

16 March 1984 • Vol. 223 • No. 4641

\$2.50

# SCIENCE

AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE



## COVER

Synchronous spawning by polyps of a staghorn coral, *Acropora listeri*. The oral discs of the polyps bulge with apricot-colored egg-sperm bundles in readiness for release. The bundles float to the surface and break apart; subsequent external fertilization leads to development of planula larvae. See page 1186. [Peter Harrison, James Cook University of North Queensland, Australia]

## Mass Spawning in Tropical Reef Corals

*Abstract. Synchronous multispecific spawning by a total of 32 coral species occurred a few nights after late spring full moons in 1981 and 1982 at three locations on the Great Barrier Reef, Australia. The data invalidate the generalization that most corals have internally fertilized, brooded planula larvae. In every species observed, gametes were released; external fertilization and development then followed. The developmental rates of externally fertilized eggs and longevities of planulae indicate that planulae may be dispersed between reefs.*

It has been widely accepted that most scleractinian corals are viviparous, often releasing larvae intermittently throughout the year (1-3). This view is supported by studies of a few species that release planula larvae in the laboratory (1, 4-10). Recent studies have shown that some corals are not viviparous, but spawn gametes during brief annual spawning periods (11-18). To determine the typical mode and timing of sexual reproduction in corals, we studied gametogenesis and spawning in a large num-

ber of hermatypic coral species from the central Great Barrier Reef Province.

Studies were undertaken on nearshore fringing reefs at Magnetic Island and Orpheus Island, and on a midshelf platform reef, Big Broadhurst Reef (Table 1). We observed gamete release in 23 species in situ and in the laboratory. In nine other species, spawning was inferred from the disappearance of mature gametes in sequential samples, or from the presence of gametes in aquaria or plankton mesh bags placed over corals in

situ (Table 1). No corals were observed to brood or release planulae. Before 1981, 46 coral species were known to brood planulae, whereas only 8 species were reported to spawn gametes. The results of this study, and other recent publications, show that more than 60 coral species spawn gametes. No further species have been reported to brood planulae. Hence, the majority of coral species for which data are available spawn gametes, rather than brood planulae.

Most of the corals studied were simultaneous hermaphrodites, with an annual gametogenic cycle (19). Microscopic examination of live, freshly broken coral pieces allowed rapid assessment of polyp reproductive status. Approximately 3 weeks before spawning, during rising sea

temperatures in the spring, oocytes of many species began changing color from white to pinkish-red, green, or tan. This change could easily be seen in the field. In the week before spawning, sperm squashes showed condensation of spermatozoa heads and increased flagellar activity.

Lunar periodicity of spawning has been described in brooding corals (4, 5, 7, 20) and in gamete releasing species (12, 14, 18). Spawning was first observed in corals in aquaria at Magnetic Island in 1981, 5 to 8 nights after a full moon in mid-October (Table 1). One lunar month later, synchronous, epidemic spawning was observed in situ on the fifth night after the full moon in mid-November (Table 1). There was only one major spawning period at Magnetic Island in

1982, 4 and 5 nights after the full moon in early November (Table 1). Spawning at Orpheus Island and Big Broadhurst Reef occurred 4 and 5 nights after a full moon in early December 1982 (Table 1).

Spawning appears to be induced by specific dark periods, characteristic for each species. *Acropora tenuis* spawned on dusk at 1900, and *Galaxea* spp. from 1945, while most of acroporiid and faviid corals spawned between 2000 and 2330. Freshly collected corals maintained in the laboratory under natural light regimes spawned simultaneously with corals in situ; experimentally extended light periods delayed spawning. As in many temperate marine invertebrates (21-23), the reproductive cycles of these corals also appeared to be broadly influenced by temperature. Cooler water tempera-

Table 1. Coral spawning dates from three reefs during 1981 and 1982. The data were collected on the nights indicated (4, 5, 6, 7, and 8) after the full moon. Dates when spawning was not observed are not included in the table. Spaces indicate either that the species were not present at the site or were not observed spawning. Abbreviations: F, spawning observed in the field; (F), spawning inferred in the field from daily samples; (.F.), spawning inferred in the field from samples taken a few days apart; A, spawning observed in aquaria; and (A), spawning inferred from presence of gametes in aquaria.

