Acropora (Anthozoa: Scleractinia) Reproductive Synchrony and Spawning Phenology in the Northern Line Islands, Central Pacific, as Inferred from Size Classes of Developing Oocytes[1]

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Abstract: Little is known of the timing of reproduction in central Pacific coral populations near the equator. Oocyte pigmentation and size comparison with sizes of mature eggs reported in published literature were used to infer intra- and interspecific synchrony and probable spawning phenology in 15 species of *Acropora* from Palmyra and Kingman atolls in the northern Line Islands. Sampling at both atolls took place in March–April 2002 and 2004. Oocyte sizes were determined from microdissections of fixed, decalcified samples. The majority (91.2%) of samples ($n = 209$) were gravid, with high levels of fertility in most (84.3%) samples. Statistically discrete oocyte size classes could be distinguished in most taxa at each atoll in each year. These discrete oocyte size classes suggest that several episodes of spawning, involving multiple species, take place over 2 or 3 months beginning in early spring. These data, which are the first observations of coral reproductive synchrony in the Line Islands, support the results of other recent studies, suggesting that reproductive synchrony can be a feature of equatorial reef assemblages where the annual ranges of sea-surface temperature and tidal amplitude are small.

THE WORLDWIDE DECLINE of coral reefs necessitates improved understanding of their intrinsic capabilities for replenishment and recovery. As one of the primary structural architects of reefs, scleractinian corals provide shelter and food for numerous other taxa of reef inhabitants. Their capacity to maintain or renew genetically diverse populations through sexual reproduction is a key attribute of reef resilience (West and Salm 2003). The dominant reproductive mode of scleractinian corals in the Pacific Ocean is broadcast spawning of gametes followed by external fertilization (reviewed in Harrison and Wallace 1990, Richmond and Hunter 1990). The phenology of spawning and degree of synchrony within and between species can vary widely among locations and along latitudinal gradients. For example, at least 133 species are known to participate in annual multi-species "mass spawning" events on the Great Barrier Reef in late austral spring (Willis et al. 1985), but corals in the Red Sea tend to spawn asynchronously (Shlesinger and Loya 1985, Shlesinger et al. 1998). It has been hypothesized that mass spawning during brief, predictable time windows is driven by large fluctuations in environmental parameters such as sea-surface temperature and tidal amplitude (Harrison and Wallace 1990), but recent studies indicate a high degree of spawning synchrony may also be characteristic of some equatorial assemblages (i.e., between 10° N and 10° S [Guest et al. 2005*a*]) where environmental fluctuations are less pronounced (Baird et al. 2001, 2002, Guest et al. 2002, 2005*a,b*, Penland et al. 2004).

Kingman (6° 25′ N, 162° 23′ W) and Palmyra (5° 53′ N, 162° 05′ W) are the northernmost atolls of the Line Islands Archipelago in the central Pacific (Figure 1).

