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RESEARCH ARTICLE

Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the Equatorial Eastern Pacific: Part V. Dendrophylliidae

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Abstract The reproductive ecology of *Tubastraea coccinea* Lesson, an azooxanthellate tropical scleractinian coral, was studied over various periods from 1985 to 2006 at four principal eastern Pacific locations in Costa Rica, Panamá, and the Galápagos Islands (Ecuador). This small (polyp diameter 0.8–1.0 cm), relatively cryptic species produced ova and planulae year round, including colonies with as few as 2–10 polyps. Of 424 colonies examined histologically, 13.7% contained both ova and sperm. Mature ova varied in diameter from ~300 to 800 μm and the time from spawning and fertilization of oocytes to release of brooded planulae was about 6 weeks. Planulae were 0.5–1.5 mm long and they settled and metamorphosed on a variety of substrates after 1–3 days. Spermaries, though more difficult to distinguish in histological sections, were present throughout the year. Spent spermaries were never observed in sections, but several colonies in Panamá and the Galápagos Islands released sperm from night one to night five after full moon, indicating the potential for cross-fertilization among colonies. Planula release was observed at Uva Island (Panamá) in March, May, June, and July, and in general planula presence was higher at warm ocean temperatures at all sites, whether or not the sites were influenced by seasonal upwelling. Annual fecundity estimates for *T. coccinea* are comparable with other high fecundity brooding species, including the zooxanthellate *Porites panamensis*, with which it co-occurs in Panamá. *Tubastraea coccinea* is widely distributed in the tropical Indo-Pacific and has colonized substrates in the western Atlantic. In addition to the reproductive characteristics described in the present study, other features of the biology of *T. coccinea*, such as an ability to withstand conditions that produce bleaching and mortality in zooxanthellate species, may account for its widespread, low-latitude distribution in multiple oceans.

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Introduction

Aspects of the sexuality, reproductive condition, lunar and seasonal spawning patterns, fecundity and planula settlement behavior of *Tubastraea coccinea* are considered here as a contribution to a series of studies on the reproductive ecology of eastern Pacific scleractinian corals (Glynn et al.

1991, 1994, 1996a, 2000; Colley et al. 2000, 2006). The principal motivation for these studies stems from the severe El Niño-Southern Oscillation (ENSO) disturbance of 1982–1983 that devastated coral reefs and coral communities in the equatorial eastern Pacific (Glynn 1984, 1990; Glynn and Colgan 1992; Guzmán and Cortés 1992; Prahl 1985; Robinson 1985) The equally strong 1997–1998 ENSO event also caused coral mortality and affected coral reproduction in the eastern Pacific (Glynn et al. 2001; Colley et al. 2006). To assess coral reef resilience following these disturbance events, it is necessary to investigate the reproductive ecology of corals, relating fecundity, spawning activity and recruitment of surviving species to community recovery.

Considering the often-high local abundance and nearly circumtropical distribution of the azooxanthellate scleractinian coral *Tubastraea coccinea*, surprisingly little is known of its reproductive biology and ecology. Listed under the junior synonym, *Tubastraea aurea* (see Cairns 2000), Fadlallah (1983), Harrison and Wallace (1990) and Richmond (1997) noted that *T. coccinea* is a brooder, i.e. it releases planula larvae. This species has also been observed to spawn gametes on the Great Barrier Reef (Ayre, personal communication in Harrison and Wallace 1990). Edmondson (1946) reported that planula release of *T. coccinea* in Hawaii occurred mainly in autumn and winter, and Richmond and Hunter (1990) and Richmond (1997) extended this release period to the summer season. Richmond (personal communication) also noted that *T. coccinea* released larvae under laboratory conditions over a 6-month period (June–November) in the Gulf of Panamá in the eastern Pacific. Richmond further observed (personal commuication in Fenner 2001) that the planulae of *Tubastraea* species could remain competent up to 100 days. Ayre and Resing (1986) found that planulae were produced asexually in Australia. Van Moorsel (1988) observed that the early (up to 2 years) maximum growth rates of *T. coccinea* were comparable to those of zooxanthellate corals on a Caribbean reef. The calcification rates of *T. coccinea* reported by Marshall (1996) were also found to be comparable with a zooxanthellate coral (*Galaxea*). *Tubastraea coccinea* is present throughout the Indo-Pacific realm, the eastern Pacific, and also occurs in the western and eastern Atlantic regions. It was possibly introduced to the Caribbean in the late 1930s, on a ship's hull from the Indo-Pacific (Cairns 2000). From its first appearance in the eastern Caribbean (Puerto Rico and Curaçao, between 1948 and 1950), it has spread relatively rapidly throughout the Caribbean, the Bahamas and most recently into the Gulf of Mexico (Fenner 2001) and south to Brazil (Figueira de Paula and Creed 2004).

Some key aspects addressed in this study relate to the high abundance and widespread distribution of *Tubastraea coccinea* on equatorial eastern Pacific reefs. How might this success be related to its reproductive ecology? It is now possible to compare the reproductive activity and fecundity of *T. coccinea* with 11 other reef corals in Costa Rica, Panamá and the Galápagos Islands (Glynn et al. 1991, 1994, 1996a, 2000; Colley et al. 2000, 2006, unpublished observations). Selection of study sites was based primarily on the diversity of environmental conditions prevalent in the equatorial eastern Pacifi: (1) Caño Island, Costa Rica, and Gulf of Chiriquí, Panamá—relatively high and constant sea surface temperature (SST); (2) Gulf of Panamá, Panamá—seasonal upwelling with marked SST declines; (3) Galápagos Islands, Ecuador—relatively low and variable SSTs frequently influenced by El Niño and La Niña activity. See Appendix 1 for more detailed information.

Tubastraea coccinea and the small nodular zooxanthellate species *Porites panamensis* are the only common brooding corals on eastern Pacific reefs. All of the other studied zooxanthellate species are broadcast spawners. A pattern that has emerged for the majority of these species is (a) extended year-round reproductive activity and (b) spawning concentrated around new and full lunar phases. However, at upwelling sites (Gulf of Panamá) or during dry/cool periods (Galápagos Islands) when water temperatures are seasonally low, reproductive activity is greatly curtailed. In this study, we offer evidence of extended seasonal reproductive activity, high fecundity, and rapid larval settlement near reproducing populations, attributes that contribute towards the prominence of *T. coccinea* on eastern Pacific coral reefs.

Materials and methods

Species and collections

Tubastraea coccinea Lesson is the most abundant and widespread azooxanthellate scleractinian associated with eastern Pacific zooxanthellate coral communities and coral reefs. While colonies are occasionally present on exposed substrates intermingled with zooxanthellate corals, they typically occur on the undersides of large rocks, in the eroded spaces under large massive corals, in caves and on rock walls. This species has appeared under various synonyms (Maragos 1977; Wells 1983; Cairns 2000), e.g. *Tubastraea aurea* Quoy & Gaimard, *Tubastraea tenuilamellosa* Milne Edwards & Haime, and *Dendrophyllia manni* (Verrill).

Collections for histological analysis were made from the mid-1980s to 1998, with varying degrees of effort in Costa Rica, Panamá, and the Galápagos Islands. Locations of collection sites are noted in Fig. 1. Sampling depths ranged from 2 to 5 m below MLLW (mean lower low water).