Species	Magnetic Island (146°51'E; 19°09'S)								Orpheus Island (146°29'E; 18°36'S)		Big Broadhurst (148°43'E; 18°57'S)	
	18 to 21 October 1981				16 November 1981		5 to 6 November 1982		5 to 6 December 1982		6 December 1982	
	5	6	7	8	5	4	5	4	5	4	5	
<b>Acroporidae</b>												
<i>Acropora austera</i>												(F)
<i>A. clathrata</i>												(F)
<i>A. cerealis</i>												(F)
<i>A. cytherea</i>						(F)						(F)
<i>A. elseyi</i>					(.F.)							
<i>A. formosa</i>	(A)		A	A	F	A (F)	F			A		
<i>A. gemmifera</i>												F
<i>A. humilis</i>		A			F	A (F)						F
<i>A. hyacinthus</i>					(.F.)	A (F)	F					(F)
<i>A. intermedia</i>					(.F.)							(F)
<i>A. listeri</i>										A		
<i>A. longicyathus</i>					(.F.)					A		
<i>A. loripes</i>												F
<i>A. millepora</i>					F	A (F)	F			A		(F)
<i>A. microphthalma</i>						A (F)						(F)
<i>A. nasuta</i>										A		F
<i>A. pulchra</i>						(F)	(.F.)					
<i>A. tenuis</i>					(.F.)		F					
<i>A. valida</i>		A				A (F)						(F)
<i>Montipora ramosa*</i>					(.F.)							
<b>Faviidae</b>												
<i>Favia pallida</i>												F
<i>F. rotumana</i>										A		A
<i>Favites chinensis</i>												F
<i>Goniastrea aspera</i>	(F) (A)	A				A				A		FA
<i>G. favulus</i>	(F) A	A				A				FA		A
<i>G. retiformis</i>												F
<i>Hydnophora exesa</i>								(.F.)	(.F.)			
<i>Platygyra sinensis</i>							F			A		FA
<b>Oculinidae</b>												
<i>Galaxea astreata</i>												A
<i>G. fascicularis</i>							F					
<b>Mussidae</b>												
<i>Lobophyllia</i> sp.		A†										
<b>Poritidae</b>												
<i>Goniopora</i> sp.		A†										

\*A. Heyward, James Cook University, personal communication.

†P. Watson, Shark World, Nelly Bay, Magnetic Island, personal communication.

Table 2. Planulae development times, settlement dates, and longevity in the laboratory.

Species	Planula (days after spawning)				Age at settlement (days)	Maximum longevity of planulae (days)
	Motile ciliated	In mid-water	In mid-water and on bottom	Benthic searching		
<i>Acropora hyacinthus</i>	1.5	2.5	3-4	7	36	91
<i>A. formosa</i>	1.5	3	4-5	5	16-20	23
<i>A. tenuis</i>	1.5	6	7			7
<i>A. millepora</i>	1.5	2-3	3-4			5
<i>Goniastrea aspera</i>	1-2	2-4	5	6		60
<i>G. favulus</i>	1-2	2	5	6	14-22	

tures at Orpheus Island and offshore reefs in November 1982 probably account for slower gamete maturation and later spawning at these sites. Thus spawning can be predicted to occur at characteristic hours, 4 to 5 nights after one or two full moons in spring, from October to December. The local sea temperature pattern in winter and spring probably determines when, and how many, spawning periods occur at each site.

Of the corals studied, only four species of *Turbinaria* did not spawn in spring. Instead they spawned in autumn in 1981 and 1982 when sea temperatures were falling (19). *Turbinaria* species were also unusual in having colonies with separate sexes and a spawning season extending over 3 months.

A range of spawning strategies was observed in the study corals, and these could influence both the degree of cross-fertilization within a population and the dispersal of gametes and embryos. In the acroporiid (Fig. 1a) and some faviid species (*Goniastrea retiformis* and *Platygyra sinensis*), the eggs and testes were compressed and slowly extruded as a positively buoyant egg-sperm bundle that rose to the surface and broke apart. In contrast, other faviid species actively expelled streams of buoyant egg-sperm bundles (*Goniastrea aspera*, Fig. 1b), or sperm followed by sticky, sinking eggs (*G. favulus*) through rapid polyp contractions.