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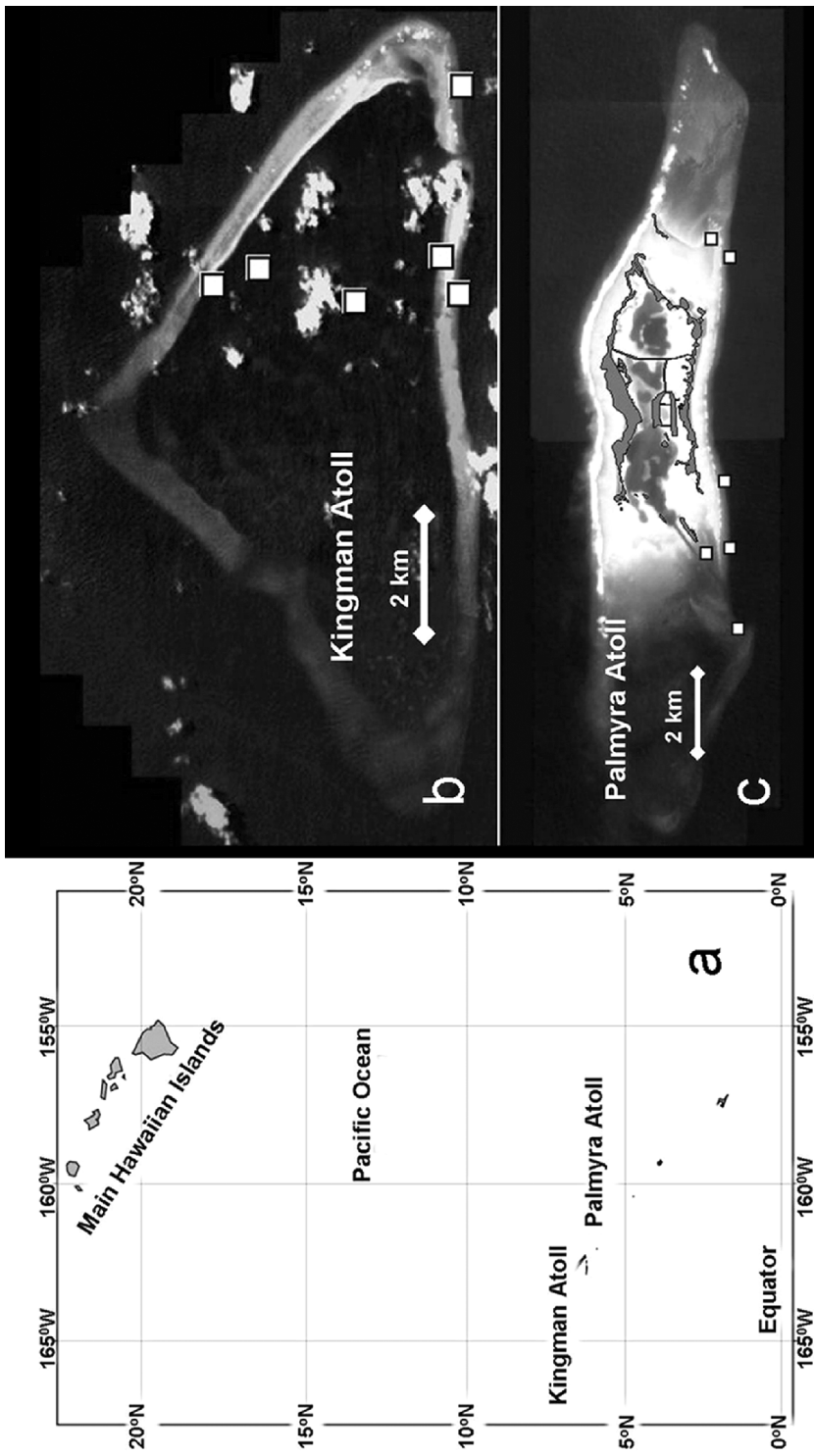
FIGURE 1. *a–c*. Location of Palmyra and Kingman Atolls in the central Pacific, and location of sample sites (squares) at each atoll using IKONOS imagery as a base map. Irregular white shapes overlying Kingman Atoll are clouds.

Both atolls are currently managed as National Wildlife Refuges by the U.S. Fish and Wildlife Service and lie beyond the proximate influence of population centers, associated pollution, and major shipping lanes. Legal access is largely restricted to scientific studies and, at Palmyra, infrequent ecotourism activities (Brainard et al. 2005).

No previous studies of coral reproduction have been conducted in the Line Islands. The aims of this study were to assess the degree of reproductive synchrony within and between species of scleractinian corals and infer probable spawning phenologies based upon the size of developing gonads. *Acropora* was chosen as the targeted study taxon because its reproductive parameters have been studied in diverse Pacific regions (e.g., Wallace 1985, Kenyon 1992, 1995, Baird et al. 2001, 2002, Guest et al. 2005*b*, Carroll et al. 2006) and thus provided the most extensive base for comparison.

