MASS SPAWNING OF SCLERACTINIAN CORALS IN THE DAMPIER ARCHIPELAGO AND THE IMPLICATIONS FOR MANAGEMENT OF CORAL REEFS IN WESTERN AUSTRALIA

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Department of Conservation and Environment Perth, Western Australia

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ABSTRACT

Mass spawnings of scleractinian corals have been observed in the Dampier Archipelago (20⁰ 30'S,116⁰42' E) during March in 1984 and 1985, and occurred exactly 12 synodic months apart on the eighth and ninth nights after the full moon. These are the first recorded observations of mass spawning of corals in the Indian Ocean, the first recorded in autumn and the first recorded outside the Great Barrier Reef Province.

Comparisons with the mass spawnings of corals on the Great Barrier Reef suggest that, apart from the timing, many features of the spawnings are similar. The breeding season in each location coincides approximately with seasonal changes in wind and current patterns, and factors related to these events may determine the annual timing of mass spawning. Spawning occurs during an ebbing tide in darkness, which may be related to predation from the many planktivores that are found in shallow coral reef communities, and over a period of neap tides which may be an adaptation for increasing the dispersal of the propagules.

The timing of mass spawning of corals in the Dampier Archipelago coincides approximately with the onset of a unidirectional poleward current (Leeuwin Current) in the adjacent offshore waters and may provide a mechanism for widespread dispersal of planulae. This raises the possibility that regionally separate coral reefs in Western Australia are interrelated.

An emergence of the epitokous (reproductive) segments of polychaete worms also occurred simultaneously during the coral mass spawning in both years, suggesting that other marine invertebrates may reproduce during this period each year.

INTRODUCTION

A review by Fadllalah (1983) on the reproduction of scleractinian corals shows that most research, before 1980, dealt with species which are fertilised internally and have been observed to release planula larvae. This emphasis led to the generalisation that viviparity, in this instance planulation, was the typical mode of reproduction in hermatypic corals and occurred intermittently throughout the year. Recent findings have shown that many species release gametes which are fertilised externally and develop outside the parent colony (Rinkevich and Loya, 1979; Szmant-Froelich *et al.*, 1980; Kojis and Quinn, 1981,1982a,1982b; Harriot, 1983; Babcock, 1984). Further work by Harrison *et al.* (1983, 1984) has invalidated the generalisation of viviparity in scleractinian corals and as a result of these studies, more coral species are now known to spawn gametes (broadcasting species) than to brood planulae (brooding species). Additionally, the spawning of many broadcasting species appears to be synchronous and confined to a single, brief annual period (Harrison *et al.*, 1984).

Multispecific, synchronous spawning, or ' mass spawning ', of scleractinian corals has been observed on the Great Barrier Reef (GBR), during late spring to early summer (October - December) since 1981 (Harrison *et al.*, 1983, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986), and occurs predominantly on the third to sixth nights after a full moon, during a period of rising sea temperatures (Babcock *et al.*, 1986). Offshore reefs appear to spawn exactly 1 lunar month later than inshore reefs, and synchronous spawning has been recorded between reefs separated by as much as 5° of latitude (Babcock *et al.*, 1986). At present, 133 species of scleractinian corals on the GBR (of a total of 356) are known to spawn during this period: it has been postulated ' it is likely that the majority of corals on the GBR participate in the annual mass spawning phenomenon ' (Willis *et al.*, 1985).

This paper describes a coral spawning event that was observed, fortuitously, in the Dampier Archipelago (DA) during March 1984, and a second mass spawning of corals observed at the same reef, in March 1985. Observations during March 1985 confirmed the coral mass spawning phenomenon in the DA, documented some species involved and characterised aspects of the physical environment during the spawning period. In this paper ' mass spawning ' is defined as the multispecific, synchronous release of gametes by scleractinian corals on one night, ' spawning period'

refers to the fifth to eleventh day after the full moon in March during 1984 and 1985, and ' breeding season ' refers to the season (spring in the GBR and autumn in the DA) in which the mass spawning occurs.

These are the first recorded observations of mass spawning of scleractinian corals in the Indian Ocean, the first recorded in autumn rather than late spring to early summer, and the first recorded outside the Great Barrier Reef Province. Environmental data collected during the spawning periods in 1984 and 1985 are presented, and possible causal factors determining the timing of mass spawning of scleractinian corals are discussed. Implications for management of coral reefs, in the DA and elsewhere in Western Australia, are outlined.

MATERIALS AND METHODS

Study sites

To determine the timing, mode, and spatial extent of scleractinian coral reproduction in the DA (20° 30'S,11°42'E), coral species were studied at 3 sites (Fig. 1). Site 1 is on an inshore subtidal fringing reef about 4m below mean sea level (MSL) on the north side of Conzinc Island and is characterised by turbid water, weak currents and intermittent long period wave action. Site 2 is on an intertidal reef (about 1m below MSL) on the eastern side of Keast Island. This site is typified by turbid water, strong currents and is protected from swell by adjacent islands. Site 3 is on the reef crest at Hamersley Shoal (about 1.3m below MSL), an offshore reef with predominantly clear water, weak currents and constant swell activity.

Reproductive status and spawning records

Polyp reproductive status was determined either by the examination of freshly broken pieces of live coral in the field (Fig.2a) or under a dissecting microscope in the laboratory (Fig.2b). The presence of pigmented eggs was used as a criterion for reproductive maturity (Harrison *et al.*, 1984).

In order to determine the reproductive status of selected coral species in the DA at the time of mass spawnings on the GBR, corals (28 species, 60 colonies) were collected at site 2 on November 12



Figure 1 . Location of the study sites in the Dampier Archipelago. Inset: location of Dampier Archipelago on the northwest coast of Australia.

and 13, 1984 (dates of mass spawning on the offshore reefs on the GBR in 1984) and examined for the presence of mature eggs. *In situ* assessment of the reproductive status of various acroporiid and faviid species were also made at site 1 on November 12, 1984. On October 17, 1985 (less than three weeks before the dates of mass spawning at inshore reefs on the GBR) corals (acroporiid and faviid species) at site 2, were tagged and 20 samples collected and examined for the presence of pigmented eggs.

