gain, estimated from the ratio of peak-to-peak amplitude of tracking to target waveforms, averaged 0.87 ± 0.10. We also found that the gain for a given tracking trial was related to the correlation coefficient between error corrected for lag and target position ($r = 0.78$, d.f. = 68, $P < 0.001$), suggesting that a bat uses different gains at different times, although what determines its choice is not clear. If the tracking signal is adjusted to bring the gain to unity for that trial before subtracting the target signal, the mean error, now corrected for lag and gain (Fig. 2f), is reduced to 1.6° ± 0.4°. Small correlations between error and target position and velocity remain ($r = 0.13 \pm 0.20$ and $r = -0.20 \pm 0.22$, respectively), but they account for relatively little of the error signal's variance, suggesting that a nonpredictive tracking strategy is a reasonable interpretation of our data. The residual error of ±1.6° is comparable to the angular resolving ability of *Eptesicus* determined with stationary targets (*3*). It also indicates that bats can locate prey at least as precisely as other highly auditory hunters, such as owls (*7*), that rely on passive listening.

W. MITCH MASTERS
ANNE J. M. MOFFAT
JAMES A. SIMMONS
Institute of Neuroscience,
University of Oregon, Eugene 97403

References and Notes

1. D. R. Griffin, *Listening in the Dark* (Yale Univ. Press, New Haven, 1958; reprinted by Dover, New York, 1974); A. Novick, in *Biology of Bats*, W. A. Wimsatt, Ed. (Academic Press, New York, 1977), vol. 3, pp. 73–287; J. A. Simmons, M. B. Fenton, M. J. O'Farrell, *Science* **203**, 16 (1979); J. A. Simmons and S. A. Kick, in *Behavioral Physiology and Neuroethology: Roots and Growing Points*, F. Huber and H. Markl, Eds. (Springer, New York, 1983), pp. 267–279.
2. F. A. Webster and O. G. Brazier, *Aerospace Medical Research Laboratories Technical Report AMRL-TR65-172* (1965); F. A. Webster, in *International Conference on Sensory Devices for the Blind* (St. Dunstan's, London, 1967), pp. 63–87.
3. J. A. Simmons *et al.*, *J. Comp. Physiol.* **153**, 321 (1983).
4. S. A. Kick and J. A. Simmons, *J. Neurosci.* **4**, 2725 (1984).
5. Experiments were normally conducted under dim light, although some control experiments were done in total darkness: this did not change the bat's tracking accuracy. We also looked at the bats' response to the support frame with the ball removed. They were unable to follow, indicating that they were indeed tracking the intended target.
6. Of the measurements reported in this paper the two bats differed significantly from each other only in calling rate, head lag, and mean error. This last difference is a consequence of the difference in tracking lag.
7. E. I. Knudsen, G. G. Blasdel, M. Konishi, *J. Comp. Physiol.* **133**, 1 (1979).
8. Silicon Detector Corporation type SD-386-22-21-251.
9. Bruel and Kjaer type 4135.
10. We thank D. Presti and F. Presti for comments on the manuscript and D. Kon for assistance. Supported by the National Science Foundation, System Development Foundation, and Whitehall Foundation grants to J.A.S. and an NIH postdoctoral fellowship to W.M.M.

5 November 1984; accepted 25 March 1985

Coral Community Reproductive Patterns: Red Sea Versus the Great Barrier Reef

Abstract. *In contrast to many corals of the Great Barrier Reef, Australia, which are synchronous multispecific spawners, the abundant coral species in the northern Red Sea, Israel, exhibit temporal reproductive isolation. Spawning dates of 12 of the 13 Red Sea species followed lunar periodicity and were consistent throughout 3 years of study. Spawning periods of all species occurred in different seasons, different months, or different lunar phases within the same month. The high abundance of the corals studied at Eilat may be due in part to the advantages gained through not having overlapping spawning periods and settlement times.*

Our understanding of coral sexual reproduction is limited, and few generalizations can be made about the physical or biological factors responsible for the observed reproductive patterns (*1*). In particular, population ecology (*2*) and community structure of scleractinian corals is not well known. Until now, the reproduction of only one Red Sea stony coral (*Stylophora pistillata*) had been studied (*3*). We examined reproductive patterns of 13 ecologically important coral species (*4*) at Eilat (northern Gulf of Eilat, Red Sea). Major reproductive ac-

Table 1. Coral spawning dates at Eilat during 1981 and 1982. Data for 1980 is illustrated in Fig. 1. The lunar month is divided into eight phases similar to those described by Atoda (*8*): 1, new moon; 3, first quarter; 5, full moon; 7, last quarter; 2, 4, 6, and 8 indicate intermediate lunar phases.

