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Reef coral reproduction in the equatorial eastern Pacific: Costa Rica, Panamá, and the Galápagos Islands (Ecuador). VII. Siderastreidae, *Psammocora stellata* and *Psammocora profundacella*

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Abstract Two zooxanthellate, scleractinian species present in the equatorial eastern Pacific, *Psammocora stellata* and *Psammocora profundacella*, were examined in terms of their reproductive biology and ecology at four study sites, non-upwelling (Caño Island, Costa Rica, and Uva Island, Panamá), upwelling (Gulf of Panamá, Panamá), and seasonally varying thermal environments (Galápagos Islands). Both species were gonochoric broadcast spawners lacking zooxanthellae in mature ova. Mature gametes and spawned gonads are present around full moon; however, no spawning was observed naturally or in outdoor aquaria. Mature gametes occurred in *P. stellata* at Caño Island for nearly 6 months, and year round at Uva Island, both non-upwelling sites. Reproductively active colonies occurred mostly in the warmer months in the Gulf of Panamá and Galápagos Islands. In the Galápagos Islands, where collecting effort was greatest for *P. profundacella*, mature gametes were also most prevalent during the warm season. Annual fecundity was high in both species, 1.3–1.8 $\times$ 10^4 ova cm^{-2} $year^{-1}$ in *P. stellata* and 1.2–2.0 $\times$ 10^4 ova cm^{-2} $year^{-1}$ in *P. profundacella*. Compared to other eastern Pacific corals, *P. stellata* was relatively resistant to ENSO-related bleaching and mortality, especially populations inhabiting deep (12–20 m) coral communities. Rapid recovery and persistence of *Psammocora* spp. can be attributed to several factors: (a) relative resistance to bleaching, (b) deep refuge populations, (c) broadcast spawning, (d) protracted seasonal reproduction, (e) high fecundity, and (f) asexual propagation.

Introduction

Knowledge of the sexual reproductive biology of eastern Pacific scleractinian corals has increased significantly since

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the 1980s. This is especially true for the equatorial eastern Pacific (Colley et al. 2000; Glynn et al. 1991, 1994, 1996, 2000, 2008, 2011) and more recently for the Mexican coral fauna (Vizcaíno-Ochoa 2003; Mora-Pérez 2005; Rodríguez-Troncoso 2006; Chávez-Romo and Reyes-Bonilla 2007; López-Pérez et al. 2007; Carpizo-Ituarte et al. 2011; Rodríguez-Troncoso et al. 2011). As in the equatorial eastern Pacific, patterns of coral sexual activity are now known for several species inhabiting upwelling and non-upwelling environments from northern- to southern-most Mexican Pacific sites.

The asexual regeneration of corals surviving disturbance events has been observed in several eastern Pacific areas and has been well documented for branching and massive species that survive ENSO disturbances (e.g., Guzmán and Cortés 2001; Vargas-Ángel et al. 2001; Glynn and Fong 2006; Glynn et al. 2009, 2011). Guzmán and López (1991) noted that pufferfish corallivores likely contribute to the propagation of *Psammocora* spp. while feeding on these colonies. The pufferfish *Arothron meleagris* is a known predator of *P. stellata* in the Galápagos Islands (Feingold 1996), and may likewise promote asexual reproduction. In contrast to other coral reef biogeographic regions, the great majority of eastern Pacific corals are broadcast, asynchronous (no multispecies spawning) spawners, and reproductively active year round in non-upwelling environments. Only two brooding corals inhabit equatorial eastern Pacific coral reefs, *Tubastraea coccinea*, an azooxanthellate cryptic species (Glynn et al. 2008), and *Porites panamensis*, a zooxanthellate small, encrusting species (Smith 1991; Glynn et al. 1994).

This study investigates the reproductive biology of two siderastreid zooxanthellate species that are widespread and often locally abundant on and adjacent to eastern Pacific coral reefs, *Psammocora stellata* and *Psammocora profundacella* (Glynn and Ault 2000; Reyes-Bonilla 2002). These species are generally not important in terms of framework construction, but *P. stellata* often forms unconsolidated mounds in both shallow and deep reef zones that provide shelter for diverse coral reef-associated species (Cortés 1990; Feingold 1996; Bezy et al. 2006). With the goal of better understanding post-disturbance resilience and recovery, the following aspects of the biology and ecology of the two siderastreid species were investigated: (a) sexual systems and mode of reproduction, (b) reproductive activity under contrasting oceanographic regimes, (c) seasonal and lunar spawning cycles, (d) fecundity, and (e) recovery of ENSO-impacted populations. With this publication, studies of the reproductive biology/ecology of 13 major scleractinian reef corals present on equatorial eastern Pacific reefs will have been completed (e.g., Colley et al. 2000; Glynn et al. 2011).

Materials and methods

Species and collections

Morphological and molecular evidence demonstrate clear and consistent differences between *Psammocora stellata* and *Psammocora profundacella* (Benzoni et al. 2007). *Psammocora stellata* displays a branching colony habit with relatively large calice diameters (mean ≈ 2.0 mm), wide enclosed petaloid septa (mean ≈ 0.25 mm), and relatively closely spaced calices without encircling ridges (Stefani et al. 2008). *Psammocora profundacella* typically grows as encrusting, submassive to massive colonies, with relatively small calice diameters (mean ≈ 1.5 mm), narrow enclosed petal septa (mean ≈ 0.15 mm), and relatively well separated calices surrounded by ridges (Benzoni et al. 2010). *Psammocora superficialis*, originally reported from various eastern Pacific localities, has been synonymized with *P. profundacella* (see Benzoni et al. 2010) and samples that we collected as *P. superficialis* are here assigned to *P. profundacella*. All collected colonies of *P. stellata* were free living, usually present on mixed sandy and rubble substrates; *P. profundacella* colonies were generally firmly cemented to stable substrates (see Electronic Supplementary Material, Appendices 1, 2).

Both species were collected over relatively large areas (50–100-m search paths along isobath), with colonies usually separated by 5–10 m or more, in order to avoid clonemates. Sampling of *Psammocora stellata* was performed by cutting or breaking sections of colonies. Samples usually included 3–5 branchlets, and sampled colonies 10–20 branches. Approximately 2-cm^2 sections were chiseled or pried from *Psammocora profundacella* colonies. Sampling was performed on 3–5 different colonies during each collection, but this was sometimes not possible for *P. profundacella* due to its relative scarcity. Repeated sampling of known colonies was not performed with one exception. A large (≈0.25 m^2) male colony of *P. stellata* at Taboga Island, Gulf of Panamá, was re-sampled in every calendar month during 1990–1991. Generally, the same populations were re-sampled on multiple occasions without any discernible effects on species' abundances.