To assess the taxonomic extent of coral reproduction during March 1985, corals were sampled randomly before (at sites 1, 2 and 3; 46 species, 139 colonies) and after (at sites 1 and 2; 43 species,

86 colonies) the dates of mass spawnings and reproductive status assessed. During the 2 nights of mass spawning, coral species observed releasing gametes were sampled for identification. Additionally, corals at site 1 (*Acropora formosa*, *Acropora hyacinthus*, *Acropora cf danai*, *Acropora cf grand*: *s*, *Acropora tenuis*, *Astreopora cf myriophthalma*, *Favites pentagona*, *Platygyra daedalea*, *Galaxea fascicularis*, *Turbinaria mesenterina*) and site 2 (*Acropora formosa*, *Acropora hyacinthus*, *Acropora hyacinthus*, *Acropora aspera*, *Acropora sp.1*, *Favites abdita*, *Favia pallida*, *Goniastrea retiformis*, *Platygyra sinensis*) were tagged and later sampled on March 13, 19 (site 1) and March 14, 15 and 16 (site 2).

To determine whether corals in an aquarium would spawn simultaneously with *in situ* corals, pieces of 6 species (*Galaxea fascicularis, Favites abdita, Platygyra daedalea, Acropora hyacinthus, Leptoria phrygia, Acropora millepora*) were removed from the reef, at site 2, at 1300h on March 14, 1985 and maintained in an aquarium under a natural photoperiod and at ambient seawater temperatures (29 °C \pm 2 °C) until March 18.

Spawning of corals in the field was determined directly by observation of gamete release *in situ* (Fig.3a), the appearance of eggs on the sea surface, or inferred from the disappearance of mature gametes in sequential samples from tagged colonies. In the laboratory, spawning was inferred by the appearance of gametes in the aquarium. The approximate size range of floating eggs was estimated from photographs (15X) of eggs collected and preserved in 10% formalin seawater during the mass spawnings on March 15, 1985 (Fig.3b). The maximum diameter of 50 eggs was determined with a digitizer (Summagraphics Corp. USA).

Environmental data

Data bggers (Windrift Instruments, WA) recording (15 minute sampling interval) instantaneous measurements of depth (\pm 0.05 m), seawater temperature (\pm 0.02 °C) and bottom irradiance (\pm 5%) were deployed during the spawning periods in 1984 and 1985. Also salinity (\pm 0.05 °/₀₀) and seawater temperature were measured during March and November in 1984 and in March 1985 with a Yeo - Kal Model 605 temperature - salinity meter. The times of sunset and moonrise were recorded on the nights of March 15, 16 and 17, 1985.

RESULTS

Taxonomic extent

Twenty-seven species of scleractinian corals were found (directly and indirectly) to release gametes between March 13-19. Eighteen species were observed, in situ, releasing gametes on two consecutive nights after the full moon in March 1985. One species (Acropora florida) spawned on both nights. Spawning in a further 9 species was inferred from the disappearance of mature eggs in sequential samples from tagged colonies (Table 1). No species were observed to release planulae. About 70% (32 species) of all corals sampled before March 15, at sites 1, 2 and 3, contained mature eggs. A similar survey at sites 1 and 2 after March 16, found 23% (10 species) with mature eggs. Six of these species (Acropora cf clathrata, Astreopora cf myriophthalma, Favia matthali, Favia stelligera, Goniastrea palauensis, Platygyra lamellina) contained low numbers of eggs with the rest (Montastrea valenciennesi, Moseleya latistellata, Galaxea fascicularis, Hydnophora microconos) having high numbers of mature eggs. In total, 62 species of scleractinian corals were sampled between March 12-20, 1985 and 46 species (74%) were found to contain ripe gonads. Five species that did not contain eggs (Caulastrea tumida, Favia flexuosa, Montastrea curta, Leptastrea cf pruinosa, Goniopora minor) were only sampled after the observed spawning periods. At sites 1, 2 and 3, 62%, 83% and 57% (respectively) of the species sampled before March 15 contained mature eggs. In addition, on March 14 at site 3, 10 colonies of Acropora hyacinthus, the dominant species at the site, were all found to contain mature eggs. Of the 46 species found to contain ripe gonads, 8 families of scleractinia were represented, although most species were confined to two families, Acroporidae (21 species) and Faviidae (18 species). Of the 27 species found to release gametes during this period 5 families of scleractinia were represented: Acroporidae (14), Faviidae (10), Merulinidae (1), Mussidae (1) and Fungiidae (1). Mature gonads were not observed in the coral samples collected at site 2 on November 12 and 13, 1984 (Table 1) or in samples collected in October 1985.

Day of spawning

Coral spawnings occurred at site 2 on March 25 and 26,1984. In 1985, scleractinian corals were observed at site 2 to be spawning on the nights of March 15 (18 species) and March 16 (1 species). These dates, in both years, occurred on the eight and ninth nights after the full moon in March (Fig.4).

 Table 1. List of coral species sampled in the Dampier Archipelago during November 1984 and March 1985.

(a) : number of colonies containing pigmented eggs (total number sampled) between March 12-14,1985 at sites 1,2,3.

(b) : spawning species : \bullet - *in situ* spawning observed at site 2 between 2010h-2100h on March 15,1985; \bullet^1 - *in situ* spawning observed between 2010h-2100h on March 15,1985 and between 2000h-2020h on March 16,1985 at site 2; \bullet^2 - spawned at site 2 between 1430h on March15 and 1545h on March 16,1985 (inferred from the disappearance of eggs in consecutive samples) ; \blacktriangle - spawned at site 1 between 1000h on March 13 and 1400h on March 19,1985 (inferred from the disappearance of eggs in consecutive samples).

(c) : number of colonies containing pigmented eggs (total number sampled) between March 17-20, 1985 at sites 1,2 : * - low number of eggs in samples; ** - high number of eggs in samples.

(d) : number of colonies containing pigmented eggs (total number sampled) at site 2 between November 12-13,1984.

(-), coral species not sampled (a,c,d) or not observed during periods of mass spawning(b).