MATERIALS AND METHODS

Due to their remote location, both Palmyra and Kingman atolls are only infrequently accessible to marine scientists. The reproductive condition of 15 *Acropora* species was examined at Palmyra Atoll and Kingman Atoll from 14 to 17 March 2002 and from 29 March to 4 April 2004. Colonies were sampled at six sites at Palmyra (depth range 1–14 m) and six sites at Kingman (depth range 6–14 m) (Figure 1). Sampled colonies measured > 30 cm in diameter to avoid sampling young colonies that had not yet reached sexual maturity. Colonies were sampled haphazardly, though care was taken to minimize sampling from clonemates by choosing widely separated or morphologically distinct colonies. All but two species were identified by reference to Veron (2000) and a list compiled by J. Maragos (unpubl. data) of corals reported from Palmyra and Kingman atolls since 1987 and 2000, respectively. Two species, designated *Acropora* sp. A and *Acropora* sp. B, could not be identified with these resources. *Acropora* sp. A formed a corymbose clump with appressed radial corallites; *Acropora* sp. B formed bushy colonies with irregularly sized corallites. Intact voucher specimens of the unidentified species were not retained due to the scarcity of samples. Branch pieces 7–12 cm long were removed with a small chisel, and the broken ends were examined by eye for conspicuous eggs. Microdissection of fixed, decalcified samples was chosen as the study approach due to limited field time, absence of land-based laboratory facilities, and the improbability of encountering spawning. Members of the genus *Acropora* are simultaneous hermaphrodites (Wallace 1985, Szmant 1986). Available evidence indicates that reproductive condition can be estimated based on the visibility and color of developing oocytes (Baird et al. 2002). Visible pigmented oocytes are mature and most likely will be released around the next full moon (Willis et al. 1985, Babcock et al. 1986, Oliver et al. 1988). Visible white oocytes are close to maturity and are likely to be spawned within 1–3 months. Colonies in which oocytes are not visible either have recently spawned or are unlikely to do so for at least 3 months (Harrison et al. 1984, Baird et al. 2002, Guest et al. 2005*b*). After visual inspection, samples were fixed in 10% formalin-seawater.

Fixed samples were decalcified in 4% acetic acid–seawater and examined with a dissecting microscope. Samples were classified as gravid if oocytes were seen through the undissected or longitudinally cut, translucent decalcified tissue. Polyps from individual colonies generally have a high degree of synchrony in gamete maturation (Wallace 1985). In gravid samples, the proportion of polyps that were fertile was estimated using a DACOR system (Dominant > 80%, Abundant 60–80%, Common 40–60%, Occasional 20–40%, Rare < 20%). For each gravid sample, five fertile polyps from a 1 cm length of tissue behind the sterile growing margin were randomly chosen for dissection (Wallace 1985, Kenyon 1992). Maximum and perpendicular diameters of each oocyte were measured, and oocyte size was computed as the geometric mean. Comparison of sizes of fixed and fresh oocytes obtained from the same colony indicates that fixation and storage in formalin for several months had no significant effect

on oocyte size (Kenyon 1992). The length of each individual testis in each polyp was also recorded. Mean oocyte size was calculated for each gravid sample and for all gravid samples of each taxon at each atoll in each sample year.

Student's *t*-test or one-way analysis of variance (ANOVA) were used to examine differences in mean oocyte size between conspecific samples at each atoll in each sample year; the number of statistical groups (i.e., oocyte size classes) was determined from pairwise multiple comparisons using the Bonferroni *t*-test. Kruskal-Wallis tests were used to examine oocyte size data that were not normally distributed, even with transformations, or had unequal variances, and the number of statistical groups was determined from pairwise multiple comparisons using Dunn's test. Statistical analyses were conducted using Sigma-Stat version 2.03 (Systat Software 2001).

For each taxon with evidence of more than one oocyte size class, mean oocyte size was computed for each statistical group. The statistical group with the highest mean was assumed to be the first spawning group for each taxon at each atoll in each year. The means of these putative first spawning groups were then compared with estimates of the size of mature oocytes of Pacific *Acropora* assembled from published literature to infer the probable phenology of spawning.

RESULTS

A total of 209 samples representing 15 *Acropora* species was collected and examined during the study (Tables 1, 2). Pigmented eggs were seen in nine (4.3%) fresh samples from three species (*A. elseyi*, *A. cerealis*, *A.* sp. B). White eggs were visible in 183 (87.5%) samples, which included 14 of the sampled taxa. Eggs could not be seen in only 17 (8.1%) samples. Thus, 91.9% of all samples were visibly gravid. The majority of gravid samples had high fertility (i.e., proportion of polyps that were fertile), as observed during microscopic examination of decalcified samples. Of the 192 gravid samples, 162 (84.3%) had estimated fertility levels greater than 60% (Ta-

bles 1, 2), the lower limit of the "Abundant" DACOR category.