The general locations of the nine principal study areas in Costa Rica, Panamá, and Ecuador (Galápagos Islands) span only about 10° latitude, but are subject to very different environmental conditions (Fig. 1). In Costa Rica, samples were collected at two fringing reefs at the northeast end of Caño Island, site 1 (Guzmán and Cortés 1989). Sampling in Panamá was performed in two areas: the Gulf of Panamá (seasonal upwelling) and the Gulf of Chiriquí (non-upwelling). Sampling in Chiriquí was performed on the Uva Island reef (site 2) or <1 km north on a rocky promontory. Additional samples were collected at Taboga Island

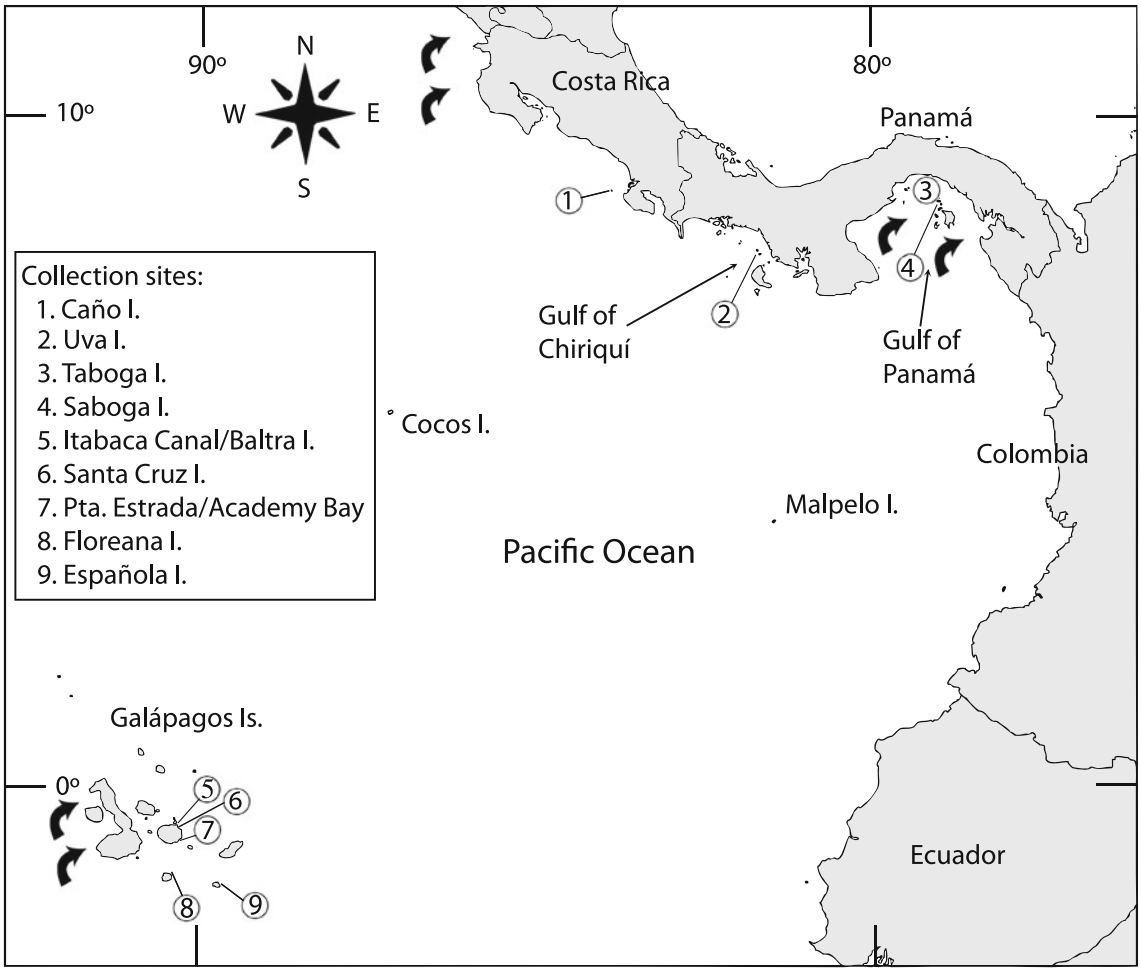

Fig. 1 Collection sites in Costa Rica, Panamá (Gulf of Chiriquí and Gulf of Panamá), and the Galápagos Islands. Galápagos Islands sites include Itabaca Canal and Baltra Island (site *5*), Robinson Cove (site *6*) and Punta Estrada/Academy Bay (site *7*) on Santa Cruz Island, north end of Floreana near Punta Cormorant (site *8*), and eastern end of Española Island, Gardner Bay (site *9*). All Galápagos study sites are thermally similar, located within the SE bioregion (Wellington et al. 2001; Edgar et al. 2002). *Solid recurved arrows* denote upwelling centers

(site 3) and Saboga Island (site 4) in the Gulf of Panamá. The Galápagos Islands sites included Itabaca Canal and Baltra Island (site 5), Robinson Cove (site 6) and Punta Estrada/Academy Bay (site 7) on Santa Cruz Island, the north end of Floreana Island near Punta Cormorant (site 8), and the eastern end of Española Island (site 9). These five central and southern island sites are located within Harris's (1969) relatively mild temperature zones 1 and 2, which demonstrate very similar seasonal patterns (Wellington et al. 2001). The collecting effort for both *Psammocora* species at all sites and years is noted in Appendix 3.

Histology

After collection, samples were transported underwater in wide-mouth bottles or netted bags during dives lasting less than 2 h. Within 1 h after collection, samples were fixed in seawater/Zenker's solution with 5 % formaldehyde for 18–24 h. Decalcification and histological tissue preparation were performed as previously described in Glynn et al. (1994, 1996, 2000). Tissues were embedded in Paraplast Plus and oriented so that the branches lay horizontally. The paraffin blocks were then sectioned into approximately 7-µm-thick slices. One slide of serial sections was prepared from each of 3 different levels of the mid-polyp region, approximately 70, 200, and 500 µm below the mouth. These tissues were then mounted on slides and stained with a slightly modified Heidenhain's aniline-blue method (Luna 1968) using Azocarmine G. One section per slide was outlined with a fine marker pen and examined under 100–400× magnification with a light microscope.

Spawning

Attempts to observe spawning in the field were performed most consistently for *Psammocora stellata* at Uva Island in Panamá from 1990 to 2003 by monitoring colonies in (1) natural reef settings, (2) buckets, aquaria, and water tables aboard ship at anchor, and (3) sealed polyethylene bags tethered to reef substrates. Procedures 1 and 2 were carried out mostly in the dry season (February, March) during lunar days 15–18 with observations concentrated between sunset and midnight. Sample size usually ranged from 10 to 15 colonies, and occasionally to 5–10 colonies. Aquaria and water tables were supplied with running sea water and colonies in 20-l buckets were freshened with approximately hourly seawater changes. Suspected spawned gametes were checked microscopically; ova appearance and colors were noted and diameters measured. Procedure 2 was also performed on several occasions in the Galápagos Islands over the course of this study.