1981		1982	
Spawning dates	Lunar phase	Spawning dates	Lunar phase
	*Stylophora pistillata**		
January–June		December–June	
	*Seriatopora caliendrum**		
4–5 May	1†	21–23 May	1†
31 May–2 June	1†	17–19 June	1†
28 June–3 July	8–1	16–20 July	8–1
27 July–1 August	8–1	13–18 August	8–1
27 August–1 September	8–1	13–18 September	8–1
26 September–1 October	8–1	12–17 October	8–1
23–28 October	8–1	12–17 November	8–1
26–28 November	1†	13–15 December	1†
	*Alveopora daedalea**		
18–24 October	6–8	5–11 November	6–8
15–21 November	6–8	4–10 December	6–8
17–23 December	6–8	2–8 January	6–8
	Pocillopora verrucosa		
1–2 July	1	19–20 July	1
31 July–1 August	1	19–20 August	1
	Galaxea fascicularis		
21–24 July	6–7	6–9 August	6–7
19–22 August	6–7	4–7 September	6–7
	Goniastrea retiformis		
24–27 July	7	9–12 August	7
	Platygyra lamellina		
30 June–5 July	1–2	19–24 July	1–2
1–3 August	1†	19–21 August	1†
	Favia favus		
21–26 June	6–7	9–14 July	6–7
20–22 July	6†	5–7 August	6†
	Astreopora myriophthalma		
16–18 July	5	3–5 August	5
15–17 August	5	1–3 September	5
	Acropora hyacinthus		
9–11 July	3	26–28 July	3
	Acropora scandens		
16–18 June	5	4–6 July	5
	Acropora humilis		
24–26 May	7	12–14 June	7
	Acropora eurystoma		
19–21 May	5	6–8 June	5

*Brooding species. †Sporadic spawning (10 to 20 percent of population).

Table 2. Time periods of development and settlement of planulae given in days from spawning until appearance of a fully developed polyp in the laboratory.

Species	Development in water column*	Minimum free-swimming period	Settlement range†	First polyp appears‡	First polyp with thecal walls
Stylophora pistillata§	0	1	1–2	6	7
Seriatopora caliendrum§	0	0.5	0.5–1	1	2
Alveopora daedalea§	0	3	3–6	16	30
Pocillopora verrucosa	1–2	3	3–5	8	16
Galaxea fascicularis	1–2	6	6–8	12	14
Goniastrea retiformis	1–2	6	6–8	14	18
Platygyra lamellina	1–2	8	8–10	11	12
Favia favus	1–2	6	6–8	12	17

*Time range from egg fertilization to first observation of swimming larvae. †Time range of active searching behavior on aquaria bottom until final settlement on substrate (dead coral branches). ‡Secretion of basal plate and first appearance of septae. §Brooding species.

tivities of these abundant species (*5*) occurred in different seasons, different months, or different lunar phases within the same month. These results are in marked contrast to the reproductive patterns described for 32 coral species in the central Great Barrier Reef (GBR) that were reported to be synchronous multispecific spawners (*6*).

Reproductive cycles were determined from in situ and laboratory observations as well as histological studies (*7*). The lack of overlap in spawning dates of the corals was consistent throughout all years of the study (Fig. 1 and Table 1). Spawning dates are thus highly predictable.

All species examined are sequential protogynous hermaphrodites and, except for *S. pistillata*, exhibit lunar periodicity of gamete or planular shedding (*8*). In most species the onset of oogenesis precedes that of spermatogenesis by 2 to 4 months. Maturation of the male and female gonads occurs simultaneously and spawning is synchronized. Broadcasting species release their gametes during periods of up to six nights, once or twice a year, whereas brooders release their planulae for 3 to 7 months (Fig. 1 and Table 1). The breeding period of most of the species studied occur throughout the summer, when water temperatures are rising or warmest (*9*) (in different months or different lunar phases within the same month).

Settlement of most of the released planulae of brooding species occurs within hours in *Seriatopora caliendrum*, 1 to 2 days in *S. pistillata*, and 3 to 6 days in *Alveopora daedalea*. In most gamete spawners, the interval between fertilization and settlement ranges from 6 to 10 days (Table 2). There are time gaps between the settlement dates of all species.