SPECIES	а	b	с	d	
ACROPORIDAE				me Men dang	
Acropora formosa	12(13)	•	0(8)	0(5)	
A. hyacinthus	19(19)	\bullet	0(4)	0(3)	
A. florida	3(3)	•1	0(1)	0(3)	
A. tortuosa	3(3)	-	-	-	
A. cf clathrata	4(5)	-	1(1)*	-	
A. latistella	• • •	•	-	0(1)	
A. cf danai	3(3)	▲	0(1)	-	
A. tenuis	2(2)	A	0(2)	0(1)	
A. cf nasuta	0(2)		0(1)	0(2)	
A. millepora	3(3)	•	0(1)	0(2)	
A. ct microphthalma	1(1)	-	-	0(1)	
A. aspera	1(1)	● 2	0(4)	0(1)	
A. cf grandis	11(11)	A	0(3)	-	
A. spicifera	1(1)	-	-	0(1)	
A. verweyi	1(1)	-	•	0(1)	
A. pulchra	1(1)		0(1)	-	
A. anthoceris	2(2)	-	-	-	
A. CI robusta	0(1)	-	-	-	
Acropora sp. 1	1(1)	●2	-	-	
Astreopora gracilis	1(1)	•	-	0(2)	
A. cf mynophthalma	4(4)	-	1(1)*	-	
Montipora verrucosa	0(1)	-	0(1)	-	
m. nispida	-	•	0(2)	0(2)	

table continued next page

Table 1 continued:

FAVIIDAE				
Caulastrea tumida	-	-	0(2)	0(2)
Cyphastrea serailia	1(3)	-	-	0(1)
Favia pallida	1(1)	●2	0(1)	-
F. matthaii	-	-	1(2)*	-
F. stelligera	1(1)	-	1(3)*	-
Favites abdita	4(4)	•	-	0(4)
E cf rotundata	0(1)	-	0(1)	-
F pentagona	3(3)	▲	-	-
F halicora	-	•	•	-
F. flexuosa	-	-	0(1)	-
Goniastrea palauensis	-	-	1(1)*	-
G. retiformis	1(1)	•	0(6)	0(3)
G. aspera	-		0(2)	-
Leotoria ohrvoia	3(3)	-	0(1)	0(2)
Montastrea curta	-	-	0(1)	-
M. maonistellata	-	•	~	0(1)
M. valenciennesi	2(2)	-	1(1)**	-
Platvovra daedalea	5(5)	A	0(5)	0(2)
P sinensis	6(6)		0(5)	0(4)
P ct pini	1(1)	ě	-	-
P lamellina	-	-	1/1)*	
Leotastrea cf oruinosa	-	-	0(2)	-
Moseleva latistellata	-	-	1(1)**	0(1)
OCULINIDAE				0(1)
Galaxea astreata	1(2)	-	-	-
G. fascicularis	1(1)	-	2(3)**	0(3)
MERULINIDAE			-(-)	0(0)
Merulina ampliata		٩	-	0(1)
Hydnophora microconos	•	-	1(1)**	-
H. exesa	0(2)	-	0(1)	-
MUSSIDAE				
Lobophyllia hemprichii	6(6)	•	0(2)	0(5)
PECTINIIDAE	-\ -/		-(-)	-(-)
Echinophyllia aspera	1(1)	-	0(1)	-
AGARICIIDAE				
Pavona decussata	0(3)	-	0(2)	0(1)
THAMNASTERIIDAE				- ()
Psammocora digitata	0(1)	-	-	-
FUNGIIDAE				
Fungia fungites	0(1)	•	0(1)	-
PORITIDĂE				•
Goniopora minor	-	-	0(2)	-
G. tenuidens	0(1)	-	0(1)	-
Porites heronensis	0(2)	-	0(2)	0(2)
P. lutea	0(5)	-	-	0(3)
P. lobata	0(3)	-	0(1)	-
DENDROPHYLLIIDAE				
Turbinaria mesenterina	0(1)	-	0(2)	-
	-			



Figure 4. Predicted astronomical tide height, date of full moon (@), and dates of mass spawning (A) for the Dampier Archipelago during March in 1984 and 1985.

During March 1984 observations were not made on the seventh or tenth nights after the full moon. In 1985, the eight tagged species at site 2 all spawned between 1430h on March 15 and 1545h on March 16 (Table 2).

	n	14/3/85	15/3/85	16/3/85	
SPECIES		1200	1430	1545	
ACROPORIDAE					
A. formosa	3	+	+	-	
A. hyacinthus	1	+	+	-	
A. aspera	1	+	+	-	
Acropora sp.1	1	+	+	-	
FAVIIDAE				۴	
Favites abdita	1	+	+	-	
Favia pallida	1	+	+	-	
Goniastrea retiformis	1	+	+	-	
Platygyra sinensis	3	+	+	• .	

TABLE 2. Reproductive status of tagged corals at Keast Island reef during March 1985. (+), eggs present; (-), eggs absent; (n), number of colonies.

The corals kept in an aquarium from 1300h on March 14 spawned between 1900h and 2000h on March 15 (D. M. Gordon, pers. comm.). On March 17 observations were maintained, at site 2, from 1700h to 2230h. No spawning was observed during this period.

Hour of spawning

The sudden appearance of large quantities of eggs (predominantly pinkish-red) floating on the sea surface in 1984 was first noticed at 1925h on March 25. On the following night spawning began at about 1930h. When observations ceased at 2200h on both nights, large numbers of floating eggs were still visible. The timing and duration of the mass spawning events observed in 1985, in relation to tide height, diel light cycles, sunset and moonrise are shown (Fig. 5). On March 15, the first eggs (pink) were observed at 1900h. Between 1900h - 1940h many *Acropora* colonies were observed releasing gametes. Between 2010h - 2100h, 18 species were observed spawning (Table 1). Spawning activity appeared to peak (maximum number of eggs on the surface) between 2000h - 2100h and by 2140h only a few eggs were visible on the sea surface. On March 16, pink egg bundles were first observed at 1923h. Between 2000h - 2020h only 1 species of *Acropora* was observed





spawning. Most of the observed eggs were pink or red, although green and white eggs were also present indicating that other unidentified coral species were spawning also. Spawning activity appeared to peak between 2030h - 2100h, and by 2200h only a few eggs were visible.

A swarming of polychaete worms, predominantly rag-worms (Polychaeta:Nereididae), occurred simultaneously with the coral mass spawning in both years. The epitokous (reproductive) stage of these worms emerged following the appearance of coral eggs on the sea surface. *Eunice* cf *australis* was present although less abundant. On the night of March 17,1985 (the night after the two consecutive nights of mass spawning) swarming was not observed.