Systematic monitoring of *Psammocora stellata* was also performed on colonies collected at Saboga Island, Gulf of Panamá, and then transported to flow-through sea water tables at Naos Island (about 60 km distant). Twenty-one colonies approximately 20 × 50 mm (height by length) were collected 3–4 days before lunar day 15 in July, September, and October 2011 and monitored continuously every 15 min from sunset to sunrise through lunar day 19. On August 4, new colonies were collected and monitored with those remaining from the July collection. Each colony under observation was positioned in a 10-cm-diameter cylinder lined with 64-μm mesh nylon netting topped with an inverted funnel and test tube egg collector.

Coral abundances

Psammocora stellata abundances are reported for five sites sampled in Costa Rica, Panamá, and the Galápagos Islands. Sampling methodologies for the Costa Rican sites are noted in Guzmán and Cortés (2001, 2007). Colony abundances were sampled annually or every 2 years in a 288-m^2 plot at Uva Island. Colony counts were made in randomly placed 15–25 1-m^2 quadrats. Two Galápagos sites were sampled repeatedly: Devil's Crown (Onslow Island), north side of Floreana Island since 1983, and Xarifa Island, east end of Española Island, since 2004. At Devil's Crown, the area covered by *P. stellata*-dominated patches was determined by field measurements from 1976 to the early 2000s (Glynn and Wellington 1983; Glynn 1994) and with high precision area measurements with CPCe (Kohler and Gill 2006) in 2011. Colony densities were determined using randomly placed 0.5 × 0.5-m quadrats in 2004 ($n = 60$) and 2011 ($n = 75$). Since 2004, at Xarifa Island, *P. stellata* abundance was determined from percent live cover and numbers of colonies from quadrat sampling in a shallow (0.5–3.0 m) 34-m^2 plot dominated by this species. This population has been present at Xarifa since first observed in the 1980s (T. DeRoy, personal communication) and has persisted through two very strong ENSO events (1982–1983 and 1997–1998).

Statistical analyses

Chi-square analyses were performed on the occurrence of spawned gonads in relation to lunar phases in histological samples, and sex ratios at all study sites. The seasonal and lunar timing of gametogenesis was tested employing chi-square analyses and the Fisher exact probability test, the latter when sample sizes were small.

Due to the limited sample sizes for calculating fecundity metrics in some collections, bootstrapping methods (Davidson and Hinkley 1997; Efron and Tibshirani 1998; Manly 2007) were used to assign unbiased measures of accuracy (e.g., standard error of the mean) to statistical estimates of coral fecundity. Bootstrap samples $y^* = y_1^*, \ldots, y_n^*$ were obtained by randomly sampling n times, with replacement, from the original data points y to produce a bootstrap sample that has the same sample size as the original sample (Appendix 4). Confidence intervals of the mean were computed using the central limit theorem where the estimate followed a normal density function. Standard graphical and statistical diagnostics, such as quantile–quantile and residual plots, and Shapiro–Wilk and Kolmogorov–Smirnov tests, were used to assess normality of the particular computed sample distributions and whether two or more sample distributions differed (Zar 1999; Crawley 2005; Kutner et al. 2005; Alder 2010). Sample distributions that failed to meet the assumption of normality were transformed to normality using the Box-Cox ladder of powers procedure (Kutner et al. 2005; Appendices 5–8). Parametric Student's t, nonparametric Kruskal–Wallis, and Wilcoxon rank sum tests were used to evaluate the equality of sample means. All statistical procedures and tests were implemented in the *R Project for Statistical Computing* (http://www.r-project.org/, Crawley 2005; Qian 2010; Alder 2010). Other details of the analysis are outlined in the fecundity 'Results' section below.

Results

Gonad development and gametocyte classification

Detailed descriptions of gamete development in female and male colonies are available in Appendices 9 and 10. No discernible interspecific differences were found in gonad development or gamete maturation in the two *Psammocora*

species. Female gamete diameters ranged from ≈10–25 μm (Stage I oocytes) to ≈90–130 μm (Stage IV ova) in histological preparations. Zooxanthellae were not observed in any mature ova. Spermary diameters ranged from ≈5–25 μm (Stage I) to ≈60–120 μm (Stage IV). Cellular organization appeared disrupted and empty in spent gonads. Several spent spermaries were observed in colonies of *Psammocora stellata* collected in Panamá (Gulfs of Chiriquí and Panamá) and the Galápagos Islands (Appendix 11).

Reproductive condition

Relatively high percentages of *Psammocora* spp. contained gonads, spanning most seasons and lunar phases. Over half of sampled colonies at non-upwelling Uva Island were reproductively active—57.8 % of *Psammocora stellata* and 64.4 % of *Psammocora. profundacella* (Table 1). The population of *P. stellata* at seasonal upwelling Saboga Island demonstrated the lowest proportion of reproductive colonies (20.4 %), but *P. profundacella* at non-upwelling Caño Island also exhibited relatively few reproductive colonies (25.0 %). All colonies but one (*P. stellata*) of both species were gonochoric. Planula larvae were never observed in histological preparations, only gametes in all stages of development and occasionally spent gonads. Nearly equal numbers of *P. stellata* male and female colonies were sampled at Caño Island (51.5 % male and 48.5 % female), and the single large colony repeatedly sampled at Taboga Island contained only spermaries. Sex ratios of *P. stellata* at Uva and Saboga Islands were significantly skewed with predominantly female colonies (85.4 and 84.2 %, respectively), and male colonies predominated in Galápagos samples (71.4 %). Female colonies significantly dominated *P. profundacella* samples at Uva Island (73.7 %). A preponderance (59.4 %) of *P. profundacella* female colonies was sampled in the Galápagos Islands, but there was no significant deviation from a 1:1 sex ratio. Too few reproductively active colonies of *P. profundacella* from Caño Island were available for reliable statistical testing.

Seasonal and lunar activity

Psammocora stellata demonstrated significant seasonal differences in the presence of mature gonads at all study sites (Figs. 2a, b, 3, 4, 5a, b; Table 2). At Caño Island, all colonies with mature ova (Stage IV) were concentrated in the wet season, with male colonies bearing mature spermaries mostly during the wet season, but also in the dry season. This pattern was reversed at Uva Island where both male and female colonies contained ripe gonads from January to March of the dry season. In the Gulf of Panamá, nearly all mature gonads occurred in the wet season following seasonal upwelling. Stage IV spermaries were present in only a single colony in February 1992. In the Galápagos Islands, mature gonads were most prevalent in male and female colonies in the wet/warm season. A few male and female colonies contained mature gonads in November 1987, during a mild El Niño year (Podestá and Glynn 2001).

The presence of mature gametes in *Psammocora stellata* was marginally significantly ($p < 0.05$) related to full moon, within 5–6 days at Caño and Uva Islands (Figs. 2c, d, 3c, d; Table 2). Gulf of Panamá (combined Saboga and Taboga sites) and Galápagos locations did not show a significant correspondence with any particular lunar phase (Figs. 4c, d, 5c, d; Table 2).