The free-swimming period of the planulae is 0.5 to 3 days in brooding species and 3 to 8 days in broadcasting species (Table 2). This difference is probably due to the time required by the larvae of the broadcasters to develop in the water column to the edwardsia stage (three to four pairs of mesenteries) or to the halcampoides stage (six pairs of complete mesenteries). These are the earliest developmental stages in which settlement has been observed. In the brooding species, planulae are already at the edwardsia or halcampoides stages when released, which may account for the shorter time period required for successful settlement.

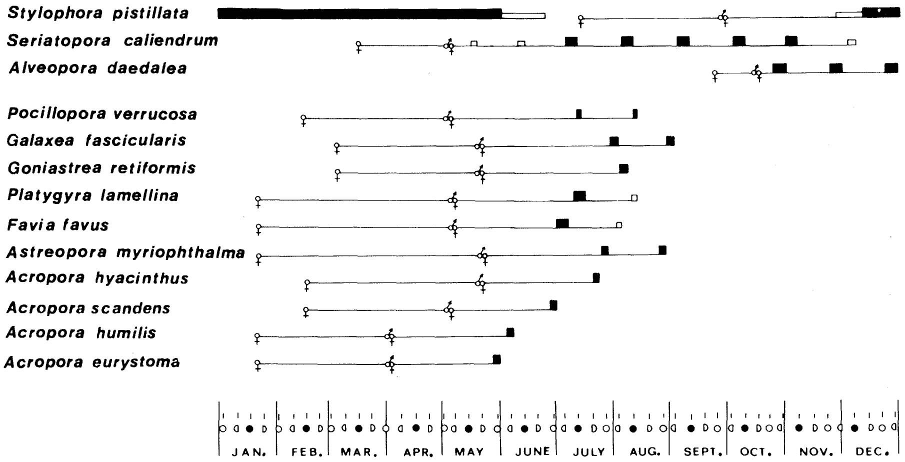

Fig. 1. Reproductive patterns of 13 scleractinian corals at Eilat in 1980. The first three species are brooders and the rest are broadcasting spawners. The results presented are in accordance with the lunar calendar, as follows: ●, new moon; ◗, first quarter; ○, full moon; and ◖, last quarter. The period of gonadal development is represented by a solid line with indications of the onset of oogenesis (♀), and spermatogenesis (♂). Further development of both gonads is indicated by the line following the ♂♀ sign. Black bars represent massive spawning (90 to 100 percent of the population), and blank bars represent sporadic spawning (10 to 20 percent of the population).

Because space for settlement and development is one of the most important limiting resources on coral reefs, there may be acute competition among coral populations (*2*, *10*) and other benthic organisms (*11*). Stony corals and benthic algae (turfs and macroscopic noncalcareous algae) have been suggested as the major competitors for space in shallow water at Eilat (*12*). The major reproductive activity of most of the corals studied coincides with the seasonal disappearance of benthic algae (*12*). Various species of algae progressively decline in abundance throughout the summer months, continuously creating more space for coral settlement during this season. During the winter algal cover on the shallow reefs is very high and space for settlement is scarce (*12*). Availability and predictability of space for settlement during summer, together with warm water temperatures (*9*), allow more favorable conditions for successful reproduction in Red Sea corals.

Levin (*13*) has suggested that selection for seasonal reproductive isolation in plants is usually a response to competition, whereas in animals it is more often a response to selection against hybridization or mismating. Most stony corals are sessile animals attached to the substrate throughout their lives; they possess many ecological features typical of both plants and animals. Selection against hybridization (more likely among sympatric species) or competition for space (or both) may have led to the evolution of temporal reproductive isolation among prominent reef corals at Eilat. Intraspecific synchronization of spawning and a discrete breeding period may be advantageous to each coral species by (i) reducing gametic wastage, hybridization, and disruptive gene flow; (ii) increasing the probability of successful fertilization; and (iii) reducing interspecific competition both among corals and between corals and algae. Hence, the success of these corals in terms of abundance and living cover (*5*) may be due in part to advantages gained by having no overlap in breeding periods (*14*).

The reproductive traits of 32 coral species from the central GBR differ from those at Eilat. Harrison *et al.* (*6*) reported synchrony of spawning both within and between coral species. Most of the species recorded spawned during a single night, a few nights after the late spring full moons, suggesting that the synchronous simultaneous spawning of corals may increase the survival chances of their larvae by satiating predators during the spawning period. To what extent gamete loss through hybridization takes place, or how gamete union is ensured in the resultant gamete melange, is not known.