Spawning behaviour and egg size

The form of spawning most commonly observed on the two nights was the slow extrusion of gametes through the polyp mouth (Type I as described by Babcock *et al.*, 1986). Size of preserved coral eggs was 356um - 661um (mean = 505um). No fertilized coral eggs were detected in samples collected during the mass spawnings on March 15,16 in 1985.

Environmental data

Environmental data collected during the spawning periods in 1984 and 1985 are summarised (Figs. 6 and 7). The full moon occurred at 1810h on March 17, 1984 and at 1014h on March 7, 1985. The time of moonrise on the nights of March 15/16, 16/17, 17/18, 1985 occurred at approximately 0130h, 0220h, 0310h respectively. Sunset occurred at about 1825h on March 14 - 17, 1985. At 1845h, on these nights, recorded irradiance levels were still above night values. The first night values were recorded at 1900h.

In the DA, spring and neap tides occur 2 - 4 days and 8 - 10 days after the full moon respectively (Fig. 4). At site 2, the eighth to tenth days after the full moon during March 1984, and the eighth and ninth days after the full moon during March 1985 were the only days during the spawning periods that this reef was not exposed. On March 15, 1985 (the first date of mass spawning), a high water occurred at 1615h. The tide began to ebb approximately 45 minutes later and low water occurred at 2345h. On







Figure 7. Environmental data recorded during the spawning period at Keast Island reef in 1985. Periods of mass spawning are marked.

the following day, a high water occurred at 1845h and the tide began to ebb at approximately 1910h with low water occurring at 0245h on March 17 (Fig. 5).

Temperature records show that the corals on this reef were subject to large (>4 °C) diel variations in seawater temperatures during the spawning period in 1985. A warming trend also occurred with a minimum of 27.0 °C, recorded at 2300h on March 12, and a maximum of 32.5 °C, recorded at 1445h on March 17. During the equivalent period in 1984, temperatures varied from 31.3 °C on March 23 to 27.6 °C on March 27. Mean temperatures during the two successive periods of mass spawning in each year were 29.3 °C and 29.4 °C in 1985 and 30.5 °C and 28.8 °C in 1984. Salinities, at site 2, during the spawning periods were $35.5 ^{\circ}/_{00} - 36.0 ^{\circ}/_{00}$ in both years.

DISCUSSION

General

Following the observation of spawning events on two consecutive nights in March 1984, a mass spawning of scleractinian corals was predicted to occur 12 synodic months (1 synodic month=1 lunar month=29.53 days) later, after dark, and on the eighth and ninth nights after the full moon.

The accuracy of this prediction confirmed the phenomenon of mass spawning of scleractinian corals in the DA, and suggested that the observed spawning events in March 1984 were mass spawnings of corals. Furthermore, this also suggests that a predictable, brief, annual period of multispecific, synchronous spawning by scleractinian corals occurs in late summer, early autumn in the DA. The presence of mature eggs in many species of corals and in many colonies of the same species, at widely separated reefs, suggest that this is a major reproductive effort in the DA . Although only 27 species of corals were found (directly and indirectly) to have spawned, a high proportion (74%) of the coral species sampled during March 12 to 20, 1985, contained mature eggs. This, and comparisons with the species composition of the mass spawnings on the GBR (Babcock *et al* ., 1986), suggest that many more of the 204 species of scleractinian corals found in the DA (L. M. Marsh, J. E. Veron, pers. comm.) are likely to be involved in mass spawning. The total absence of mature eggs in the corals sampled in the DA on November 12 and 13,1984, and on October 17,1985, and the observed mass

spawning in March 1985 confirm that the mass spawning of corals on the GBR and in the DA are not synchronized, and support findings on the GBR that the observed mass spawnings are an annual event. The presence of high numbers of apparently mature eggs in some non-acroporiid species after the nights of mass spawning in 1985 suggest that these species may have spawned at a later date (that is, a 'split' spawning occurred). 'Split' spawnings have been observed at Magnetic Island on the GBR in 1981 and 1984 (Willis *et al.*, 1985).

Comparisons with mass spawnings on the Great Barrier Reef

Many characteristics of the mass spawnings observed on the east and west coasts of Australia are similar. Most species spawn after a full moon, on 2 - 3 consecutive nights, during a period of neap tides and for 3 - 4 hours between sunset and moonrise. In addition, spawning appears to be an annual event, in both locations, and most species observed to spawn or contain ripe gonads during March 1985 in the DA are known spawning species on the GBR (Harrison *et al.*, 1984; Willis *et al.*, 1985;Babcock *et al.*, 1986; this paper). Time elapsed between consecutive annual mass spawnings in 1983 and 1984 on the GBR, and 1984 and 1985 in the DA, was exactly 12 synodic months, and the two main spawning families are common to both areas (that is, Acroporidae, Faviidae) (Willis *et al.*, 1985; this paper). The colours, general buoyancy (Babcock *et al.*, 1986; this paper) and size range (Marshall and Stephenson, 1933; Kojis and Quinn, 1981, 1982a, 1982b; Harriot, 1983; Babcock, 1984; this paper) of mature eggs, and the most common spawning behaviour also appear to be similar (Babcock *et al.*, 1986; this paper). The synchronous spawning of corals kept in aquaria with *in situ* corals (Harrison *et al.*, 1984; this paper) and the possibility that a 'split' spawning occurred during 1985 in the DA consistent with the 'split' spawning observed at Magnetic Island in 1984 (Willis *et al.*, 1985; this paper) are further similarities.

The seasonal timing of the mass spawnings, and as a consequence, the different environmental conditions that exist during the periods of gametogenesis and spawning are, therefore, the most significant differences that exist between both locations; for example, mass spawning on the GBR occurs after a period of rapidly rising sea temperatures and at temperatures well below the mean maxima for these locations (Babcock *et al.*, 1986) while spawning in the DA occurs after a period of



Figure 2. (a) Polyp of *Lobophyllia hemprichii* split through the centre exposing gonads (G); **2**(b): polyps of *Platygyra sinensis* split through the centre exposing gonads containing pigmented ooyctes (O). Photographs: C J Simpson.