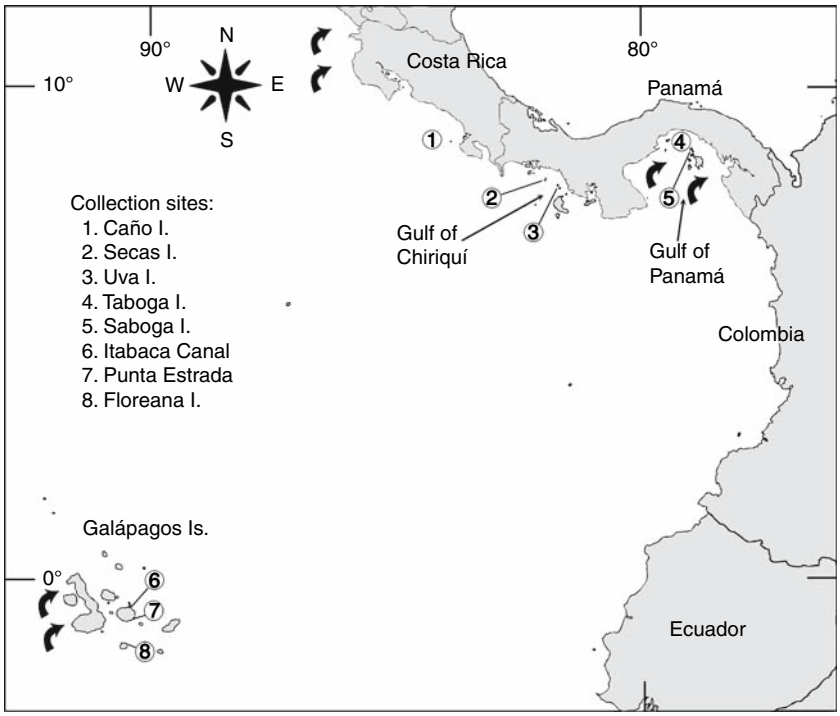

Fig. 1 Study sites in the equatorial eastern Pacific: Costa Rica, Caño Island (*1*); Panamá, Gulf of Chiriquí, and unnamed island in the Secas Islands group (*2*); Uva Island (*3*); Panamá, seasonally upwelling Gulf of Panamá, Taboga Island (*4*); Saboga Island (*5*); Galápagos Islands, Itabaca Canal (*6*); Punta Estrada (*7*); Floreana Island (*8*). *Thick black arrows* denote upwelling centers

Sampled colonies generally ranged from 10 to 30 polyps each. Studies directed toward planula swimming behavior, settlement, size at first reproduction, and planula release and fecundity were performed mainly from 2000 to 2006 in Panamá and the Galápagos Islands. Information on dates, numbers of collections, colonies sampled and site-specific environmental conditions is available in Appendix 1.

Histology

Preparation of tissues for histology followed the methods in Glynn et al. (1994, 1996a, 2000). Decalcification of *Tubastraea* tissues is slow (often requiring several days) due to the density and intricate structure of the skeleton. Staining times with azocarmine and aniline blue were limited to 15 min because of the absorptive characteristics of the tissues. Sectioning was performed with a very sharp microtome blade since mature eggs and planulae had a tendency to pull from ovarian tissues.

Observations of live colonies

Field observations were conducted mostly at the Secas and Uva reefs in the Gulf of Chiriquí, Panamá, where numerous colonies occurred on vertically exposed dead *Pocillopora* spp. frameworks. Observations of planulae, recruits and mature colonies were carried out in (1) flow-through sea water tables and 4-l containers supplied with aeration aboard ship, (2) 1.5-l flow-through plastic buckets assembled at the Coiba Island field facility, (3) flow-through sea water tables at the Smithsonian marine laboratory, Naos Island, Panamá, and (4) recirculating tanks at the Rosenstiel Marine School in Miami, Florida. Coral rock and adult colonies with attached bare rock bases were placed in all containers to provide potential settlement sites. Mature colonies were fed *Artemia salina* nauplii (stage 2) in the recirculating tanks in Miami.

Analysis

To assess temporal patterns of gametogenesis, all histologically sampled colonies were scored with respect to the presence or absence of gametocytes, and for each collection the abundance of colonies with gametocytes present was expressed as a percentage of the total number of colonies examined on that date. The seasonal and lunar occurrence of mature gonads also was expressed as a percentage of all gonads observed on a given Julian or lunar date. Values were then plotted to inspect for patterns. Since >95% of colonies contained oocytes and/or ova, data only for hermaphroditic colonies (with spermaries) and colonies containing planulae were plotted. In this study, oocytes are defined as developmental Stages I, II, and III; ova as stage IV (see "Gamete and planula development" below).

Chi-square analyses were performed to test for sex ratio differences and trends in seasonal and lunar reproductive activity. To detect seasonal patterns, observations in Costa Rica and Panamá were divided into dry (mid-December through mid-April, 4 months) and wet (mid-April through mid-December, 8 months) season periods. These seasonal

patterns were reversed for the Galápagos analyses with the year subdivided into wet/warm (mid-December through mid-April) and dry/cool (mid-April through mid-December) seasons. To detect possible lunar patterns, the lunar month was divided into four quarters: days 26–4, 5–11, 12–18 and 19–25. This ordering deviates from earlier studies (e.g. Glynn et al. 2000) because it was reasoned that these periods would more accurately capture reproductive activity around the new and full lunar phases. Analyses included only data from colonies with spermaries (hermaphrodites) and/or planulae.

Polyps are elevated and widely separated by thick, deep thecal walls. Coralla are round to elliptical, ranging from two to hundreds of polyps arranged in bouquet fashion. Most mature polyps are about the same height within a colony, and are 0.8–1.0 cm in diameter. Therefore, the number of mature ova polyp^{-1} was reported rather than per surface area of tissue as recommended by Harrison and Wallace (1990). However, sexual products per cm^2 are also presented in the final fecundity estimates for comparison with other studies (e.g. Hall and Hughes 1996).

Polyps from all study sites were decalcified and dissected to determine total numbers of mesenteries, reproductive mesenteries and Stage IV ova per reproductive mesentery. Polyp lengths and widths were measured before removal of epidermal and gastrodermal layers. One to three polyps were examined for each selected date (12–33 polyps per location from various colonies). All Stage IV ova polyp^{-1} were counted when present. Interior polyp volumes were estimated from the volume of a cylinder, $V = \pi r^2 2h$ (r = 0.5 polyp diameter, h = polyp height), and were compared with numbers of Stage IV ova polyp^{-1} volume employing the Pearson Product Moment test.

Fecundity measurements were also derived from longitudinal sections of polyps. Stage IV ova diameters were measured in histological sections to distinguish ova from planulae. Ovum and planula size measurements in histological preparations are underestimates due to 20–30% shrinkage (Harriott 1983). Stage IV ova and Stage I planulae could not always be confidently separated in dissected preserved material. However, mature planulae readily fell away from dissected polyps. Ovum volumes were calculated from ovum diameters by employing the volume of a sphere ($V = 4/3\ \pi r^3$). One slide of Stage IV ova was used to measure ovum diameters for each colony with Stage IV ova for all collection locations. Since most samples contained Stage IV ova, ovum diameter measurements were made from colonies that contained partially spawned ovaries, spermaries, planulae or both in order to include the most mature ova. A random number table was used to select ova for measurement except in samples from Taboga Island where ovum numbers were too few. Planula length measurements were taken from 30 live, free-swimming larvae in Panamá (Gulf of Chiriquí) on 18 September 2006. These were compared with the same ethanol (70%)-preserved specimens after 3 weeks. Live mean (±SE) lengths were 1.21 ± 0.06 mm and dead mean lengths were 1.02 ± 0.04 mm. These differences amounted to 15.7% shrinkage. Planula volumes were estimated from the equation, $V = (h + l)\ \pi r^2$, assuming a cylindrical midbody region and parabolic end caps where l is the length of midbody, r the radius, and h the length of paraboloid end cap (see Harris and Stocker 1998).

Ova per mesentery counts were obtained from both histological, longitudinal sections and dissected specimens. As noted above, Stage IV ova polyp^{-1} was determined from dissected polyps. However, due to difficulties in discerning Stage IV ova from early planulae in dissected tissues, mean ova polyp^{-1} was also calculated from Stage IV ova per mesentery counts from histological tissues multiplied by the mean number of mesenteries (24, determined from dissected tissues). This was completed for each location and sometimes for all locations pooled.

Planulae polyp^{-1} was estimated from counts within preserved, dissected polyps. The number of reproductive cycles per year was inferred from patterns of reproductive activity in histological and dissected tissues, and from spermatozoa and planula release from live colonies. Annual volume production of planulae was determined from size measurements and calculated Stage IV planula volumes, counts of planulae polyp^{-1}, number of polyps cm^{-2}, and number of reproductive cycles years^{-1}.

Colony size series collections, from 1 to ~100 polyps colony^{-1}, were obtained to determine the minimum reproductive sizes. Corals from three sites in Panamá (Uva, Taboga and Saboga Islands), collected during known periods of planula release, were preserved immediately, decalcified, and then dissected and examined microscopically. Numbers and sizes of polyps and colonies, and the developmental stages of reproductive products were noted. The relationship between coral size (number of polyps and colony surface area) and the presence of oocytes, ova, and planulae was tested employing the Spearman rank correlation coefficient and Model I least squares regression analysis.