Psammocora profundacella demonstrated a significant increase in reproductive activity at Caño Island during the dry season, from mid-December to the end of February (Fig. 6a, b; Table 3). No lunar pattern was detected in Costa Rica (Fig. 6c, d; Table 3). The limited collections (4 mo) from Uva Island indicated reproductive activity in the dry and wet seasons, but without statistical significance (Fig. 7a–d, Table 3). The prevalence of Stage IV gametes during lunar days 14–20 suggests a spawning period near full moon (Fig. 7d; Table 3), but not at a statistically significant level. In the Galápagos Islands, *P. profundacella* contained a significantly high proportion of gametes (Stages I–IV) in the wet/warm season (Fig. 8a, b; Table 3). Mature gametes were detected at nearly all lunar phases in the Galápagos Islands (Fig. 8c, d).

Limited spawning was observed under artificial conditions at Uva Island, Panamá, and at Devil's Crown (Onslow Island), Galápagos Islands. Two of 10 colonies of *Psammocora stellata* confined to sealed transparent bags overnight at 4 m depth on the Uva reef spawned numerous large (120–150 μm diameter) ova during lunar days 21 and 22, February 2–3, 1994. These eggs were either pearly white or muddy green with a corona of microvilli in the latter. Two colonies of *P. stellata* spawned at Devil's Crown on April 9, 1992 at 16:03 h (6 days after new moon). These were collected at 15 m depth and held in aerated buckets following staining with Alizarin Red S vital stain. Microscopic examination of the spawn was not possible, but it appeared to be sperm.

Empty gonads, presumably recently spawned, were observed in histological samples from several colonies of *Psammocora stellata* over a wide range of lunar phases at all major study sites (Appendix 11). Nearly equal numbers of males and females demonstrated this condition. Statistical testing failed to reveal a clustering of spent gonads at any of four lunar phase periods (Chi-square test, $p > 0.90$). Spawned gonads were found in just a single female colony of *Psammocora profundacella* during new moon at Caño Island.

Table 1 *Psammocora stellata, Psammocora profundacella*

Location	*n*	% with gonads	No. of colonies with ooc/sperm		Sex ratio	
			Male	Female	♂:♀	χ^2 (*p*)
Psammocora stellata						
Caño	78	42.3	17	16	1:0.94	0.8026
Uva Island	154	57.8	13	76	1:5.85	<0.0001
Saboga	93	20.4	3	16	1:5.33	0.0028
Taboga	95	37.9	36	0	1:0	<0.0001
Galápagos Islands	93	45.2	30	12	1:0.4	0.0055
Psammocora profundacella						
Caño	28	25.0	5	2	1:0.4	0.257
Uva Island	59	64.4	10	28	1:2.8	0.0035
Galápagos Islands	88	36.4	13	19	1:1.46	0.289

Percent colonies with gonads, sex ratios, and Chi-square analyses. Number of colonies sampled (*n*), percentage of colonies with gonads, and number of colonies with oocytes or spermaries (ooc/sperm) from five (*P. stellata*) and three (*P. profundacella*) sampling localities. Deviation of sex ratio from 1:1 (♂:♀) was tested with χ^2 analyses

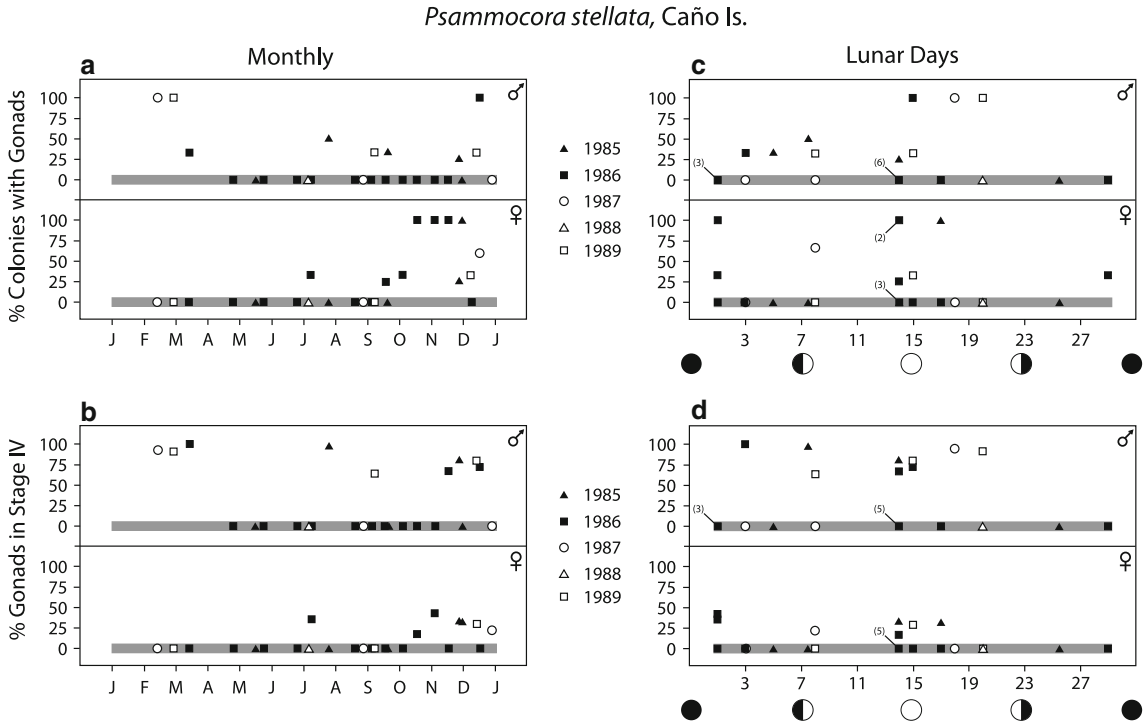

Fig. 2 *Psammocora stellata.* Reproductive activity at Caño Island, Costa Rica, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 25 collections and 78 colonies examined (1985–1989). All male (*top panels* in each set) and female (*bottom panels*) colonies that contained gonads at any stage of development were included in **a** and **c**; only colonies with mature (Stage IV) gonads were included in **b** and **d** (Embedded numbers in *parentheses* denote number of overlapping data points; 5 and 6 denote multiple collections within a given year); **c**, **d** *abscissas* lunar days, full moon occurred near Lunar Day 15. *Gray bar* denotes zero values

Fecundity

Empirical sample data from four locations (1) Caño Island, Costa Rica; (2) Uva Island, Panamá; (3) Gulf of Panamá, Panamá; (4) Galápagos Islands, Ecuador, were analyzed for six variables: (1) ovum diameter; (2) ovum volume; (3) number of mesenteries per polyp; (4) number of ova per cross-section of mesentery; (5) number of ova per longitudinal section of mesentery; and (6) number of polyps per cm^2 colony surface area. Histological distinction between polyps was often difficult because mesenteries appeared to be shared among several polyps. Gastrodermal canals extended across corallites whose walls were absent or weakly defined (Wells 1956).