Figure 3. (a) in situ spawning of Acropora millepora showing the release of buoyart egg and sperm bundles (ES) between 2010h-2100h on March 15,1985 at Keast Island reef. Photograph: C J Simpson;

Simpson; 3 (b): unfertilised eggs (E) and egg bundles (EB) collected from the sea surface at Keast Island reef between 2000h-2050h on March 16,1985; colour of eggs at the time of collection was mainly pink. Photograph : E I Paling. high, relatively constant temperatures and coincides with the period of maximum temperatures (Fig. 8). Furthermore, mass spawning occurs on different nights after a full moon and although the state of the tide is similar (that is, neap tides), the periods of darkness between sunset and moonrise will be different due to the later rising (about 50 minutes) of the moon on successive nights after the full moon.

Environmental factors co-related with the timing of spawning

Korringa (1947) listed annual sea temperature changes, monthly tidal or moonlight cycles and diel light or tidal cycles as the factors that determine the timing of reproduction in marine invertebrates. Babcock *et al.* (1986) suggest ' the synchrony, predictability and brevity of the mass coral spawning appear to be linked to successive environmental cues which operate on increasingly fine time scales: annual sea temperature patterns, monthly lunar or tidal cycles, and diel light cycles'. Environmental conditions (for example, annual sea temperature cycles), at a given location, can vary markedly from year to year (Babcock *et al.*, 1986) and as a result, it is unlikely that the timing of reproduction is a response to exogenous factors alone. Olive and Garwood (1983) suggest that all reproductive cycles have an endogenous component. Willis *et al.* (1985) made a preliminary analysis of the mass spawning phenomenon on the GBR since 1981, and have identified lunar and diel light cycles as zeitgebers for spawning synchrony.

Annual rhythms

(i) Sea temperature cycles

Korringa (1947) suggests that 'most probably temperature conditions preponderate in establishing the breeding season' in marine animals. Babcock *et al.* (1986) suggest that the seasonal variation in sea temperatures, on the GBR, may influence gametogenic cycles in corals and that mass spawning of corals occurs after a period of rapidly rising sea temperatures in spring. They suggest that the corals on the inshcre reefs, on the GBR, spawn 1 lunar month earlier than corals on the offshore reefs as a result of an earlier and more rapid rise in sea temperatures at the shallower, inshore reefs. Kojis and Quinn (1981) have associated seawater temperature changes with annual periodicity of spawning in scleractinian corals and also suggest that the spawning of corals at Lord Howe Island, where spring sea

temperatures are lower (by over 4 °C) than in the DA, is delayed until January due to a second -



Figure 8. Comparison of spring sea water temperatures at Magnetic Island (A) on the Creat Sarrier Reef (Babcock et al., 1986) with the Dampier Archipelago :(•), mean monthly sea temperatures near Conzinc Island;(•), instantaneous sea temperatures at Keast Island reef in 1984.

Seawater temperatures in the DA show a pronounced seasonal pattern and compressions with Magnetic Island (Babcock *et al.*,1986) during spring to early summer in 1982 and 1983 *relicate that the differences were generally less than 1°C (Fig. 8). This is less than the diurnal variation in sea temperature in the DA, which can exceed 4 °C on the shallower reefs (Fig. 7a). Trase small differences in sea temperature during spring appear insufficient to explain the difference of 5 months in the timing of mass spawning between these two locations, and suggest that winual sea temperature patterns may not play a key role in determining the timing of the breeding season of scleractinian corals. The inter-year variability in spring sea temperatures in both locations. Note that winus before spawning (Fig.8), in contrast to the rapidly rising temperatures during the equivalent for do n the GBR, also support this hypothesis. The apparent similarity to the highly predictable spawing rhythm of the Pacific palolo worm *Eunice viridis*, in Samoa, where sea temperatures are equable Sroughout the year (Korringa, 1947), is further evidence that annual sea temperatures alone may restermine

the breeding season in tropical marine invertebrates that reproduce in brief, annual periods. Johannes (1978) states that seawater temperature does not appear to play a key role in the timing of spawning of coastal tropical marine teleosts and cites examples where the collective spawning peaks, at different locations, occur during periods of minimum, maximum and intermediate sea temperatures.

It would be premature, however, to exclude the possibility that different sea temperatures may locally delay spawning (for example, on the offshore reefs on the GBR) within the breeding season.

(ii) Wind and current cycles

Mass spawning of corals in spring to early summer on the GBR and in autumn in the DA, coincide approximately with periods of calms associated with changes in seasonal wind patterns. During November, winds on the central GBR change from the southeast trade winds that predominate during March to November to the northwest monsoons that occur from December to February (Pickard *et al.*, 1977; Williams *et al.*, 1984). In the DA, winds from the west and southwest (monsoons) predominate from September to March and change to the southeast trades from March to August (Hollaway and Nye, 1985).

Approximately coincident with this change in wind patterns is a change in the large scale water circulation patterns in both locations. Some evidence suggests that a unidirectional, poleward flow of surface water occurs in late spring to early summer along the northern and central GBR and this pattern remains until about March/April when more complex patterns occur and persist until November (Pickard *et al.*, 1977; Williams *et al.*, 1984). On the west coast of Australia a unidirectional, poleward flow of surface water (the Leeuwin Current) occurs during autumn and early winter (Cresswell and Golding, 1980; Legeckis and Cresswell, 1981; Thompson and Cresswell, 1983; Thompson, 1984; Hollaway and Nye, 1985). This current is strongest during March to June with the speed and direction of the surface water being more variable during the remainder of the year (Hollaway and Nye, 1985).

These periods of relative calm, coinciding approximately with changes in large-scale circulation patterns, appear to occur annually in each location and at the approximate time of the breeding season

of scleractinian corals. Do these physical events or co-related factors determine the bineding sesson? If so, the inter-year variability in the timing of these physical events in contrast *v_i* the precisely predictable periods of mass spawning suggests that an endogenous, rather than an exception. control is exerted. The existence of an endogenous annual rhythm, interacting with environmental cues, as an adaptation to factor/s related to similar meteorologic/oceanographic, events in toth locations, but at different times of the year, may explain the large differences in the errors of reproductive activity in many tropical, coastal teleosts has been found to coincide with (errors of carries of Basheerudin and Nayar, 1962; Bapat, 1955; Prasad, 1958). Watson and Leis (1974) to charges in the local current patterns that occur at these times of the year. Johannes (1978) wind collective spawning peaks in 13 out of 18 locations (5 locations had insufficient data to draw voncusions) to occur at times of the year when prevailing winds or prevailing currents are the weakest.