Results

Gamete and planula development

Histological preparations were used to distinguish the four stages of oogenesis, spermatogenesis, and planula development. The maximum diameters of mature Stage IV ova were ~800–1,000 μm. Stage IV spermaries, 150–200 μm in diameter, were packed with minute spermatids. Fully

developed planulae ready for release exhibited an oral pore, and short mesenterial filaments on 12 stubby mesenteries. In dissected preserved polyps, mature planulae were loosely associated with maternal mesenteries and floated free when exposed. Detailed descriptions of gametes and planula development are available in Appendix 2.

Reproductive condition

Reproductive activity occurred nearly in all samples (99.5%) from all five locations. Only two specimens from Taboga Island, one collected in December 1992 and one in January 1993 (2.9%, $n = 70$) did not contain gametes. All reproductive samples contained oocytes, ova and/or planulae of various stages, and most also contained Stage IV ova. Up to 15 ova per mesentery were observed in preserved but non-histologically processed specimens. A total of 424 colonies were analyzed with usually 3–5 (and up to 10) whole colonies collected per sampling to total 120 collections covering all months of the year at some locations. All reproductive samples were female with 12.9% of these also containing male gonads (hermaphroditic). Sex ratio (female:hermaphrodite) ranged from 3.3:1 (Caño Island) to 10.3:1 (Taboga Island) (Table 1). All Chi-square analyses were highly significantly biased toward females. Skewed sex ratios may be a result of male gametocytes forming and maturing over a brief period compared with the length of oogenesis. Also, male gametes are difficult to distinguish due to their light staining and lack of contrast with the deeply staining ova and other tissues. Spermaries are relatively small compared to the large yolky ova and are usually at the same stage of development. Spermaries are intermingled in small clusters adjacent to ova on female mesenteries. Spawned spermaries were not observed in histological sections. Sperm release was observed in monitored live colonies in Panamá and the Galápagos Islands (see "Lunar activity" below). Percent colonies with spermaries observed within sample sets for each location were Caño Island, 23.1% ($n = 26$); Uva Island, 13.7% ($n = 73$); Saboga Island, 12.3% ($n = 73$); Taboga Island, 8.6% ($n = 70$); Galápagos Islands, 12.7% ($n = 181$). Caño Island, the location with the least sampling effort, displayed the greatest percentage of hermaphroditic colonies. Hermaphroditic colonies in the Galápagos Islands, the study location with the greatest sampling effort, approximated the percentages observed at both Uva and Saboga Islands.

Spawned ovaries were present in some histological samples, but had likely released Stage I planulae since these were found in the polyp gastrovascular cavities. Spermaries may occur seasonally, but planula release (those with mesenterial filaments) appears to be monthly depending on the location. Planulae were found in the gastrovascular cavities of polyps in 85 (~20%) samples (Table 1).

Ovum maturation appears to occur continuously throughout the year. Available data for male gonad activity is relatively sparse; however, sperm maturation appeared to occur over several months in the Gulf of Panamá (May–November) and the Galápagos Islands (February–September).

The minimum colony size capable of producing ova and planulae is unexpectedly small. Two of four decalcified and dissected colonies with only two polyps revealed mature ova and planula larvae (Fig. 2). The colony and polyp diameters were 11 and 17 mm, and 8 and 9 mm, respectively. No sexual products were found in five individuals with single polyps, but the proportion of ova and planulae present in colonies ranging from 2 to 10 polyps were similar (ova, $r_s = 0.376$, $P > 0.20$; planulae, $r_s = 0.460$, $P > 0.10$, Spearman rank correlation test).

In support of the results from dissected preserved polyps, several live colonies with 6–10 polyps released planulae around the new lunar period. Moreover, small colonies demonstrated a significantly higher planula release rate polyp^{-1} than large colonies ($r_s = 0.422$, $0.05 > P > 0.02$). Five small colonies (18–28 mm diameter) released between 1.3 and 5.3 planulae polyp^{-1}(Fig. 3). Mean (±SE) planula release polyp^{-1} in colonies with ten or fewer polyps was 1.51 (±0.67) and 0.26 (±0.09) in colonies with >10 polyps. This trend was still significant with the elimination of the seven-polyp colony outlier ($r_s = 0.39$, $0.05 > P > 0.02$).

Table 1 *Tubastraea coccinea*

Location	Reproductive (%)	*n*	Female only	Hermaphrodite	No. with planulae	♀:H	χ^2	*P*
Caño Isl.	100	26	20	6	2	3.3:1	7.54	< 0.01
Uva Isl.	100	74	64	10	19	6.4:1	39.96	« 0.001
Saboga Isl.	100	73	64	9	15	7.1:1	41.44	« 0.001
Taboga Isl.	97.1	70	64	6	16	10.3:1	49.53	« 0.001
Galápagos Isl.	100	182	154	23	33	6.7:1	80.58	« 0.001

Percentage of colonies reproductive (with gametes and/or planulae), number of colonies sampled (*n*), number of female and hermaphroditic colonies, and number of colonies with planulae from Costa Rica (Caño Isl.), Panamá (Uva, Saboga and Taboga Isl.), and Galápagos Islands. Deviation of sex ratio from 1:1 was tested with Chi-square analysis (χ^2)

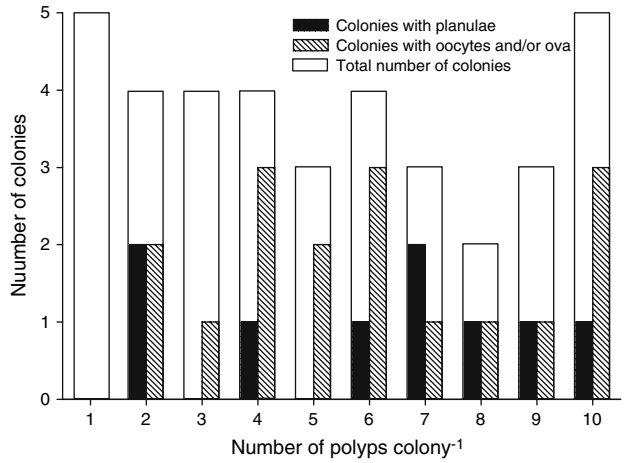

Fig. 2 *Tubastraea coccinea*. Presence of oocytes, ova, and planulae in dissected polyps with up to 10 polyps col^{-1} ($n = 37$). Corals collected during reproductive period at the Secas, Uva and Saboga reefs (2002–2005)

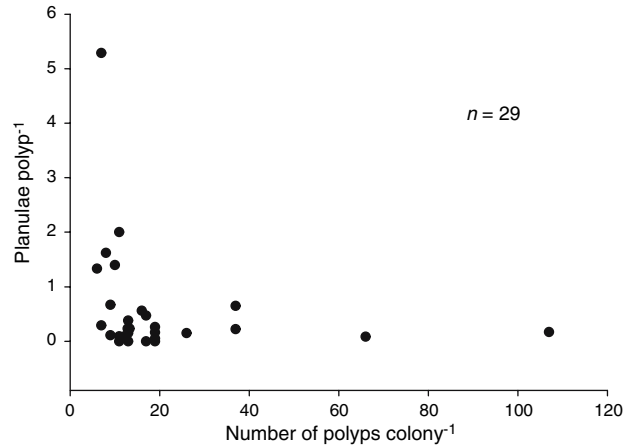

Fig. 3 *Tubastraea coccinea*. Numbers of planulae polyp^{-1} released in relation to colony size (number of polyps col^{-1}) during new moon period in the Gulf of Chiriquí, March 2002, 2003 and 2005

Several attributes relating to ovum and polyp size, and numbers present were quantified for later estimates of fecundity at the various study sites. Stage IV ovum diameters were measured from histologically prepared slides to better determine the dimensions of this particular developmental stage. Mean ovum diameters at the various study locations ranged from 459 to 526 µm from a total of 1,706 ova measured overall (Appendix 3). Mean ovum volumes, calculated from the ovum diameter data, ranged from 0.069 to 0.092 mm^3 at the five study sites. Statistically significant ($P < 0.001$) differences were evident with Taboga and Galápagos ovum diameters and volumes the greatest among sites.

Mesenteries were counted in dissected fixed/decalcified polyps ($n = 96$) from all locations. The number of mesenteries polyp^{-1} ranged from 10–40 depending on polyp size. Mean mesentery counts at the five collection sites ranged from 22 to 26 with an overall mean of 24.1 mesenteries polyp^{-1} (Appendix 3). These site differences were non-significant. Since all mesenterial cycles (1–3) supported gamete development, a mean of 24 mesenteries polyp^{-1} was used in fecundity calculations below.