Average polyp fecundity (number of oocytes per polyp) varied among taxa, ranging from 4.9 (*A. cytherea*, Kingman Atoll 2004, Table 2) to 11.2 (*A. cerealis*, Kingman Atoll 2002, Table 2). For most taxa that were sampled in more than one atoll or year (i.e., *A. cerealis*, *A. cytherea*, *A. humilis*, *A. hyacinthus*, *A. nobilis*, *A. valida*), average polyp fecundity values were quite consistent between atolls and years. Only *A. verweyi* samples showed notable variation in average polyp fecundity between sample years (Table 1).

Mean oocyte size calculated from all gravid samples varied among taxa, ranging from 210 μm (*A. verweyi*, 2002) to 591 μm (*A. nobilis*, 2004) (Table 1). For all taxa sampled in both years at either atoll, mean oocyte size was greater in 2004 than in 2002, as might be expected because sampling occurred about 2 weeks later in 2004 than in 2002. For all but one taxon (*A. verweyi*, Palmyra, 2002) at both atolls in both years in which more than one colony was sampled, there was a significant difference ($P \leq .002$) among colonies in mean oocyte size, with two or three discrete oocyte size classes distinguished by multiple comparison tests (Tables 1, 2). For taxa that were sampled at more than one site at each atoll, the oocyte size classes did not correspond to different sample sites (Figure 1). The majority (>98%) of dissected polyps ($n = 960$) had well-developed, loculated testes (two "large" and two "small" [Wallace 1985]) in which the maximum length varied by taxon (range 1,250–3,000 μm) (Tables 1, 2).

DISCUSSION

The available evidence of sample fertility, polyp fecundity, and oocyte size classes suggests that *Acropora* corals at Palmyra and Kingman atolls possess a high degree of intra- and interspecific synchrony in reproductive development, and that there are two or more spawning episodes per year beginning in early spring, each of which may be synchronous. Indeed, the proportion of gravid colonies (91.8%) documented from both years in this study exceeded the proportion

TABLE 1
Reproductive Status of *Acropora* Corals Sampled at Palmyra Atoll

Sample Dates	Species	No. of Colonies Sampled	% Gravid Samples	Gravid Sample Fertility, D:A:C:O:R[a]	Polyp Fecundity: No. Oocytes/Polyp (Mean ± SE)	No. of Oocytes Measured	Oocyte Diameter, μm (Mean ± SE), All Gravid Samples	P Value	No. of Oocyte Size Classes	Oocyte Diameter, μm (Mean ± SE), Putative First Spawning Group	Maximum Testes Length, μm
14–16 March 2002	*A. clathrata*	4	100	4:0:0:0:0	6.7 ± 0.1	134	430 ± 4.5	<.001[b]	2	451 ± 5.0	2,000
	A. cytherea	16	75	6:2:3:1:0	5.4 ± 0.3	322	502 ± 17.5	<.001[c]	2	513 ± 3.4	2,000
	A. elseyi[e]	1	100	1:0:0:0:0	5.4 ± 0.5	27	571 ± 9.8	—	1	571 ± 9.8	2,000
	A. gemmifera	1	100	1:0:0:0:0	8.4 ± 0.5	42	437 ± 9.9	—	1	437 ± 9.9	2,250
	A. humilis	9	100	9:0:0:0:0	6.8 ± 0.4	307	517 ± 2.7	<.001[c]	2	540 ± 2.8	1,750
	A. hyacinthus	15	100	12:1:2:0:0	7.8 ± 0.4	589	409 ± 3.4	<.001[c]	3	489 ± 5.6	2,500
	A. nobilis	8	100	8:0:0:0:0	6.6 ± 0.3	262	458 ± 4.7	<.001[b]	3	510 ± 4.7	2,000
	A. samoensis	1	100	1:0:0:0:0	6.2 ± 0.9	31	553 ± 8.8	—	1	553 ± 8.8	1,500
	A. tenuis	4	100	4:0:0:0:0	12.9 ± 0.6	257	369 ± 3.7	<.001[c]	2	396 ± 4.6	1,500
	A. valida	11	100	10:1:0:0:0	6.4 ± 0.4	350	482 ± 3.3	<.001[c]	2	508 ± 4.4	2,000
	A. verweyi	3	67	0:2:0:0:0	8.6 ± 0.7	84	210 ± 4.1	.81[d]	1	210 ± 4.1	2,000
	A. sp. A	1	100	1:0:0:0:0	9.2 ± 1.2	46	344 ± 6.5	—	1	344 ± 6.5	1,250
	Total	74	93	57:6:5:1:0		2,405					
29–31 March 2004	*A. cerealis*[e]	13	100	11:0:0:2:0	9.7 ± 0.6	632	505 ± 2.3	<.001[c]	3	546 ± 2.6	3,000
	A. cytherea	11	82	6:1:2:0:0	6.2 ± 0.4	277	550 ± 3.7	<.001[c]	2	574 ± 4.5	2,500
	A. humilis	5	60	2:0:1:0:0	5.8 ± 0.4	87	526 ± 13.7	<.001[c]	2	607 ± 10.2	1,750
	A. hyacinthus	8	100	6:2:0:0:0	6.2 ± 0.3	248	460 ± 4.4	<.001[c]	3	506 ± 5.2	1,750
	A. nobilis	14	100	13:1:0:0:0	5.3 ± 0.1	377	591 ± 3.1	<.001[b]	2	630 ± 4.5	2,500
	A. polystoma	5	80	2:1:1:0:0	5.9 ± 0.3	119	465 ± 9.8	<.001[c]	2	562 ± 9.6	2,250
	A. verweyi	10	60	0:0:2:2:2	5.8 ± 0.3	175	412 ± 4.7	<.001[c]	2	476 ± 6.2	1,250
	A. sp. B[e]	3	100	1:0:2:0:0	6.9 ± 0.5	103	532 ± 6.8	<.001[c]	2	566 ± 7.2	2,500
	Total	69	83	41:5:8:4:2		1,915					