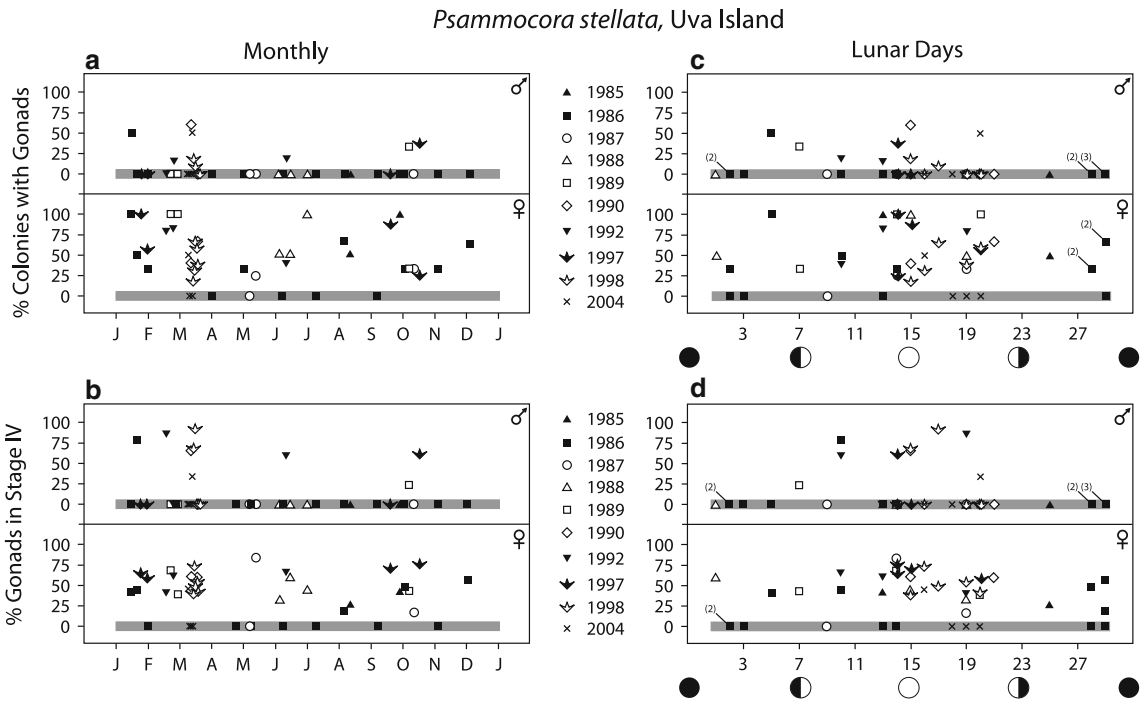

Fig. 3 *Psammocora stellata.* Reproductive activity at Uva Island, Gulf of Chiriquí, Panamá, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 41 collections and 154 colonies examined (1985–2004). Further details as in legend to Fig. 2

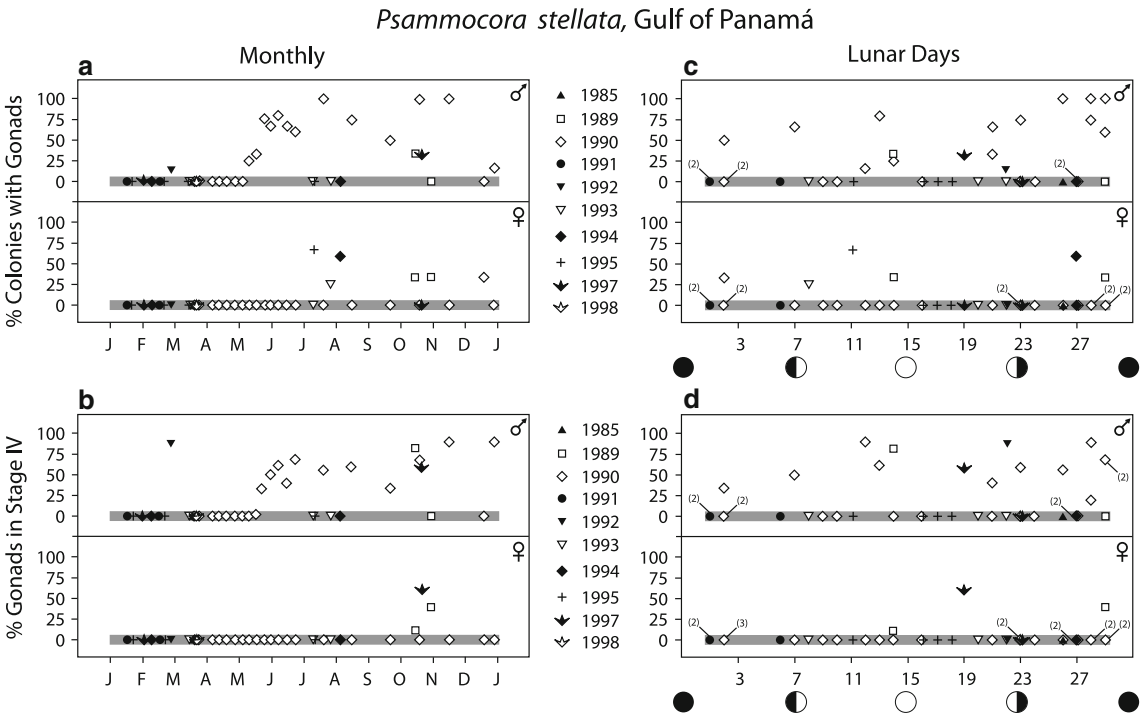

Fig. 4 *Psammocora stellata.* Reproductive activity in Gulf of Panamá (Saboga and Taboga Islands), Panamá, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 40 collections and 188 colonies examined (1985–1998). Further details as in legend to Fig. 2

Therefore, in some gravid samples with low *n*, it was not possible to match ova numbers in mesenteries with their corresponding polyps.