A possible explanation for the differences in the reproductive patterns of corals in the two localities may be the marked differences in the respective environmental regimes. The range and amplitude of most environmental variables on the GBR are more extreme (*15*) than at Eilat. During the summer months at the Eilat study area (2 to 6 m depth), most environmental variables are almost constant (*16*). This might be one reason why the major reproductive season of corals at Eilat is much longer (3 to 4 months during summer) (Table 1) than that of GBR corals (1 to 2 months during spring). Also, within the same coral species, the time interval for gamete spawning is longer at Eilat: two to six nights once or twice a year (Table 2) compared to a single night annually in most of the central GBR corals (*6*). It is possible that mass spawning of GBR corals at a particular time of year may be induced by a precise combination of optimal environmental conditions, maximizing reproductive success. The evolution of discrete breeding periods in a coral community, as opposed to synchronous multispecific spawning, poses important theoretical questions regarding differences in stability and predictability of environmental conditions between the two areas during their evolutionary history. The high plasticity in reproductive traits of scleractinian corals, both on local and geographical scales, may account in part for their success in tropical seas.

Y. SHLESINGER
Y. LOYA

Department of Zoology,
George S. Wise Center for Life
Sciences, Tel Aviv University,
Tel Aviv, Israel 69978

References and Notes

1. Y. H. Fadlallah, *Coral Reefs* **2**, 129 (1984).
2. J. H. Connell, in *Biology and Geology of Coral Reefs*, O. A. Jones and R. Endean, Eds. (Academic Press, New York, 1974), vol. 2, pp. 205–245.
3. B. Rinkevich and Y. Loya, *Mar. Ecol. Prog. Ser.* **1**, 133 (1979).
4. Y. Loya, *Mar. Biol.* **13**, 100 (1972); *Nature (London)* **259**, 478 (1976); *Ecology* **57**, 178 (1976).
5. Although the 13 species studied make up only 13 percent of the total number of coral species known from Eilat, they are among the most abundant species, contributing approximately 60 to 70 percent of the total living cover of coral communities in shallow water (*4*).
6. P. L. Harrison, R. C. Babcock, G. D. Bull, J. M. Oliver, C. C. Wallace, B. L. Willis, *Science*, **223**, 1186 (1984). The GBR species studied make up approximately 10 percent of the total number of species known there.
7. The spawning of all species was observed in the field. In the laboratory living samples were studied with a stereoscope for gross detection of gonadal development (changes in size, color, and volume) enabling the evaluation of approximate spawning periods. Six to eight large colonies were then collected from depths of 2 to 6 m and held separately in aquariums with changing seawater for observations on release of gonadal products. For the histological study, four to six colonies of each coral species were sampled weekly during 1980 and monthly during 1981 and 1982. Histological procedures followed that of Rinkevich and Loya (*3*).
8. The lunar month is divided according to K. Atoda [*Sci. Rep. Tohoku Univ.* **18**, 48 (1947), table 4].
9. Fadlallah (*1*) shows that on a global scale, most corals reproduce throughout the spring and summer, when seawater temperatures are rising or are the highest of the year.
10. J. C. Lang, *Bull. Mar. Sci.* **23**, 260 (1973); J. W. Porter, *Science* **186**, 543 (1974).
11. J. B. C. Jackson, *Am. Nat.* **111**, 743 (1977); K. P. Sebens, *ibid.* **120**, 189 (1982).
12. Y. Benayahu and Y. Loya, *Helgol. Wiss. Meeresunters.* **30**, 362 (1977); *Bull. Mar. Sci.* **31**, 514 (1981). In many localities living cover contributed by stony corals and algae reaches 80 to 90 percent in shallow water.
13. D. A. Levin, *Am. Nat.* **104**, 571 (1970); *Taxon* **20**, 91 (1971).
14. Throughout the study we collected and observed additional species and at no time was synchronous multispecific spawning observed. Nevertheless, we do not rule out the possibility that the spawning periods of some uncommon species coincide with the ones reported here.
15. See J. Morrissey, *Aquat. Bot.* **8**, 91 (1980); J. D. Collins, thesis, James Cook University, North Queensland, Australia (1978).
16. See G. M. Friedman, *J. Sediment. Petrol.* **38**, 895 (1968); N. Paldor and D. A. Anati, *Deep Sea Res.* **26**, 661 (1979).
17. We thank J. Pearse, D. Potts, B. Rinkevich, and L. B. Slobodkin for critically reviewing the manuscript and offering valuable comments. This work was partly supported by the Tel Aviv University Fund for Basic Research and the Fund for Basic Research Administered by the Israel Academy of Sciences and Humanities.

12 October 1984; accepted 4 March 1985