[a] In gravid samples, an estimate of the proportion of polyps that were fertile. D > 80%, A 60–80%, C 40–80%, O 20–40%, R < 20%.
[b] Comparison of diameter means made using one-way ANOVA and number of oocyte size classes determined from pairwise multiple comparisons using Bonferroni *t*-test.
[c] Comparison of diameter means made using Kruskal-Wallis test and number of oocyte size classes determined from pairwise multiple comparisons using Dunn's test.
[d] Comparison of diameter means was made using Student's *t*-test.
[e] Pigmented oocytes in some fresh specimens.

TABLE 2

Reproductive Status of *Acropora* Corals Sampled at Kingman Atoll

Sample Dates	Species	No. of Colonies Sampled	% Gravid Samples	Gravid Sample Fertility, D:A:C:O:R[a]	Polyp Fecundity: No. Oocytes/Polyp (Mean ± SE)	No. of Oocytes Measured	Oocyte Diameter, μm (Mean ± SE), All Gravid Samples	P Value	No. of Oocyte Size Classes	Oocyte Diameter, μm (Mean ± SE), Putative First Spawning Group	Maximum Testes Length, μm
17 March 2002	A. cerealis	6	100	6:0:0:0:0	11.2 ± 0.6	337	423 ± 2.6	<.001[c]	2	428 ± 2.8	2,500
	A. cytherea	8	100	5:2:0:1:0	5.9 ± 0.3	237	501 ± 4.8	<.001[c]	2	516 ± 4.4	2,000
	A. humilis	4	100	4:0:0:0:0	6.4 ± 0.3	127	513 ± 3.8	<.001[b]	2	527 ± 5.1	2,000
	A. hyacinthus	8	100	7:1:0:0:0	7.7 ± 0.5	306	441 ± 3.2	<.001[c]	2	471 ± 3.7	1,750
	A. valida	2	100	1:1:0:0:0	6.5 ± 0.3	65	463 ± 6.2	.002[d]	2	482 ± 5.2	1,750
	Total	28	100	23:4:0:1:0		1,072					
2–4 April 2004	A. cytherea	7	86	2:1:2:1:0	4.9 ± 0.4	148	550 ± 4.7	<.001[b]	2	601 ± 12.8	1,750
	A. humilis	7	71	2:0:1:2:0	5.9 ± 0.3	147	557 ± 4.7	<.001[b]	2	582 ± 6.8	1,750
	A. hyacinthus	8	100	8:0:0:0:0	6.9 ± 0.4	277	510 ± 2.8	<.001[b]	3	532 ± 3.6	2,000
	A. nobilis	6	100	3:1:1:1:0	5.1 ± 0.6	156	538 ± 5.1	<.001[b]	2	600 ± 9.0	2,000
	A. tenuis	10	100	10:0:0:0:0	9.6 ± 0.6	470	487 ± 14.6	<.001[b]	3	567 ± 3.2	3,000
	Total	38	92	25:2:4:4:0		1,198					