Lunar rhythms

The spawning of corals in the DA in 1984 and 1985 occurred on the eighth and ninth fights after a full moon. On the GBR most species spawn in the week following a full moon. These data suggest that within the breeding season corals display lunar periodicity. Lunar periodicity has that previously recorded in both brooding (Lewis, 1974; Rinkevich and Loya, 1979; Richmond and Josef, 1984) and spawning (Kojis and Quinn, 1981,1982a; Harriot,1983; Babcock, 1984; Harrison *et al.*, 1984; Willie *et al.*, 1985; Babcock *et al.*, 1986) coral species.

Tidal rhythms

Babcock *et al.* (1986) suggest that the release of gametes occurs after nightfall following the first full moon subsequent to the maturation of gonads. If this were so, spawning would be expirated to occur on the same nights after the full moon irrespective of the geographical location. This does not happen. Most species spawn on the third to fifth nights after the full moon on the instrument reefs on the central GBR, and on the fourth to sixth nights after the full moon on the offshore reefs (Expcock *et al.*, 1986). In the DA, spawning has been observed only on the eight and ninth nights after he full moon.

Tidal records (Anonymous, 1984) for Townsville (for inshore reefs), Bugatti Reef (for offshore reefs) and Dampier indicate that these spawning periods coincide with the occurrence of neap tides, which suggests that following the occurrence of the full moon within the breeding season the mass spawning of corals is synchronised by a tidal rhythm. Many marine organisms display a tidal rhythm in reproductive behaviour (Korringa, 1947). In particular, the Pacific palolo worm, *Eunice viridis*, which also spawns during a brief period each year, displays a similar tidal periodicity (that is, spawns on neap tides) following the first full moon within the breeding season (Caspers, 1984).

Daily rhythms

In the DA, the release of gametes on March 15, 1985 coincided with the onset of darkness during a falling tide. On the following night, spawning commenced about 10 minutes after the onset of the ebbing tide during darkness (Fig.5). These data indicate that the spawning period displays lunar periodicity, subsequent to gonad maturation but that the specific time of spawning may be synchronised by a tidal rhythm, interacting with the light/dark cycle. The observed differences in the timing of spawning at night may be due to phase differences in the tides. Evidence to support this hypothesis can be seen from the timing of spawning of many corals on the GBR. Harrison et al. (1984) and Babcock et al. (1986) have shown that many acroporiid and faviid corals at Magnetic Island spawn 2-4 hours after sunset. This period coincides approximately with high water and an ebbing tide in Townsville (Anonymous, 1982). Observations by the author at Magnetic Island on November 1,1985 noted that many acroporiid corals appeared to spawn between 2100h-2200h. Predicted high tide at Townsville on November1,1985 occurred at 1958h (Anonymous,1984). Further evidence can be seen in the timing of spawning of Goniastrea favulus in two locations on the GBR. This faviid coral spawns during daylight (1600h-1800h) at Heron Island (Kojis and Quinn, 1981a) but after dark on reefs near Townsville (Babcock et al., 1986). Tides at Heron Island are at least 30 minutes earlier than at Townsville (Babcock et al., 1986).

The reproductive swarming of the polychaete worm, *Eunice viridis*, on Tutuila reef in Samoa, also starts at the end of the nocturnal flood tide which occurs at about 0030h (Caspers, 1984). This timing, in relation to the state of the tide, is identical to the swarming of polychaete worms in the DA and is

additional evidence to support the importance of tides in determining the time of the day that spawning takes place.

An endogenous rhythm may partly explain the simultaneous spawning of corals in aquaria with *in situ* corals (Harrison *et al.*,1984; this paper). This does not explain, however, the change in the hour of spawning of *Goniastrea aspera* in aquaria, as a result of the manipulation of light/dark cycles (Babcock, 1984).

Possible factors determining the timing of spawning

The precise timing of mass spawning during periods of relative calm, after a full moon, over neap tides, on an ebbing tide, and after dark is an unusual and significant feature of the mass spawning phenomenon. The synchronous spawning of gametes within populations of a single species has the obvious advantage of promoting cross fertilization. Many marine invertebrates employ this reproductive strategy (Korringa, 1947) and, in particular, the spawnings of the crinoid, Comanthus japonica (Kobota, 1980), and the Pacific palolo worm, Eunice viridis (Caspers, 1984), are well documented examples of predictable, synchronized spawning that occur for a few days each year. The advantages of multispecific synchronous spawning are less clear. Harrison et al. (1984) suggest that epidemic spawning of many species would increase the chances of survival for planktonic larvae by satiating predators and filter feeders. The general buoyancy of propagules and the timing of spawning during darkness would also reduce predation by benthic filter feeders and visual feeders respectively. Predation by planktivorous fishes such as the blue sprat, Spratelloides robustus, which was observed eating coral eggs (subsequently confirmed by gut analysis) in the DA, increased when lights were shone on the water during spawning. Spawning on an ebbing tide would facilitate the flushing of propagules to deeper, offshore waters and may also be related to the need to reduce the threat of predation from the many planktivores that occur in shallow coral reef communities (Johannes, 1978).

Babcock et al., (1986) suggest that spawning on low tides may be related to the advantage of reducing the dispersal of gametes prior to fertilization and Stimson (1978) proposed that the

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reproduction of shallow water reef corals during low tides facilitates the retention of planulae near the natal reef. In addition, Kojis and Quinn (1982b) suggested that the propagules of the faviid corals *Favites abdita* and *Leptoria phrygia* are likely to remain in the vicinity of the natal reef because spawning of these two corals takes place on neap tides.

Mills *et al.* (1986) has shown that the net excursion of water during the week of neap tides in the DA can be an order of magnitude greater than during the week of spring tides (Fig.9). This is a result of the decreased influence of the tidal (oscillatory) current component and the relative increase of the winddriven (non-oscillatory) current component. Thus, spawning on neap tides is more likely to disperse (periods of wind being more likely than periods of calm during the days following spawning) rather than retain larvae in the vicinity of the natal reef and may be an adaptation for increasing the dispersal of the ensuing adults. Similarly, Johannes (1978) states that, in relation to considerable year to year variation in recruitment of some tropical marine fishes,' it might prove revealing to compare the relative strength of the prevailing currents and winds during years of high and low recruitment'. The positive, rather than negative, buoyancy of the propagules, the low level of endemism of coral species found on isolated shelf atolls such as the Rowley Shoals (15 °-16 °S,119 °E) and the similarity of the coral fauna on regionally separate Western Australian coral reefs (for example, Ningaloo Reef (22 °-24 °S,113 °E) and the Abrolhos Islands (28 °-29 °S,114 °E); J. E. Veron , pers. comm.) also support the hypothesis that coral larvae may have an extended pelagic phase.