A mean ovum diameter of 98.8 μm in *Psammocora stellata* at Caño Island was significantly greater (Kruskal–Wallis rank sum test, $p < 0.001$) than in Panamá

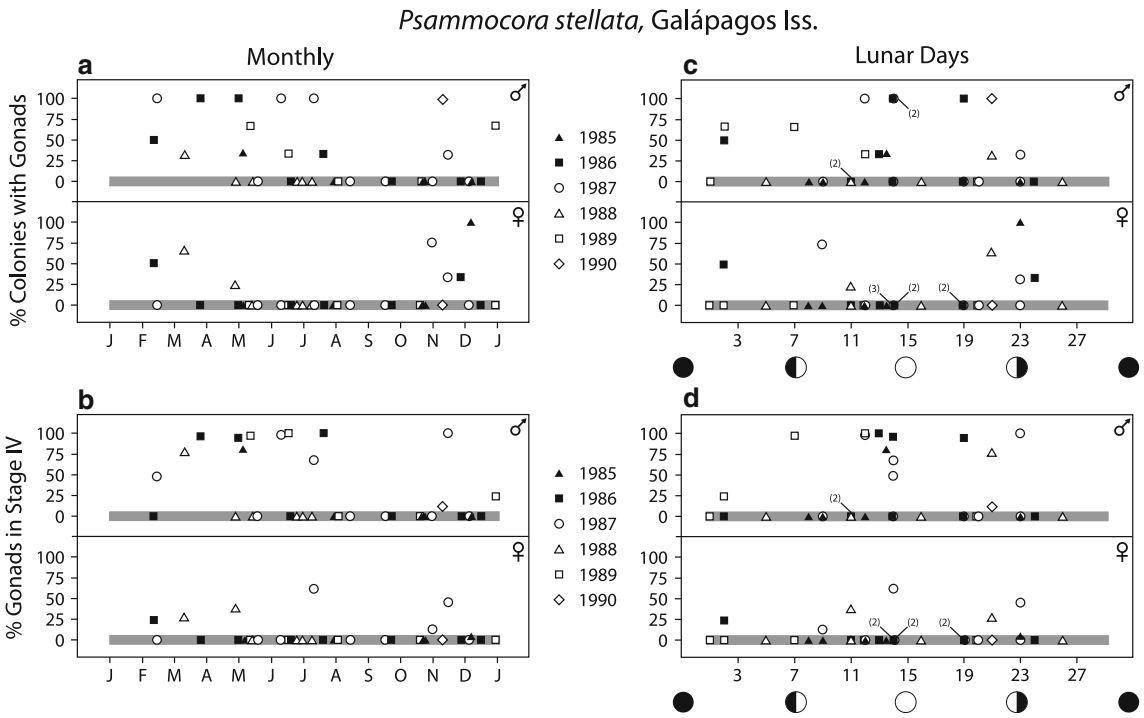

Fig. 5 *Psammocora stellata.* Reproductive activity in Galápagos Islands, Ecuador, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 34 collections and 93 colonies examined (1985–1990). Further details as in legend to Fig. 2

(Uva Island) or the Galápagos Islands (Appendix 12). At collection sites in Panamá (Uva Island and Gulf of Panamá) and the Galápagos Islands, mean ovum diameters ranged from 92.5 to 94.7 μm and there was no statistically significant difference between them. Mature ova diameters in *Psammocora profundacella* at 3 sites (Caño Island, Uva Island, and Galápagos Islands) ranged from 90.5 to 94.7 μm and were not statistically different (Kruskal–Wallis test, $p = 0.234$; Appendix 13). Mean gamete-bearing mesenteries in both species ranged between about 9 and 11. In the Gulf of Panamá, *P. stellata* polyps contained about one additional fecund mesentery than polyps at Uva Island. There was no statistically significant difference in numbers of fecund mesenteries in *P. profundacella* among localities.

Bootstrapped probability distributions were computed for various sample sizes to produce unbiased estimates for the means and standard errors (Appendices 12, 13). Two additional joint probability estimates of reproductive output were subsequently computed by combining certain individual variable estimates consisting of 10,000 bootstrapped trials each to produce unbiased estimates of overall multiplicative mean and standard error. These were number of stage IV ova per polyp (attribute #7, Appendices 12, 13):

$$\#3 \times \#4 \times \#5 = \frac{mes^2}{polyp} \times \left(\frac{ova}{cs} \times \frac{ova}{ls}\right) = \frac{mes^2}{polyp} \times \frac{ova}{mes^2} = \frac{ova}{polyp} = \#7 \qquad (1)$$

and, ova-per-unit surface area (cm^2) of colony (attribute #8, Appendices 12, 13):

$$\#6 \times \#7 = \frac{polyps}{colony} \times \frac{ova}{polyp} = \frac{ova}{colony} = \#8 \qquad (2)$$

A visual example of the sequence of bootstrapped distributions individually generated to compute the synthesized fecundity estimates is shown for *Psammocora stellata* at Caño Island for attribute #7 in Appendix 5 and attribute #8 in Appendix 6. Parametric statistical tests of significance of mean differences in computed fecundity (e.g., attribute #8) for *P. stellata* and *Psammocora profundacella* required transformation of the original bootstrapped estimates (Appendices 7, 8) using the Box-Cox procedure.

Boxplots of the distributions of the bootstrapped estimates of fecundity (number of stage IV ova cm^{-2} of colony surface) are shown for the two species (Appendix 14a, b). All among-site fecundity estimates demonstrated highly significant differences for *Psammocora stellata* ($X^2 = 19{,}717$, $p < 2.2 \times 10^{-16}$), with median values ranging from <1,000 ova cm^{-2} at Uva Island to >3,000 mature ova cm^{-2} in the Gulf of Panamá (Appendix 14a). A posteriori testing indicated significant site differences in fecundity in descending order (Appendix 14a): Gulf of Panamá, Caño Island, Galápagos Islands, Uva Island (Kruskal–Wallis test, $p < 2.2 \times 10^{-16}$). *Psammocora profundacella* also demonstrated highly significant intersite

Table 2 *Psammocora stellata*

Environmental setting location	Samples (*n* colonies)			Test		*p*
	Totals	With gametes	With stage IV	Period	Gamete stages	
Stable thermal regime						
Caño Is., Costa Rica	78	33	29	Wet/Dry	I–IV	<0.005
					IV	<0.001
				Lunar	I–IV	<0.05
					IV	<0.05
Uva Is., Gulf of Chiriquí	154	88	83	Wet/Dry	I–IV	<0.05
Panamá					IV	<0.05
				Lunar	I–IV	NS
					IV	<0.05
Seasonal upwelling						
Saboga Is., Gulf of Panamá	93	19	9	Wet/Dry	I–IV	<0.001
Panamá					IV	<0.001
				Lunar	I–IV	<0.001
					IV	<0.005
Taboga Is., Gulf of Panamá	95	36	34	Wet/Dry	I–IV	<0.001
Panamá					IV	<0.001
				Lunar	I–IV	<0.05
					IV	<0.01
Combined, Gulf of Panamá	188	55	43	Wet/Dry	I–IV	<0.001
Panamá					IV	<0.001
				Lunar	I–IV	NS
					IV	NS
Variable thermal regime						
Galápagos Is., Ecuador	93	42	37	Wet/Dry	I–IV	<0.001
					IV	<0.005
				Lunar	I–IV	NS
					IV	NS

Seasonal and lunar patterns of gametogenesis at six equatorial eastern Pacific study sites. Fisher exact test employed in all analyses except for Uva Island, and Gulf of Panamá lunar periods for both stages I–IV and IV, which were tested employing Chi-square analyses. When $p \leq 0.05$, reproductive activity was non-random over period tested [I–IV presence of Stages I–IV inclusive; IV presence of Stage IV gametocytes alone; wet/dry wet season, 15 April to 14 December (8 months) and dry season 15 December to 14 April (4 months) (in Galápagos, wet and dry seasons occur at opposite times of year to Costa Rica and Panamá); lunar four equal periods with lunar cycle beginning with new moon]

differences in fecundity ($X^2 = 19{,}717$, $p < 2.2 \times 10^{-16}$) with a high median value of slightly <4,000 ova cm^{-2} at Uva Island and a low median of just >2,000 ova cm^{-2} in the Galápagos Islands (Appendix 14b).