Polyp volume size, also derived from dissected material, was calculated from the volume of a cylinder from length and width measurements of 105 polyps. This resulted in a mean of 1,591.2 mm^3 polyp^{-1} when data from all locations were pooled (range 502.4–4,991.0 mm^3). In dissected tissues, the numbers of mesenteries increased significantly with increasing polyp volume ($P \ll 0.001$, $r = 0.378$, $n = 41$ polyps, Pearson product-moment correlation). Stage IV ova mes^{-1}, however, did not differ significantly ($P = 0.139$, $r = 0.229$, $n = 42$ polyps). Although polyps may contain many developing oocytes and ova (10–15 on all mesenteries), only a small percentage was in Stage IV. In histological slides made from entire polyp lengths, mean numbers of Stage IV ova mes^{-1} ranged from 1.3 to 3.7 at the five locations (Appendix 3). Overall, the 42 polyps examined (258 mesentery counts) averaged 2.7 Stage IV ova mes^{-1}. While a significant ($P = 0.021$, ANOVA) difference among locations was evident, a site difference was not detected in a posteriori testing. Mean Stage IV ovum counts mes^{-1} from each of 42 polyps were multiplied by 24 to arrive at a mean number of ova polyp^{-1} for each location. Ova polyp^{-1} ranged from 31.2 (Caño) to 88.1 (Uva) with an overall mean of 60 ova polyp^{-1}.

Occurrence of planulae in colonies and the numbers of planulae colony^{-1}, determined from histological material, demonstrated high among-site differences (Table 2). Mean percent colonies with planulae ranged from 6.7% at Caño Island to 25.4% at Uva Island (Gulf of Chiriquí). The mean number of planulae colony^{-1} was lowest at Caño Island (1.0) and highest in the Galápagos Islands (15.2), but none of these differences was significant.

Seasonality

Spermaries were found throughout the collection period at Caño Island (January–August, no sampling was completed from September through December). Planulae (Stages I–III) were found in a single collection (25% of colonies) in August. The few collections from Caño Island revealed mature spermaries (Stage IV) only in May. No Stage IV planulae were found at this location. None of these occurrences was statistically significant (Table 3, see also Appendix 4). At Uva Island, male colonies were also collected from January to August even though the collection effort included the entire year (Fig. 4a). Planulae were present during a large part of the year (January–March, June, July, December). Mature

Table 2 *Tubastraea coccinea*

Comparison	Location				Significance
	Caño Isl.	Uva Isl.	G. Panamá	Galápagos Isl.	
Mean (range) % colonies with planulae	6.7 (0–40)	25.4 (0–40)	21.0 (0–33)	17.0 (0–100)	0.70 > *P*> 0.50
0.95 conf. lim.[a]	0–0	0–40	0–33	0–0	K–W
n collections	6	18	43	53	
Mean (range) no. planulae colony^{-1} [b]					
	1.0 (1–1)	5.9 (1–24)	5.7 (1–31)	15.2 (1–110)	0.20 > *P*> 0.10
0.95 conf. lim.	1	1–7	1–6	2–4	K–W
n collections	2	19	35	33	

[a] Based on colonies with planulae

[b] 0.95 confidence limits of median estimated from $K = 50/100\ (n + 1) - \sqrt{n}$, where K is the number of units from each end of the ranked distribution towards the median

Mean percent planulae present in colonies and number of planulae colony^{-1} at four sites. All data are from histological slides

Table 3 *Tubastraea coccinea*

Environmental setting Location	Test		Samples (*n* colonies)			Spermaries		Planulae	
	Period	Reproductive stages	Total	With spermaries	With planulae	χ^2	*P*	χ^2	*P*
Stable thermal regime									
Caño Isl., Costa Rica	Wet/dry	I–IV	26	6	2	0.219	NS	1.430	NS
		IV		1	0	0.709	NS	–[a]	–
	Lunar	I–IV				1.475	NS	8.390	<0.05
		IV				0.000	NS	–[a]	–
Uva Isl., Gulf of Chiriquí	Wet/dry	I–IV	73	9	19	5.985	NS	0.032	NS
		IV		3	2	10.700	<0.005	2.926	NS
	Lunar	I–IV				0.740	NS	1.203	NS
		IV				5.665	NS	1.860	NS
Seasonal upwelling									
Gulf of Panamá, Panamá	Wet/dry	I–IV	143	15	25	6.696	<0.01	15.384	<0.001
		IV		6	7[b]	6.000	NS	2.333	NS
	Lunar	I–IV				2.750	NS	4.067	NS
		IV				6.000	NS	12.000	<0.01
Variable thermal regime									
Galápagos Isl. Ecuador	Wet/dry	I–IV	183	28	33	6.760	<0.01	15.094	<0.001
		IV		24	8	10.680	<0.005	14.287	<0.001
	Lunar	I–IV				3.620	NS	3.011	NS
		IV				4.167	NS	3.033	NS

[a] No stage IV planulae observed

[b] Exact number difficult to discern because of possible parasitic infections

Chi-square (χ^2) analysis of seasonal and lunar patterns of spermatogenesis and planula development at four principal study sites: when $P \leq 0.05$, reproductive activity was non-random over period tested [*I–IV* presence of Stages I to IV inclusive; *IV* presence of Stage IV spermaries or planulae; *wet/dry* wet season, 15 April–14 December (8 months), and dry season 15 December–14 April (4 months), respectively (in Galápagos, wet and dry seasons occur at opposite times of year to those in Costa Rica and Panamá)]; *lunar* four equal periods within lunar cycle beginning with two days before new moon: 26–4, 5–11, 12–18, 19–25. Chi-square critical probability values: $\alpha_{0.1} = 2.71$, $\alpha_{0.05} = 3.84$, $\alpha_{.025} = 5.02$, $\alpha_{0.01} = 6.64$, $\alpha_{0.005} = 7.88$, $\alpha_{0.001} = 10.83$ (1 df, wet/dry period); and $\alpha_{0.1} = 6.25$, $\alpha_{0.05} = 7.82$, $\alpha_{0.025} = 9.35$, $\alpha_{0.01} = 11.35$, $\alpha_{0.005} = 12.84$, $\alpha_{0.001} = 16.27$ (3 *df*, lunar period)

spermaries were present in samples collected in June and July, and Stage IV planulae in colonies during January and July. The occurrence of Stage IV spermaries during the first part of the wet season was highly significant ($P < 0.005$, Table 3). Of the planulae examined in January, 75% were in Stage IV development. In July, 33% of

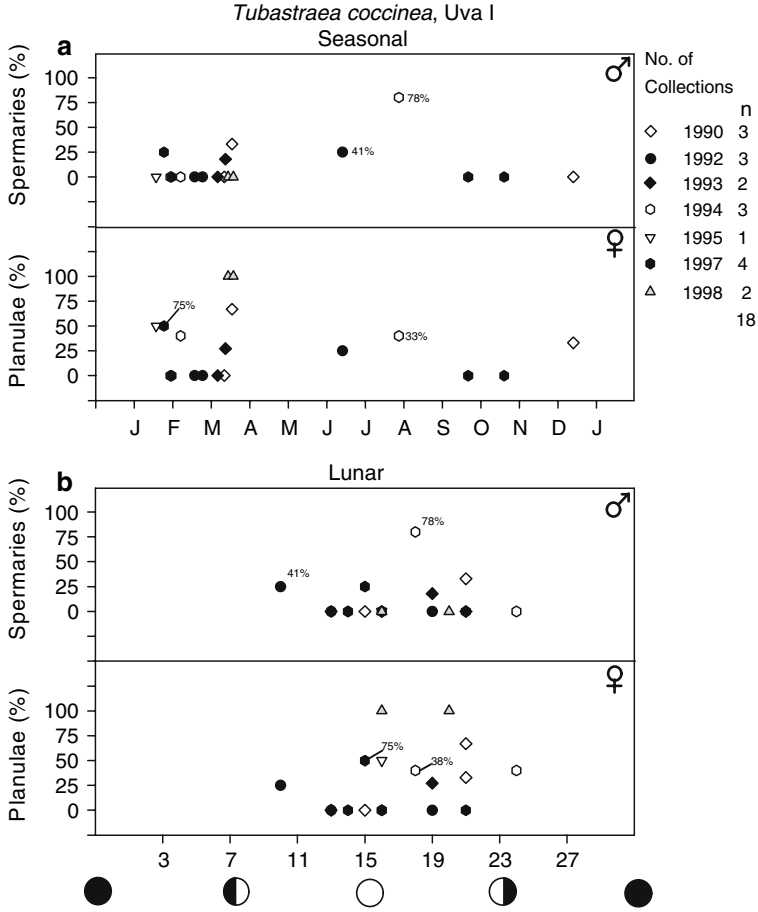

Fig. 4 *Tubastraea coccinea*. Reproductive activity at Uva Island, Gulf of Chiriquí, Panamá, as function of season (**a**) and lunar phase (**b**), based on 18 collections and 73 colonies examined (1990–1998). *Top halves* of both plots refer to percent colonies with spermaries, *bottom halves* to percent colonies with planulae. Percentage values noted beside collections indicate the proportions of spermaries or planulae in Stage IV development. *Abscissas* Julian and lunar days (full moon occurred near Lunar Day 15)

the planulae were fully developed. These temporal occurrences were nonsignificant.