[a] In gravid samples, an estimate of the proportion of polyps that were fertile. D > 80%, A 60–80%, C 40–80%, O 20–40%, R < 20%.
[b] Comparison of diameter means made using one-way ANOVA and number of oocyte size classes determined from pairwise multiple comparisons using Bonferroni *t*-test.
[c] Comparison of diameter means made using Kruskal-Wallis test and number of oocyte size classes determined from pairwise multiple comparisons using Dunn's test.
[d] Comparison of diameter means was made using Student's *t*-test.
[e] Pigmented oocytes in some fresh specimens.

TABLE 3

Comparison of Mean Diameters (µm) of Mature Oocytes of Pacific *Acropora* Species and Conspecific First Spawning Group Oocytes in This Study

Species	Published Literature[a,b]					This Study[a]	
	Australia	Hawai'i[2]	Guam[3]	Okinawa[3]	Palau[4]	Palmyra	Kingman
A. carduus					531 (50)		
A. clathrata					566 (50)	451 (68)	
A. cytherea	600 (18)[5]	622 (132)		547 (40)		513 (270)	516 (149)
	556 (50)[3]					574 (174)	601 (22)
A. digitifera			588 (75)	457 (25)			
A. elseyi				650 (20)		571 (27)	
A. florida	584 (998)[1]				562 (50)		
A. granulosa	534 (486)[1]				698 (50)		
A. hyacinthus	622 (1,250)[1]					489 (85)	471 (155)
						506 (99)	532 (125)
A. humilis	467 (50)[3]	714 (73)				540 (159)	527 (61)
						607 (26)	582 (64)
A. longicyanthus	591 (1,755)[1]						
A. loripes	560 (1,711)[1]						
A. nasuta				439 (25)			
A. nobilis	571 (886)[1]			495 (25)		510 (134)	600 (20)
						630 (137)	
A. pulchra	575 (18)[5]						
A. robusta			570 (50)				
A. samoensis	550 (100)[3]						
A. sarmentosa	652 (663)[1]						
A. tenuis	514 (50)[3]					396 (138)	567 (41)
A. valida	633 (672)[1]	642 (348)	598 (50)			508 (198)	482 (31)
	596 (17)[5]						

[a] Number of oocytes measured is given in parentheses.
[b] References 1, 2 report fixed microdissections 1–2 weeks before spawning; references 3, 4, 5 report freshly spawned oocytes.
[1] Wallace (1985), [2] Kenyon (1992), [3] Kenyon (1994), [4] Kenyon (1995), [5] Babcock et al. (2003).

recorded along the north, central, or southern Great Barrier Reef (63%, 73%, and 77%, respectively) 2 weeks before an expected mass-spawning event (Baird et al. 2002). The presence of statistically distinguishable oocyte size classes in all but one taxon in which more than a single colony was sampled suggests that spawning among conspecifics is synchronized in any given month. Species with small sample sizes (one to three colonies) may have revealed a larger number of oocyte size classes if sample size had been greater. The presence of up to three oocyte size classes in 15 species suggests at least several episodes of spawning that each include multiple species.