Willis *et al.* (1985) postulate that different populations of corals reach, concurrently, a state of reproductive maturity to take advantage of favourable environmental conditions for larval development. The occurrence of periods of relative calm weather that follow mass spawning events on the east and west coasts of Australia support this hypothesis.

Management implications of mass spawning

Timing and mode of reproduction

The timing and mode of reproduction in scleractinian corals is of fundamental importance to the management of coral reefs. The risks to the annual reproductive effort of corals that breed in brief,





Figure 9 .(a) Continuous vector plot of current speed and direction at 7m (Mills *et al.*,1986); (b) wind direction and (c) speed recorded near site 1 (Mills and Pitt, 1985). Full moon occurred on 14/9/81 and neap tides on 23/9/81.

annual periods is greater than to species that breed intermittently throughout the year. If a wide range of species reproduce synchronously, and the reproductive propagules are mostly buoyant, the entire reproductive effort of a reef is vulnerable to certain sea surface perturbations. This was clearly demonstrated at Magnetic Island, on the GBR, in November, 1981 when a heavy rain squall coincided with a multispecific synchronous spawning event. Harrison *et al.* (1984) state 'propagules on the surface were destroyed, probably by reduced salinity, thereby negating the entire reproductive effort of those corals for the year.'

The full moon preceding spawning, occurs 10-12 days earlier in successive years (Fig.4; Willis *et al.*,1985). To maintain reproductive seasonality spawning must be delayed at some stage. Willis *et al.*(1985) suggest that this occurs every three years (that is, when the full moon is approximately 1 synodic month earlier) and that 13 synodic months will elapse between consecutive spawnings involving adjustment years. Additionally, spawning in the year preceding this adjustment is 'split' over two periods following consecutive full moons. The presence of mature eggs in corals, mainly non-acroporiid species, after the spawning periods in March 1985 and the apparent lower number of eggs observed on the sea surface in 1985 suggest that 1985, in the DA, may have been a 'split' spawning year. If this is correct then 13 synodic months will elapse before the 1986 spawning in the DA and the reproductive effort of corals will be at risk for two brief periods in 'split' spawning years.

The mass spawning of scleractinian corals in the Dampier Archipelago in 1985 coincided with the opening days (March15,16) of the Abrolhos Islands rock lobster season. This suggests that, if mass spawning occurs in the Abrolhos Islands, it is likely to occur during the fishing season (March 15-June 30). The possible effects of intense boating and fishing activity on the mass spawning of corals are unknown.

Possible effects of 'stress' on coral reproduction

The gametogenic cycle of some scleractinian corals, on the GBR, ranges from about 4 months for some faviid species to about 9 months for some acroporiid species (Babcock *et al.*, 1986). If the duration of gametogenesis is similar in the DA, then November to March each year is a period of major

reproductive effort. This is also a period of natural environmental extremes (Simpson, 1985) with some evidence (that is, bleaching) to suggest that some coral species are under stress (Goreau, 1964; Lasker *et al.*, 1984). Prolonged high sea temperatures (>30 °C) and high levels of sediment deposition (on some inshore reefs) occur during this period each year (Simpson, 1985). Thus, it is possible that the tolerance of corals in the DA to human environmental perturbations may be lower than at more 'typical' coral reefs. Additional environmental stress, such as sedimentation from dredging operations, may lower the fecundity of corals due to energy for reproduction being diverted to cope with the 'stress', for example to actively reject sediment. Kojis and Quinn (1984) have shown that fecundity in the brooding species, *Acropora palifera* is inversely related to sedimentation, turbidity, depth and high seawater temperatures and suggest that reduced fecundity of corals as a response to human environmental perturbations, may be useful as a biological indicator of sub-lethal stress on coral reefs.

Distribution of coral reefs in the Dampier Archipelago in relation to recruitment

Heyward and Babcock (1985) have shown that, for 19 species of scleractinian corals that spawned on the GBR in 1984, fertilization occurred 0.5-1.5 hours after spawning, that mobile planulae had developed within 48-60 hours and that settlement, if planulae were transferred to aquaria, occurred 4-7 days after spawning. For these species, at least, the direction and net excursion of water, for the 4-7 days after spawning, will influence recruitment (supply of planulae) to the parent and other local reefs. In the DA, the movement of water during this period will be influenced largely by the wind speed and direction. Wind directions, in 1984 and 1985, during the week following spawning were predominantly from the east and west respectively. Under these conditions, the net excursion of water would be southward into Mermaid Sound (Fig.1) in 1984 and northward out of Mermaid Sound in 1985 (D. A. Mills, pers. comm.). As a result, planulae from the 1984 spawning are more likely to have settled on reefs within the archipelago than in 1985. During years when planulae are carried out to sea and presumably do not settle on reefs within the archipelago, the relative contribution to overall recruitment by the less extensive, but more diverse, inshore reefs (for example, Conzinc Island) increases due to their further proximity from the open ocean. In areas, such as the DA, where a high proportion of the live corals occur as extensive reefs on the seaward periphery of the archipelago and

where the planulae from these reefs may often be carried out to sea, these inshore reefs may be providing a high proportion of the recruits for the reefs within the archipelago. If this hypothesis is correct, the preservation of these inshore coral communities may be more critical to the maintenance of the coral reefs in the DA than the offshore reefs.

Location of coral reefs in the Dampier Archipelago in relation to recruitment

The location of reefs in relation to local water circulation at the time of spawning will influence the level of recruitment to these reefs. 'Downstream' reefs are likely to receive more planulae than 'upstream' reefs. This interdependence or otherwise of reefs is related to the ability of coral reefs to recover from natural (for example *Acanthaster* infestations or cyclonic wave damage) or human environmental perturbations.