In the upwelling Gulf of Panamá, male gonads showed a statistically significant ($P < 0.01$) occurrence during the nonupwelling season (Fig. 5a; Table 3). Two collection dates with spermaries present during the upwelling season were from Saboga Island, but spermaries at Taboga Island were not found until after the upwelling season (May). In the Gulf of Panamá, planulae (Stages I–IV) were highly significantly ($P < 0.001$) concentrated in the wet season. Mature spermaries and planulae (Stage IV) did not demonstrate a significant seasonal trend.

In the Galápagos Islands, with seasonally marked sea temperature differences, spermary and planula development (all stages) were statistically most common in the warm season and tapered off as the waters began to cool (Fig. 6a; Table 3). Seasonality of Stage IV development of both spermaries and planulae was also highly statistically significant. Stage IV spermaries were mainly present in samples collected from February to May. During this period the proportion of colonies with mature spermaries ranged from 11 to 100% in several collections (Fig. 6a).

Lunar activity

At Caño Island male colonies were found around new and full moon, and Stage IV spermaries were present in one colony, 2 days before full moon. Sampling effort, however, was too small to allow for rigorous statistical testing. The only significant ($P < 0.05$) lunar trend was the occurrence of planulae (Stages I–III) 5 days after new moon.

Only a relatively narrow window of sampling was accomplished over the lunar period at Uva Island. Hermaphroditic colonies were found throughout the collection period (lunar days 10–24). The occurrence of Stage IV spermaries 3 days after full moon was high in one collection (78%, 1994), but not statistically significant (Fig. 4b; Table 3). The presence of planulae in histologically processed tissues was common immediately following and up to 1 week after full moon (Fig. 4b). Stage IV planulae were found only in samples at full moon and shortly thereafter. However, planula release in confined colonies did not coincide with the histological evidence (see below).

In the Gulf of Panamá, hermaphroditic colonies were found throughout the lunar cycle (Fig. 5b). No significant trend was evident for presence of male colonies or Stage IV

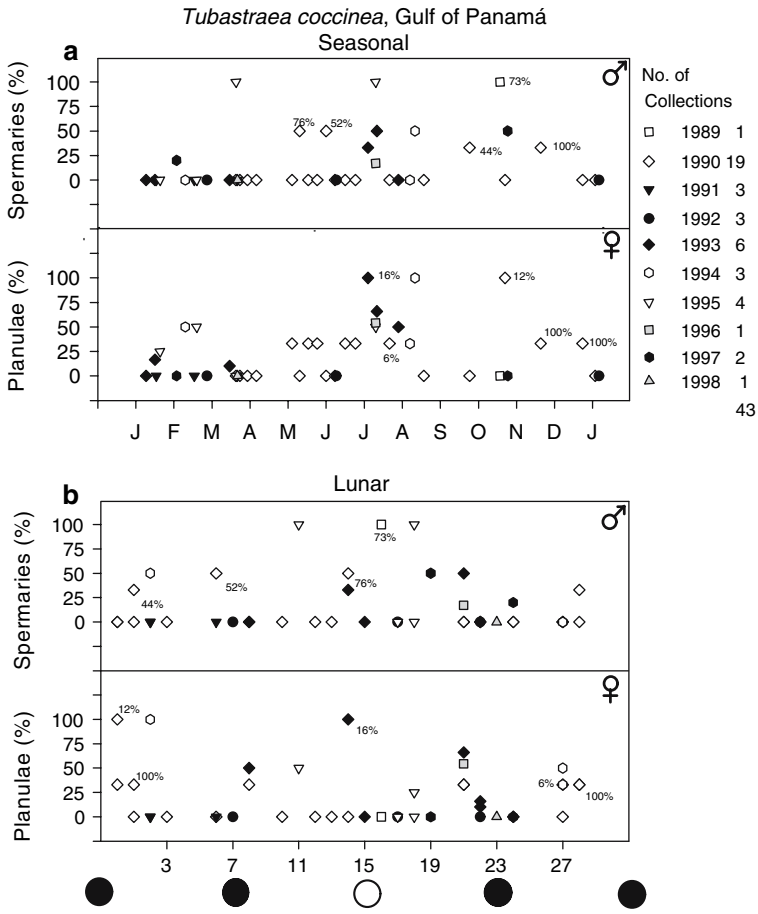

Fig. 5 *Tubastraea coccinea.* Reproductive activity in the Gulf of Panamá, Panamá as function of season (**a**) and lunar phase (**b**), based on combined analyses from 18 collections and 73 colonies examined (1989–1998) at Saboga Island, and from 25 collections and 70 colonies examined (1990–1994) at Taboga Island; further details as in legend to Fig. 4

spermaries. Planulae also were present throughout the lunar cycle. Stage IV planulae demonstrated a significant ($P < 0.01$) presence at new and full moon (Fig. 4b; Table 3).

Hermaphroditic colonies were found throughout the lunar cycle in the Galápagos Islands (Fig. 6b). No significant trends in spermary development were evident (Table 3). Planula presence also showed no significant temporal trend at this location; however, Stage IV planulae were present in some samples around new and full lunar phases.

Planulae were released a day or two before and after new moon. At Uva Island, however, Stage IV planulae were present in histological samples at full moon and 3 days later (Fig. 4b). A few planulae (<10 overall) also were released a day or two after full moon during two monitoring periods, but the greatest activity occurred around new moon (Fig. 7a). Overall, more than 100 planulae were released by 11 colonies, a few nights after new moon. Over the full moon period of March 2006, 7 of 32 colonies (21.9%) spawned sperm (Fig. 7b, see Appendix 5A).

Fecundity

The annual volumes of mature ova produced at the five study sites were marginally significantly different, ranging from 16.2 ± 0.09 mm^3 cm^{-2} at Caño Island to 82.8 ± 0.05 mm^3 cm^{-2} at Taboga Island (Table 4). Due to small sample sizes, it was not possible to determine which sites differed significantly in annual ovum production.