Inferences of probable spawning phenology at Palmyra and Kingman atolls can be made based upon comparing the mean size of developing oocytes with values reported for mature *Acropora* oocytes in published literature (Table 3). For individual taxa, the range of sizes from different geographic regions is as great at 247 µm (i.e., *A. humilis*), though most interregional size differences are considerably less. Most oocyte size means in this study fell within the range (439–714 µm) previously reported as mature for Pacific *Acropora*, but the means of some sample sets did not (Palmyra: *A. gemmifera*, *A. hyacinthus* 2002, *A. tenuis*, *A. sp. A*, *A. verweyi*; Kingman: *A. cerealis*) (Tables 1, 2). However, when mean oocyte size was computed for individual oocyte size classes for each taxon at each atoll in each year, for most taxa the highest mean fell within the range of sizes associated with maturity (Tables 1–3) and is presumed to represent the first spawning group. Colonies

from three species sampled at Palmyra Atoll (*A. elseyi*, *A. cerealis*, *A*. sp. B) had pigmented eggs, suggesting that they spawned after the next full moon of the sample years. In 2002, full moon occurred on 28 March; in 2004, full moon occurred on 5 April. Colonies with white eggs representing the putative first spawning group likely attained maturity and spawned following the second full moon after sampling in each year. For taxa in which two or more oocyte size classes were statistically distinguished, spawning likely occurred in as many months. Split spawning, in which individual taxa spawn over at least two consecutive months, has been documented in other *Acropora* populations (Wallace 1985, Willis et al. 1985, Kenyon 1994, Wolstenholme 2003, Guest et al. 2005*b*). Only *A. tenuis* and *A. verweyi* at Palmyra Atoll did not show evidence of near-mature oocyte sizes in concert with other sampled taxa (Tables 1, 3); hence their first spawning period may be delayed relative to other sampled taxa, or the range of sizes associated with maturity in Pacific *Acropora* may be broader than is currently documented. Mature egg sizes derived from histological sections of Caribbean *Acropora* species can be smaller (i.e., ∼325 μm) than those reported from the Pacific (Szmant 1986, Vargas-Angel et al. 2005). For all taxa, maximum testes length was within the size range associated with maturity or near-maturity (Kenyon 1992).

Early studies from higher latitudes suggested that ranges in sea-surface temperature and tidal amplitude might be causal factors underlying reproductive synchrony, and it was predicted that seasonality and synchrony would be reduced in equatorial regions where the range of these parameters is often small (Oliver et al. 1988, Richmond and Hunter 1990). However, more recent studies on near-equatorial reef assemblages have revealed that reproductive seasonality and multispecies spawning synchrony are features of diverse equatorial reefs and that a large range in annual sea-surface temperature or tidal amplitude is not required (Kenyon 1995, Edinger et al. cited in Tomascik et al. 1997, Baird et al. 2002, Guest et al. 2002, 2005*a,b*, Penland et al. 2004). The study reported here extends this growing body of evidence

to additional equatorial reef assemblages in the central Pacific. The proportion of gravid colonies (91.8%) documented from both years in this study surpasses the proportion of gravid colonies (58.5%) documented off Singapore (1° N) shortly before a multi-species spawning event over several nights following the March 2002 full moon (Guest et al. 2002). It also exceeds the proportion of gravid colonies (42%) reported from the Solomon Islands (8° S) shortly before observed multispecies spawning (Baird et al. 2002). The higher proportion of gravid colonies in the study reported here may derive, in part, from assessing reproductive status with the use of a dissecting microscope rather than visual inspection of fresh samples alone, as was done in the two cited studies. At Palmyra and Kingman atolls, the annual range in sea-surface temperature is 3°C, though shallow sites with poor circulation can show large diel variations (Brainard et al. 2005; R. E. Brainard, unpubl. data). The range of spring tides is 0.8 m (http://tidesandcurrents.noaa .gov). Values of both environmental parameters are comparable with those in the Solomon Islands (8° S), where multispecies spawning including 12 coral species has been documented (Baird et al. 2001).

The study reported here, which provides evidence suggesting several episodes of synchronous multispecies spawning over a period of at least 2 or 3 months, represents a first look at coral reproduction in the northern Line Islands. High sample fertility observed in this study (Tables 1, 2) indicates a robust reproductive potential. However, the 15 sampled species represent a small percentage of the scleractinian taxa currently reported from Palmyra (164 species, 41 genera) and Kingman atolls (144 species, 39 genera) (J. Maragos, unpubl. data). In situ observations of spawning as well as studies including other taxa over more extended time periods are clearly needed before generalizations can be made about reproductive seasonality and the degree of interspecific synchrony.

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