The majority of gametes in each colony were shed on only one night, and entire populations spawned over one or two nights annually (24). Synchronous spawning within a population is advantageous for corals with external development as it maximizes fertilization and allows for genetic exchange through cross-fertilization. However, this does not explain why many species from different families spawn synchronously, or why spawning occurs predominantly 4 to 5 nights after the full moon. Epidemic spawning may increase the survival chances of planktonic larvae by satiating

active predators and filter feeders during the spawning period. The risks of single epidemic spawning to corals with buoyant propagules were clearly demonstrated at Magnetic Island in November 1981 when a heavy rain squall coincided with spawning. Propagules on the surface were destroyed, probably by reduced salinity, thereby negating the entire reproductive effort of those corals for the year. Synchronous spawning of congeneric corals may also pose problems for

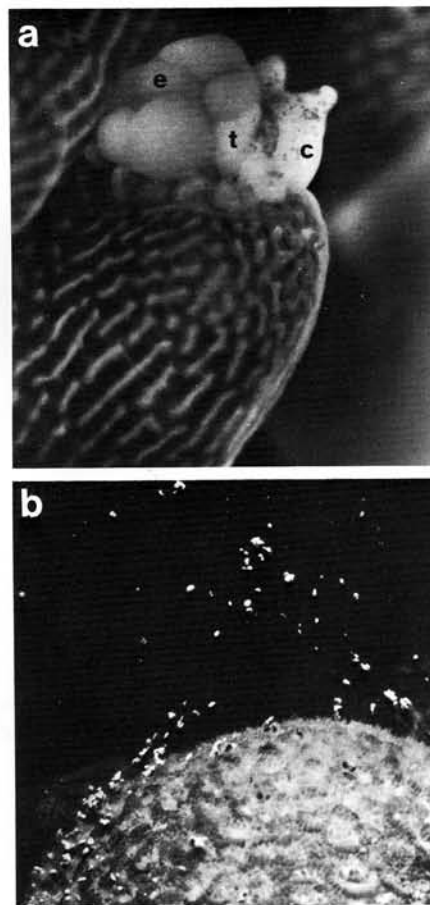


Fig. 1. Gamete release in corals. (a) *Acropora formosa* polyp slowly pushing an egg-sperm bundle through the mouth; e, egg mass; t, testis; c, contracted tentacles. The egg-sperm bundle is approximately 1.5 mm wide ( $\times 20$ ). (b) *Goniastrea aspera* colony rapidly ejecting buoyant egg-sperm bundles, synchronously, over small portions of the colony ( $\times 0.8$ ).

the recognition of conspecific gametes. Sperm chemotaxis has been documented in many species of hydromedusae that exhibit simultaneous spawning, possibly to compensate for the multispecific spawning and high dilution of gametes (25). If coral eggs do not release sperm attractants, fertilization must rely upon chance encounters of conspecific gametes.

In the laboratory, motile planulae from four acroporiid and two faviid species developed within 2 to 3 days after spawning, and active benthic searching behavior began after 5 to 7 days (Table 2). Planulae settled between 14 and 36 days after spawning, and one *Acropora hyacinthus* planula survived for 91 days (Table 2). In plankton tows near Magnetic Island during the spawning periods in 1981, planulae were found up to 2.5 km from the nearest reef. Recent speculation that reefs are primarily self-seeded (26) was based on the rapid settlement times of a few hours to 2 days recorded for brooded planulae, which are well developed when released. However, the longer period required for development of externally fertilized eggs into planulae, and the observed dispersal of larvae, indicate that most of the planulae might be dispersed away from the parent reef. This suggests that reefs in the Great Barrier Reef Province are interdependent. Indeed, a survival period of 91 days shows that at least one species of *Acropora* is capable of surviving long enough to support the hypothesis that recruitment of *Acropora* to the Hawaiian Islands may occur by larval dispersal from Johnston atoll 720 km away (27).

As a result of this study, more coral species are now known to spawn gametes than to brood planulae, suggesting that viviparity may be the exception rather than the rule in coral reproduction. In addition, these corals do not breed continuously throughout the year, but spawn seasonally, most of them during a single brief annual period. The extremely short spawning period contradicts widespread assumptions about the lack of seasonality among tropical organisms. These observations are the first to show that synchronous multispecific spawning occurs in many corals and that the time of mass spawning is predictable.