Fecundity estimates were also calculated from planula abundances and volumes based on ethanol-preserved dissected samples and from planulae released by live colonies observed over a 7-day period. The dissected and live colonies in Panamá (Gulf of Chiriquí) represent estimates made from 9 and 6 days before new moon, respectively. While planulae released from live colonies began 6 days before new moon, observations were continued for 7 days following the initial release. The dissected samples from the Galápagos Islands are from colonies collected 4 days before new moon. The histological results showed that *Tubastraea coccinea* was reproductively active during March and September in Panamá (Gulf of Chiriquí) and in May in the Galápagos Islands. Mean planulae polyp^{-1} in the Galápagos Islands (28.48 ± 4.95) was significantly higher than either of the two collections in Panamá (0.23 ± 0.03, 4.13 ± 0.49) (Table 5). Another inter-locality difference was polyp size, which was significantly greater in Galápagos than Panamá corals. As a consequence, colonies of equal size had fewer polyps in Galápagos compared with

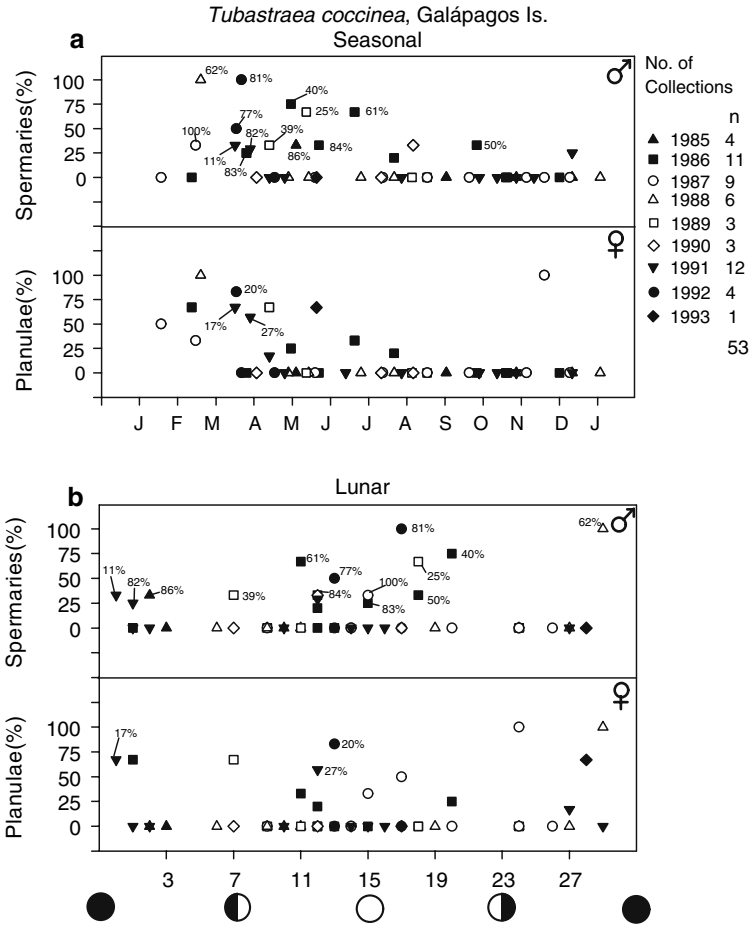

Fig. 6 *Tubastraea coccinea.* Reproductive activity in the Galápagos Islands as function of season (**a**) and lunar phase (**b**), based on 53 collections and 182 colonies examined (1985–1993); further details as in legend to Fig. 4

Panamá collections. Adjusting for seasonal reproductive activity, this is equivalent to 333.53 ± 11.58 planulae cm^{-2} $year^{-1}$ in the Galápagos and from 4.58 ± 0.09 to 80.79 ± 1.32 planulae cm^{-2} $year^{-1}$ in Panamá (Table 5).

Other informative measures of fecundity are based on planula volumes (Table 6). Individual planula volumes demonstrated similar mean values among sites, ranging from about 0.20 to 0.22 mm^3. Adjusting for the numbers of planulae $polyp^{-1}$ (Table 6), surface area of polyps (Appendix 3), and cycles of planula release $year^{-1}$ (Table 4), mean planula production in Panamá was estimated to be 0.95–17.77 mm^3 cm^{-2} $year^{-1}$ and in the Galápagos 68.07 ± 0.18 mm^3 cm^{-2} $year^{-1}$. Combining mature ovum and planula production, mean volume fecundity estimates for Panamá were 53.17 ± 0.08 and 69.99 ± 0.09 mm^3 cm^{-2} $year^{-1}$ and for Galápagos 109.85 ± 0.18 mm^3 cm^{-2} $year^{-1}$ (Table 6).

Planulae dissected from Panamá and Galápagos size series collections were regressed against colony polyp surface areas to determine the relationship between fecundity and colony size. No statistically significant trend was evident in the Panamá data set ($r^2 = 0.117$, $P = 0.635$, $n = 12$), however, the Galápagos collection demonstrated a significant linear relationship between planula production and increasing colony size ($r^2 = 0.676$, $P = 0.019$, $n = 23$).

Larval settlement and recruitment

While no planulae were observed exiting a polyp's mouth, some were seen soon after release adhering to the oral disc where they remained a few minutes before swimming free. Planula release occurred at all hours of the day, but was more frequent at night. Larvae tended to swim at or near the surface for minutes to a few hours before descending to the bottom. The time spent swimming over substrates before settlement varied from 1 to 3 days. Most planulae settled on the bare calcareous undersides of zooxanthellate corals, but some also settled on crustose coralline algae and a few even settled among filamentous algae. Within 1–3 days, post settlement corals were radially symmetrical, displayed a centrally located mouth with 6–12 surrounding tentacle anlagen.

Tubastraea coccinea are typically aggregated spatially with numerous small individuals tightly clustered around a few large adult colonies (Appendix 5B, see also Fig. 4 in Maté 2003). The numbers of individuals in five clusters at the Secas Island reef (10 March 2002) ranged from 63 to 432 with densities of 32–216 ind m^{-2}. The majority of the small colonies were within ~30 cm of the larger colonies with more distant recruits no more than about 1 m away. These clusters were often dominated by small

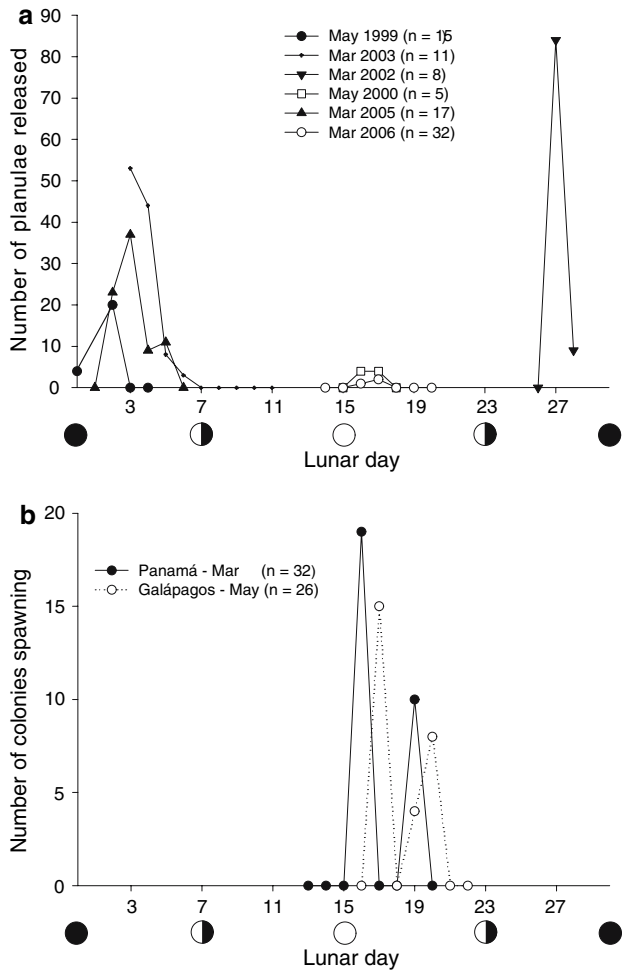

Fig. 7 *Tubastraea coccinea*. Numbers of planulae released in relation to lunar days (**a**). Data are from live colonies collected in the Gulf of Chiriquí over varying periods during March and May. Colonies were observed in tanks with running seawater, and counts were from several colonies held in the same tanks. Numbers of colonies spawning sperm in relation to lunar days (**b**). All colonies were maintained in intermittently running sea water held in separate containers. All observations in **b** performed in 2006

individuals (1.0–3.0 mm diameter) of one to a few polyps (Appendix 5C).

The early growth of recruits was determined for planulae released from colonies held in flow through tanks from a Secas Islands (Panamá) population in March 2002. The mean diameter of recruits that settled within a 24 h period was 1.26 mm (±0.15, $n = 12$). Twelve days after settlement, the mean diameter was 2.66 (±0.13, $n = 83$). Thus, the growth increment was 1.40 mm, which is equivalent to an increase in diameter of 3.5 mm month^{-1}.