Three lines of evidence from histological analyses indicated multiple annual spawning cycles at all study sites: (1) a high incidence of mature gonads in most collections, (2) prevalence of spent gonads, and (3) presence of mature testes throughout most of the year in a frequently sampled large colony. First, Stage IV gonads were present in 192 of 218 (88.1 %) samples of *Psammocora stellata* and in 69 of 77 (89.6 %) samples of *Psammocora profundacella* (Tables 2, 3). This suggested the presence of several generations of mature gametes in a colony at any given time, indicative of continuous gamete production. Secondly, spent gonads occurred in several colonies of *P. stellata* in 7 of 12 calendar months during sampling in the 1980s and 1990s (Appendix 11). Finally, approximately biweekly sampling of a single male colony of *P. stellata* at Taboga Island (Gulf of Panamá) revealed the presence of Stage IV spermaries over a nearly 8-month non-upwelling period (Fig. 4b). Based on this evidence, probable lunar and annual spawning activities were denoted for both species of *Psammocora* at the four study sites (Table 4). There was a tendency for spawning to occur around new and full lunar phases, but this was often shifted by a few days as noted previously. Spawning in *P. stellata* occurred during most of the year and year round at Uva Island, and in *P. profundacella* from a few to 6 months in the Galápagos Islands.

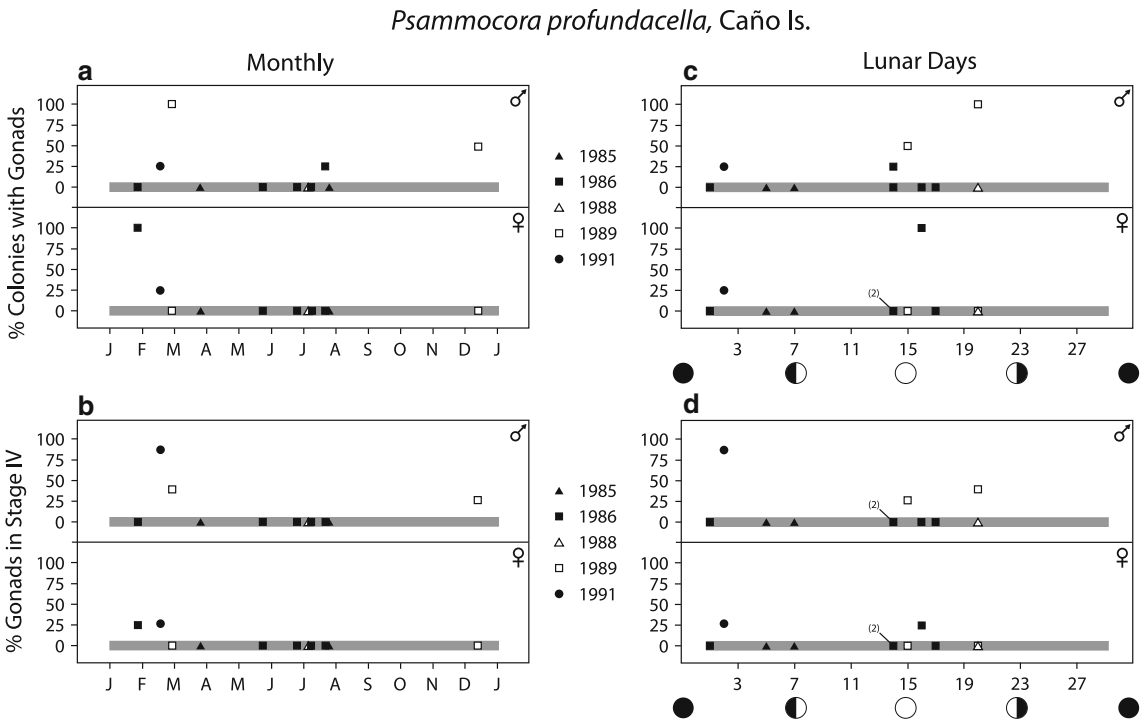

Fig. 6 *Psammocora profundacella.* Reproductive activity at Caño Island, Costa Rica, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 11 collections and 28 colonies examined (1985–1991). Further details as in legend to Fig. 2

Table 3 *Psammocora profundacella*

Environmental setting location	Samples (*n* colonies)			Test		*p*
	Totals	With gametes	With stage IV	Period	Gamete stages	
Stable thermal regime						
Caño Is., Costa Rica	28	7	6	Wet/Dry	I–IV	NS
					IV	<0.05
				Lunar	I–IV	NS
					IV	NS
Uva Is., Gulf of Chiriquí	59	38	38	Wet/Dry	I–IV	NS
Panamá					IV	NS
				Lunar	I–IV	NS
					IV	NS
Variable thermal regime						
Galápagos Is., Ecuador	88	32	25	Wet/Dry	I–IV	<0.05
					IV	NS
				Lunar	I–IV	NS
					IV	NS

Seasonal and lunar patterns of gametogenesis at three equatorial eastern Pacific study sites. Fisher exact test employed in all analyses. See caption in Table 2 for details regarding *p* and durations of seasonal and lunar periods

Recovery

Changing abundances of *Psammocora stellata* at several equatorial eastern Pacific sites, mainly in response to ENSO warming disturbances, have resulted in persistently low to moderate to high population densities (Appendix 15). Two shallow nearshore (5–9 m) sites at Caño Island, Costa Rica, have demonstrated no increases in live coral cover or number of colonies over a 15-year period following the 1982–1983 and 1997–1998 bleaching events. Two deep (9–14 m) sites demonstrated recovery of live coral cover and colony abundances after 1984, but then