PETER L. HARRISON  
RUSSELL C. BABCOCK  
GORDON D. BULL, JAMES K. OLIVER  
CARDEN C. WALLACE  
BETTE L. WILLIS

Department of Marine Biology, James Cook University of North Queensland, Townsville, Q. 4811, Australia

#### References and Notes

1. S. M. Marshall and T. A. Stephenson, *Sci. Rep. Great Barrier Reef Exped. 1928-1929* **3**, 219 (1933).
2. L. H. Hyman, *The Invertebrates*, vol. 1, *Protozoa through Ctenophora* (McGraw-Hill, New York, 1940).
3. T. W. Vaughan and J. W. Wells, *Geol. Soc. Am. Spec. Pap.* **44**, 1 (1943).
4. N. Abe, *Pulao Trop. Biol. Sta. Stud.* **1**, 73 (1937).
5. K. Atoda, *Sci. Rep. Res. Inst. Tohoku Univ. Ser. D* **20**, 105 (1953).
6. J. Harrigan, thesis, University of Hawaii (1972).
7. J. B. Lewis, *J. Exp. Mar. Biol. Ecol.* **15**, 165 (1974).
8. J. S. Stimpson, *Mar. Biol.* **48**, 173 (1978).
9. B. Rinkevich and Y. Loya, *Mar. Ecol. Prog. Ser.* **1**, 133 (1979).
10. ———, *ibid.*, p. 145.
11. A. Szmant-Froelich *et al.*, *Biol. Bull. (Woods Hole, Mass.)* **158**, 257 (1980).
12. B. L. Kojis and N. J. Quinn, *Bull. Mar. Sci.* **31**, 558 (1981).
13. ———, *Proceedings of the 4th International Coral Reef Symposium, Manila, Philippines* **2**, 145 (1981).
14. B. L. Kojis and N. J. Quinn, *Mar. Ecol. Prog. Ser.* **8**, 251 (1982).
15. A. M. Bothwell, *Proceedings of the 4th International Coral Reef Symposium, Manila, Philippines* **2**, 137 (1981).
16. P. R. G. Tranter, D. N. Nicholson, D. Kinchington, *J. Mar. Biol. Assoc. U.K.* **62**, 845 (1982).
17. Y. H. Fadlallah, *Oecologia (Berlin)* **55**, 379 (1982).
18. V. J. Harriott, *Coral Reefs*, in press.
19. Of the 32 species in Table 1; 22 species were regularly sampled and showed no evidence of a second gametogenic cycle throughout the year.
20. R. H. Richmond and P. L. Jokiel, *Bull. Mar. Sci.*, in press.
21. A. C. Giese and J. S. Pearse, in *Reproduction of Marine Invertebrates*, A. C. Giese and J. S. Pearse, Eds. (Academic Press, New York, 1974), vol. 1, pp. 2-49.
22. P. Korringa, *Geol. Soc. Am.* **67**, 917 (1957).
23. R. D. Campbell, in *Reproduction of Marine Invertebrates*, A. C. Giese and J. S. Pearse, Eds. (Academic Press, New York, 1974), vol. 1, pp. 133-199.
24. This was determined by extensive sampling (more than 20 colonies) for 9 species (6 *Acropora*, 2 *Goniastrea*, and 1 *Platygyra*). In a further 11 species, random samples were taken after the spawning event to verify the absence of eggs throughout the population. This was also confirmed for a population of *Montipora ramosa* by A. Heyward (personal communication).
25. R. L. Miller, in *Advances in Invertebrate Reproduction*, W. H. Clark and T. S. Adams, Eds. (Elsevier/North-Holland, New York, 1980), pp. 289-317.
26. T. J. Done, *Coral Reefs* **1**, 95 (1982).
27. R. W. Grigg, *Pac. Sci.* **35**, 15 (1981).
28. We thank J. D. Collins for assistance with fieldwork in 1982. C. G. Alexander, J. S. Lucas, J. R. Ottaway, M. M. Pichon, V. J. Harriott, B. A. Harrison, and D. G. Reid made valuable comments upon the manuscript. We also thank P. Watson of Shark World, Nelly Bay, Magnetic Island, for his cooperation and logistic support in 1981. Funded in part by a grant from the Great Barrier Reef Marine Park Authority in 1981, and an MSTGS grant to C.C.W.

5 July 1983; accepted 1 November 1983