Low recruitment may partly explain the low cover of live coral (less than 3% on the upper seaward reef slope, Simpson, unpublished data) on Sailfish Reef (Fig.1). Prior to 1975 extensive coral communities flourished on this reef (L. M. Marsh, pers. comm.). During 1972-1974, reefs at Kendrew Island (Fig.1), at the south-western end of Sailfish Reef, were 'infested' by the crown-of-thorns starfish, *Acanthaster planci*, (Wilson and Marsh, 1974;1975). Marsh (1978) attributes the decline in the coral communities on these reefs to the effects of this 'infestation' and cyclonic wave damage that occurred in February,1975. Either of these events, or a combination of both, may have caused the apparent reduction in live coral on Sailfish Reef. In contrast, Hamersley Shoal (Fig.1) has a high cover (approximately 80%) of live coral on parts of the upper seaward reef slope (Simpson, unpublished data). The possible 'unfavourable' location of Sailfish Reef in relation to larval recruitment may partly explain the slow recovery of this reef and suggests that different reefs in a given locality may vary considerably in ability to recover from perturbations. The degree of interdependence of reefs is important in determining the location and size of 'sanctuaries' or 'seed' areas essential for the maintenance of coral communities.

Mass spawning and the Leeuwin Current

During autumn and winter a unidirectional, poleward flow of water of tropical origin, the Leeuwin

Current, occurs along the Western Australian coastline. Observations on the southern with a the Australian North-West Shelf, between January 1982 and July 1989 recate that the the start th

The timing of coral mass spawning during autumn in the DA, coincides accurately with the initiation of this current. Planula larvae that have been transported out to sea may be dispersed southward by this current. Data on the maximum longevity of coral planulae in the larvatory (Harrison *et al.*,1984) and surface (20m) speeds of the Leeuwin Current from satelling racked drogues (CSIRC, unpublished data), suggest that some coral reefs in Western Austration may be interrelated on A regional scale and may explain the occurrence of 4 genera of reef builders corals near Esperance (3). ^o S, 122 ° E) (Wilson and Marsh,1980). In addition, the dispersal of what from tropical roots (fin example, Ningaloo Reef), via the Leeuwin Current, may partly explain the existence of the extensive high latitude coral reefs at the Abrolhos Islands (28° S-29° S). These rest are exceptionally diversed for this latitude: 37 genera have been identified (Wilson and Marsh,1987), and support an extensive commercial rock lobster fishery (Johannes *et al.*,1983). At the end of law cantury, Saville-Kontt (1897) suggested that the corals found at the Abrolhos Islands may have been carried there by a southwant flow of tropical water. The autumn timing of mass spawning of scarstinian corals in the DA, approximately coincident with the onset of the Leeuwin Current, provides the first scientific diversed to support this hypothesis.

SUMMARY

Mass spawning of scleractinian corals has been observed to occur on the sight and ninth nights all of the full moon in March for the past two years. The widespread occurrence of mature eggs in many of the species sampled during March 1985 suggest that many of the 20 pecies that court in the Dampier Archipelago may participate in the mass spawning phenomenon

The seasonal timing of the breeding season appears unrelated to see mperatures and may have

related (directly or indirectly) to the seasonal changes in wind and current patterns that occur in spring on the Great Barrier Reef and in autumn in the Dampier Archipelago. Spawning during darkness and on an ebb tide may be related to the need to reduce the threat of predation from the many planktivores that exist in shallow coral reef communities. Spawning during a period of neap tides may be an adaptation for increasing the dispersal of the ensuing adults.

The autumn timing of the mass spawning of corals in the Dampier Archipelago and the presence of a poleward flowing current in the adjacent offshore waters provide a possible mechanism for widespread dispersal of planulae larvae and raise the possibility that regionally separate coral reefs in Western Australia are interrelated.

The mass spawning of corals has been observed on the Great Barrier Reef and in the Dampier Archipelago. It is not known if it occurs elsewhere. The timing of spawning in different geographical locations may help identify the factors that determine the timing of this phenomenon. Further research is necessary to determine the degree of spawning synchrony within and between populations of corals. Additionally, the relationships between reefs (local and regional), in relation to recruitment and to recovery of reefs damaged by natural or human environmental perturbations, need to be understood if the coral reefs in Western Australia are to be managed effectively.

CONCLUSIONS

1. Multispecific synchronous spawning of scleractinian corals has been observed in the Dampier Archipelago on the eighth and ninth nights after the full moon in March for the past two years. A simultaneous emergence of epitokous segments of polychaete worms also occurred, in both years, suggesting that other marine invertebrates may reproduce during this period each year.

2. The disappearance of mature eggs in sequential samples of tagged coral species, at different sites, suggests that spawning occurs simultaneously at different locations in the Dampier Archipelago.

3. In situ observations and the presence of mature eggs in many colonies of the same species before

spawning and the absence of mature eggs after spawning, suggest that spawning within populations of scleractinian corals is synchronised.

4. The distribution of spawning species within families of Scleractinia in the Dampier Archipelago and similar comparisons with the Great Barrier Reef, suggest that many more species of corals, in the Dampier Archipelago, are likely to be involved in the mass spawnings.

5. Comparisons between the Great Barrier Reef and the Dampier Archipelago show that many features of the mass spawning in these locations are similar.

6. The lack of mature gonads in Dampier Archipelago corals sampled on November 12-13,1984 (dates of offshore spawnings on the Great Barrier Reef) and in October 1985 (three weeks before 'inshore' spawnings on the Great Barrier Reef) suggest that, like the spawnings on the Great Barrier Reef, the spawnings in the Dampier Archipelago are an annual event.

7. The timing of spawning in the Dampier Archipelago appears to be related to successive environmental cues: seasonal changes in wind/current patterns, monthly lunar cycles, fortnightly tidal cycles and daily tidal/light cycles.

8. The presence of mature eggs in some species after the dates of mass spawning in March suggest that 1985 may have been a 'split' spawning year, that is, these species may have spawned at a later date.

9. Most of the reproductive propagules are buoyant and may be vulnerable to surface pollutants for at least 4-7 days after spawning (that is, before the planulae settle).

10. The timing of coral spawning in the Dampier Archipelago, the presence of a poleward current (Leeuwin Current) in the adjacent offshore waters and the longevity of certain species of planulae in the laboratory, suggest that some coral reefs in Western Australia are interrelated on a regional scale.

11. It is predicted that thirteen synodic months will elapse from March 1985 to the spawning period in the Dampier Archipelago in 1986. The next dates of mass spawning in the Dampier Archipelago will be April 3 and 4 ,1986, and will occur after dark on these nights.

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