Discussion

It is unclear whether all colonies of *Tubastraea coccinea* develop spermaries, if maleness is a short-lived stage or if only a relatively small proportion of the population (~9–23%) becomes hermaphroditic. Skewed sex ratios may be a function of male gametocytes forming and maturing over an abbreviated period as compared with the length of oogenesis. As well, male gametes are difficult to distinguish due to their light staining characteristics and lack of contrast with the deeply stained prominent ova and other tissues. Spermatozoa are relatively small compared to the large yolky ova and are usually in the same stage of development. Spermaries are intermingled in clusters adjacent to ova on female mesenteries. It appears that they may also form near the end of ova maturation, just prior to fertilization. Spawned spermaries were not observed in any histological sections even though mature sperms were present. The spawning of copious amounts of spermatozoa by several colonies monitored in Panamá and the Galápagos indicate that outcrossing is a likely possibility. Broadcast spawning in *T. coccinea* has been observed on the Great Barrier Reef as well (D. Ayre in Harrison and Wallace 1990). However, since Ayre and Resing (1986) provided genetic evidence for the production of planulae through asexual means, some degree of selfing may also occur in eastern Pacific populations.

As for the great majority of scleractinian corals in the Indo-Pacific region (Harrison and Wallace 1990; Richmond and Hunter 1990; Hayashibara et al. 1993; Penland et al. 2004; Guest et al. 2005), the reproductive mode of most known eastern tropical Pacific corals is also broadcast spawning (Glynn et al. 1991, 1994, 1996a, 2000). Similar to *Tubastraea coccinea*, only the small endemic zooxanthellate coral *Porites panamensis* broods and releases planula larvae (Glynn et al. 1994; Smith 1991). Harrison and Wallace (1990) noted that brooding species tend to breed and release planulae over extended periods, and Guest et al. (2005) extended this observation to conclude that brooding corals demonstrate more continuous breeding at lower compared with higher latitudinal locations. Year round reproductive activity was observed in both *T. coccinea* and *P. panamensis* at eastern Pacific sites (Glynn et al. 1994) in spite of marked seasonal variations in temperature, cloud cover and rainfall. However, in both the species planula release was greater in the warmer months where populations were present in upwelling environments or under seasonally cool conditions. Guest et al. (2005) also demonstrated a strong link between rising SST and spawning seasonality in corals in the equatorial (~1°N) waters of Singapore. Other workers at low latitude localities, where annual SST excursions are slight, have found a strong relationship between coral spawning and the rise toward and fall from annual solar insolation maxima (Pendland et al. 2004). This environmental variable is in need of study in the eastern Pacific.

Evidence presented here suggests that *Tubastraea coccinea* becomes sexually active at a very early age. Colonies

Table 4 *Tubastraea coccinea*

Attribute	Caño Isl.	Uva Isl.	Saboga Isl.	Taboga Isl.	Galápagos Isl.
Volume stage IV ova polyp^{-1} (mm^3)	2.225 ± 0.024	6.044 ± 0.131	3.694 ± 1.002	7.190 ± 0.190	4.246 ± 0.472
Period stage IV ova present (month)	7	12	12	12	12
Annual fecundity (no. stage IV ova polyp^{-1})	218.4	1,057.2 ± 37.1	547.2 ± 158.0	934.8 ± 49.9	579.6 ± 24.9
Annual fecundity (ova cm^{-2})	227.1 ± 1.3	761.0 ± 0.1	437.8 ± 0.3	897.4 ± 0.1	475.3 ± 0.1
Annual volume (mm^3 stage IV ova polyp^{-1})	15.58 ± 0.06	75.53 ± 0.45	44.33 ± 3.47	86.28 ± 0.66	50.95 ± 1.64
Annual volume (mm^3 ova cm^{-2})	16.2 ± 0.1	52.2 ± 0.03	35.5 ± 0.1	82.8 ± 0.1	41.8 ± 0.04

Fecundity estimates of annual ovum production. Mean (SE) Stage IV ovum volumes polyp^{-1}, ovum volumes polyp^{-1} year^{-1}, and ovum production polyp^{-1} surface area (cm^2) at five localities

Fecundity estimates of annual planula production in Panamá (Gulf of Chiriquí) and the Galápagos Islands, 2006. Mean (±SE) planula numbers polyp^{-1}, colony^{-1} and polyp^{-1} surface area (cm^2). Panamá and Galápagos samples from March and May represent estimates from preserved and dissected polyps collected 9 and 4 days before new moon respectively. The September sample from Panamá shows estimates from planulae released by live colonies over a 7-day period starting 6 days before new moon

Table 5 *Tubastraea coccinea*

Attribute	Panamá		Galápagos Isl.	Significance
	20 Mar 06	16 September 06	23 May 06	
Planulae polyp^{-1} ± SE (*n* col, *n* polyps)	0.23 ± 0.03 (37, 223) SD = 0.51	4.13 ± 0.49 (30, 290) SD = 8.32	28.48 ± 4.95 (36, 155) SD = 61.66	K–W test, $P < 0.01$; $P_m < P_s < G$; $P_s = G$
Planulae polyp^{-1} year^{-1} ± SE (*n* cycles year^{-1})	2.81 ± 0.12 (12)	49.52 ± 1.69 (12)	227.80 ± 14.01 (8)	Dunn's MCP
Planulae col^{-1} year^{-1} ± SE (*n* polyps col^{-1}, col diam cm)[a]	14.04 ± 0.26 (5, 3)	247.62 ± 3.78 (5, 3)	1139.00 ± 31.33 (5, 3)	
Polyp diam (mm)[b] (*n* col, *n* polyps)	8.84 ± 0.09 (35, 88) SD = 0.88	–[c]	9.32 ± 0.07 (36, 97) SD = 0.68	*t* test, $P < 0.001$
Planulae cm^{-2} year^{-1} (polyp area, cm^2)	4.58 ± 0.09 (0.61)	80.79 ± 1.32 (0.61)	333.53 ± 11.58 (0.68)	

[a] Number of polyps colony^{-1} and colony diameter for Panamá, $N = 0.798e^{0.581x}$ ($r^2 = 0.910$); Galápagos, $N = 0.687e^{0.894x}$ ($r^2 = 0.565$)

[b] Minimum polyp diameter with sexual products ≥ 8 mm

[c] Polyp diameters not measured in September; assumed to not differ significantly from March sample

Fecundity estimates of annual planula production in Panamá (Gulf of Chiriquí) and the Galápagos Islands, 2006. Mean (± SE) planula numbers polyp^{-1}, colony^{-1} and polyp^{-1} surface area (cm2). Panamá and Galápagos samples from March and May represent estimates from preserved and dissected polyps collected 9 and 4 days before new moon, respectively. The September sample from Panamá shows estimates from planulae released by live colonies over a 7-day period starting 6 days before new moon. P_m Panamá 20 Mar 06; P_s Panamá 16 Sep 06; *G* Galápagos Islands

with only two polyps, ranging from 1.6 to 2.5 cm in diameter, contained ova or planulae. We have attempted to follow the growth of juvenile cohorts in the field to determine the onset of reproductive activity, but without success. The frequent release of planulae, mostly around new moon and also to a lesser extent around full moon, causes the mixing of different age classes making it difficult to identify discrete cohorts. If the Panamá recruits approximate the maximum diameter extension rates of *T. coccinea* of 2.1 to 2.4 mm month^{-1} in Curaçao (Van Moorsel 1988), after 9 months colonies in Panamá would range from 1.9 to 2.2 cm in diameter. Actually, the mean diameter growth increment of Panamanian recruits was calculated at 3.5 mm month^{-1} over a 12-day period after settlement. Providing polyp sizes attain ≥8 mm in diameter, this would place the colonies in a potentially reproductive size range. If these estimates were verified, the minimum size and age at first reproduction would rank among the lowest reported. The smallest reproductively active brooding zooxanthellate species noted in Harrison and Wallace (1990) are *Acropora cuneata* and *Cyphastrea ocellina* with colony diameters ≥2 cm. The age noted for *C. ocellina* is ≤2 years. At least four zooxanthellate scleractinians are known to release planulae at 1 year of age (species in the genera *Pocillopora*, *Seriatopora* and *Favia*). These are considered to be opportunistic species, i.e. with high mortality rates and quick to invade open habitat space.

Due to the remote locations of our sampling sites, it was not possible to monitor planula release continuously through all seasons. However, with the exception of the

Table 6 *Tubastraea coccinea*

Reproductive variable	Panamá		Galápagos Isl.	Significance
	20 Mar 06	16 September 06		
Planula volume, mm^3 [a] (*n* col, *n* planulae)	0.21 ± 0.01 (12, 29)	0.22 ± 0.02 (30, 31)	0.20 ± 0.02 (22, 63)	$P = 0.7598$, ANOVA
Planulae vol $polyp^{-1}$, mm^3	0.05 ± 0.01	0.91 ± 0.04	5.81 ± 0.09	
Planulae vol $polyp^{-1}$ $year^{-1}$ (*n* cycles $year^{-1}$)	0.58 ± 0.02 (12)	10.90 ± 0.13 (12)	46.49 ± 0.25 (8)	
Planulae vol cm^{-2} $year^{-1}$	0.95 ± 0.07	17.77 ± 0.09	68.07 ± 0.18	
Vol (mm^3) cm^{-2} col^{-1} $year^{-1}$ (*n* polyps col^{-1}, col diam cm)[b]	4.75 ± 0.16 (5, 3)	88.87 ± 0.20 (5, 3)	340.37 ± 0.40 (5, 3)	
Total vol eggs + plan (mm^3 cm^{-2} $year^{-1}$)[c]	53.17 ± 0.08	69.99 ± 0.09	109.85 ± 0.18	$P_m < P_s < G$; $P < 0.05$

[a] All planulae measurements from specimens preserved in 70% ethanol

[b] See footnote c in Table 6

[c] Probably an underestimate because egg volumes calculated from histological material.

Fecundity estimates of mean (± SE) annual planula production and combined ova + planulae in Panamá (Gulf of Chiriquí) and the Galápagos Islands. P_m Panamá 20 Mar 06; P_s Panamá 16 Sep 06; *G* Galápagos Islands

Caño Island site in Costa Rica, year round sampling in Panamá and the Galápagos Islands over several seasons provided ample material for histological analyses, which added confidence to the fecundity estimates provided and the observed variation. The numbers and volumetric measures of planula release varied greatly in *Tubastraea coccinea* within and among the study sites in Panamá and the Galápagos Islands. In the Gulf of Chiriquí (Panamá), fecundity estimates based on wet season larval release were about 16 times greater than those observed in the dry season (~5 vs. 80 planulae cm^{-2} $year^{-1}$). Since no significant seasonal differences were noted in mature planula presence in histological samples, the extrapolated higher value may be a valid upper estimate of annual fecundity. The number of planulae released by Galápagos corals was more than four times the highest estimate of Panamanian corals (~330 planulae cm^{-2} $year^{-1}$). Since a significant seasonal decline in planula presence in the Galápagos was observed in the histological samples during the cool season, the annual estimate is probably inflated. The exceptional November 1987 cool season collection, with planulae present in all colonies, was sampled during a moderate El Niño event (Podestá and Glynn 1997) when some zooxanthellate corals demonstrate enhanced reproductive activity during periods of elevated temperature (Colley et al. 2006). The fecundity estimates based on planula volume demonstrated a similar trend.

Compared with the zooxanthellate brooding species listed in Harrison and Wallace (1990), *Tubastraea coccinea* tends toward the higher annual fecundity estimates both numerically and volumetrically. The higher values of planula release in the eastern Pacific (80–330 larvae cm^{-2} $year^{-1}$) ranged from 2 to 6 times higher than those reported for acroporid and agariciid species. Annual planula volumes produced in Panamá (1–18 mm^3 cm^{-2} $year^{-1}$) were within the range of values (7–21 mm^3 cm^{-2} $year^{-1}$) listed in Harrison and Wallace (1990). The fecundity of *T. coccinea* is comparable with other notable fecund brooding species, e.g. *Porites panamensis* reported by Glynn et al (1994) in Panamá and *Stylophora pistillata* noted by Loya (1976) in the Red Sea, and by Hall and Hughes (1996) on the Great Barrier Reef. The only species known to greatly exceed *T. coccinea* in planula production is *Pocillopora damicornis* in the Central Pacific (Hawaii), in which 10 cm diameter colonies release upwards of ~27,000 larvae per year (Jokiel 1985).

Although high, the planula fecundity values reported in our study may be underestimated. Planula production was calculated assuming monthly release around new moon. However, evidence from histological analyses and live colonies indicates that some planulae were also released at and following full moon. This was the case at upwelling and nonupwelling sites in Panamá and the Galápagos Islands. In Taiwan, Lin (2005) found that *Tubastraea coccinea* released planulae mostly around new moon, but large numbers also were released around full moon over a 4-month (February–May) seasonal period. A similar cyclic pattern was demonstrated by D. Holstein (personal communication) for *T. coccinea* in south Florida, with colonies releasing planulae approximately every 2 weeks in synchrony with new and full lunar phases. Smaller numbers of planulae were released daily in Taiwan, but planula release in Florida was restricted mostly to a few days following the new and full lunar phases.

Tubastraea coccinea is one of the most abundant and widely distributed azooxanthellate scleractinians in the tropical Indo-Pacific and Atlantic regions (Cairns 1994, 2000; Fenner 2001). In the eastern Pacific, *T. coccinea* occurs abundantly in the Gulf of California (Reyes Bonilla

et al. 1997), throughout Central America (Cortés and Jiménez 2003; Maté 2003; Reyes Bonilla and Barraza 2003), along the coasts of Colombia and Ecuador (Reyes Bonilla 2002; Glynn 2003), and at the Galápagos Islands (Glynn and Wellington 1983). Gerrodette (1981) suggested that the ~2,000 km range of the temperate dendrophylliid coral *Balanophyllia elegans*, with demersal larvae capable of only limited dispersal (<0.1 m year^{-1}), achieved its broad distribution through passive dispersal or rafting. A possible example would be the dispersal of an adult coral on a rock held in a drifting kelp holdfast. According to Cairns (2000) rafting, perhaps attached to a ship's bottom, may well have been how *T. coccinea* was introduced from the Indo-Pacific into the Caribbean (Puerto Rico and/or Curaçao) in the late 1930s. Rafting, particularly on oilrigs or ship's hulls, has also been suggested by Fenner and Banks (2004) and Ferreira et al. (2004) and Figueira de Paula et al. (2004) to explain the subsequent spread of *T. coccinea* throughout the western tropical Atlantic. Since *T. coccinea* first colonized artificial structures instead of coral reef substrates as it spread throughout the western Atlantic, Fenner and Banks (2004) concluded that such surfaces were the preferred habitat of this species. Creed and Figueira de Paula (2007) have also demonstrated experimentally that *T. coccinea* is capable of successfully settling on five different artificial substrate types. This nonspecific substrate selection behavior may contribute importantly toward its success in dispersal and rapid range extension (Baird and Morse 2004).

There is a large difference in the distribution and abundance of *Tubastraea coccinea* compared with the zooxanthellate coral *Porites panamensis.* Unlike *T. coccinea*, which is typically abundant and with a nearly continuous distribution throughout the eastern tropical Pacific (Reyes Bonilla et al. 1997*), P. panamensis* is only abundant at certain localities (e.g., Panamá, Guzman et al. 2004) and uncommon, rare or absent from 11 of 14 eastern and central Pacific sites listed in Glynn and Ault (2000). Even remote localities in the eastern Pacific, such as Clipperton Atoll (Glynn et al. 1996b; Carricart-Ganivet and Reyes-Bonilla 1999), support abundant populations of *T. coccinea*. Cairns (1994) noted that *T. coccinea* is a pantropical cosmopolite, widespread throughout all tropical waters including a temperate region in Japan (Cairns 2000). *Porites panamensis* is known only from the eastern Pacific region (Veron 2000).

Besides an extended seasonal reproductive period, early maturation, high fecundity, accelerated early growth, and a capacity for widespread dispersal, at least three additional attributes would appear to favor high abundances and persistence of adult *Tubastraea coccinea* populations. The first of these involves resistance to environmental stress. Robinson (1985) reported that *T. coccinea* was one of the few scleractinian corals that did not bleach or experience mortality during the severe 1982–1983 El Niño event in the Galápagos Islands. Secondly, invasive *T. coccinea* in Brazil has been shown to damage the native zooxanthellate coral *Mussismilia hispida* when growing in close proximity (Creed 2006). These two species overlap in habitat distribution and where they occur in close proximity (≤5 cm) *T. coccinea* causes necrosis to the near side of *M. hispida*. This effect is not reciprocal. Finally, Koh and Sweatman (2000) have demonstrated that *Tubastraea faulkneri*, a close relative of *T. coccinea*, produces chemical compounds that are toxic to larvae of at least 11 zooxanthellate scleractinian species. If similar allelochemical effects can be demonstrated in *T. coccinea*, this would add yet another effective means in dealing with potential competing species.

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