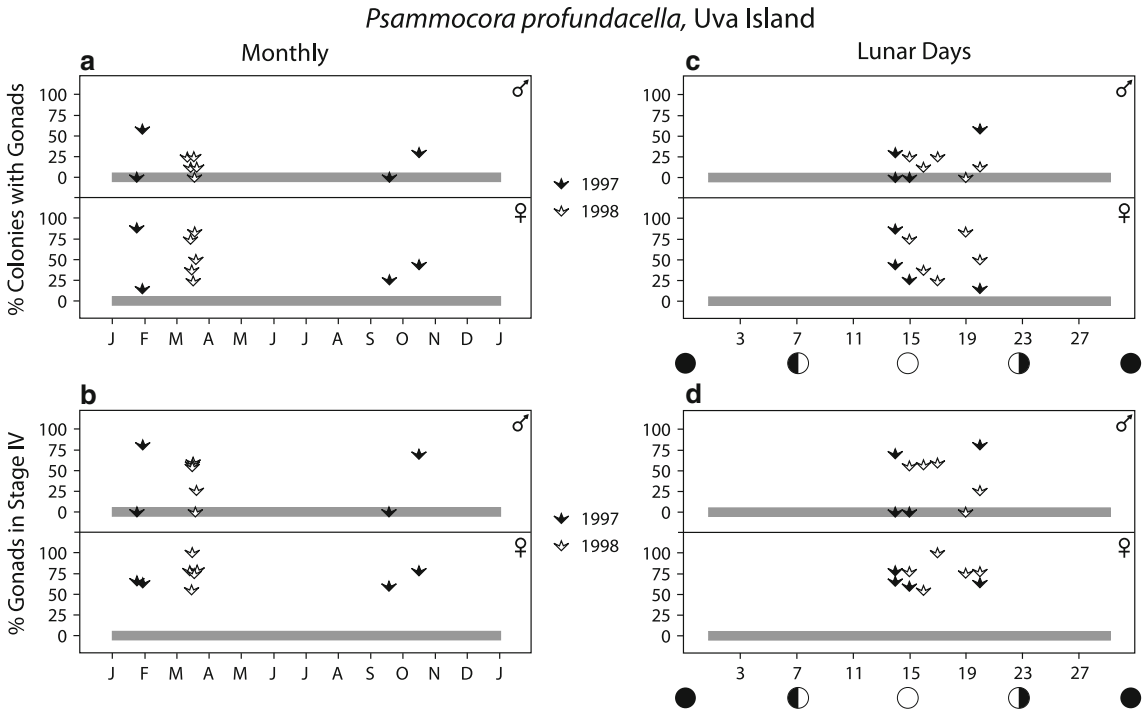

Fig. 7 *Psammocora profundacella.* Reproductive activity at Uva Island, Gulf of Chiriquí, Panamá, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 9 collections and 59 colonies examined (1997–1998). Further details as in legend to Fig. 2

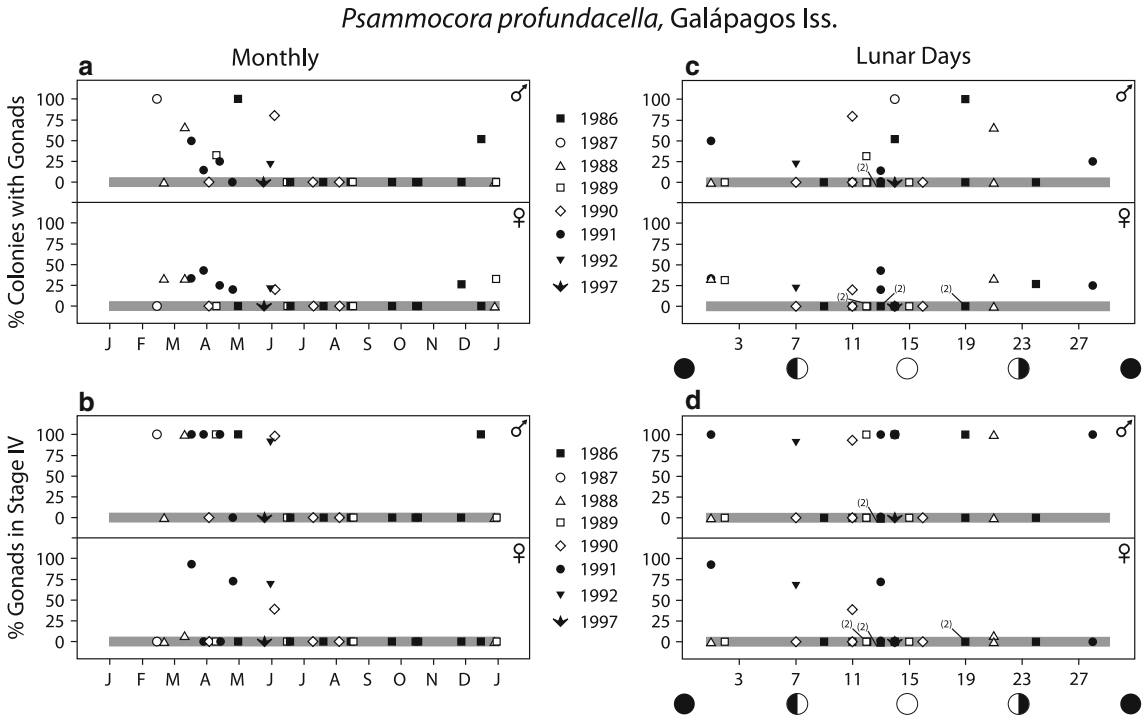

Fig. 8 *Psammocora profundacella.* Reproductive activity in Galápagos Islands, Ecuador, in relation to season (**a**, **b**) and lunar phase (**c**, **d**), based on 27 collections and 88 colonies examined (1986–1997). Further details as in legend to Fig. 2

experienced declines following the 1997–1998 ENSO event. At Cocos Island, two shallow sites (3–18 m) experienced declines in live cover while there was an increase at the deep site (9–24 m); overall, there was a minor change in cover (Guzmán and Cortés 2007). At Uva Island, Panamá, a 288-m^2 shallow (2–3 m) plot monitored since

1983 demonstrated a gradual increase from 0 to 10.6 colonies m^{-2} over a 19-year period. Although present in this plot before the 1982–1983 ENSO mortality event, abundances are unknown pre-1982. In the Galápagos Islands, an aggregate area of *P. stellata* of 2,295 m^2 at the Devil's Crown patch reef in 1976 experienced total mortality in 1983 and has since recovered to about one-third of its former cover after 28 years (Appendix 16). A second site in the Galápagos (Xarifa Island) has demonstrated substantial increases in live cover (≈48 %) and mean number of colonies (≈138 %) over a 7-year period (Brown and Feingold unpubl data, Appendix 16).

Discussion

The two eastern Pacific *Psammocora* species in this study (*P. stellata and P. profundacella*) are gonochoric as are the majority of species in the Siderastreidae (Richmond and Hunter 1990; Baird et al. 2009a; Harrison 2011; Kerr et al. 2011). Indirect evidence suggested that *P. stellata* in Hawaii was a brooder. Swimming planulae were observed in an aquarium with isolated colonies of *P. stellata,* which were assumed to be the maternal source colonies of the larvae (Kolinski and Cox 2003). Our study strongly suggests, however, that *P. stellata* in the eastern Pacific is a broadcast spawner, based on four lines of evidence: (1) observed spawning of colonies, albeit under stressed conditions, (2) presence of ova in sealed polyethylene bags containing corals, (3) presence of male and female spawned gonads in histological preparations taken throughout the calendar year, and (4) absence of planula larvae in hundreds of examined histological samples. Although only a single colony of *Psammocora superficialis* (= ? *profundacella*) was sampled at the Solitary Islands in eastern Australia, Wilson and Harrison (2003) also concluded that this species was a broadcast spawner.

Both brooding and broadcast spawning corals are known in the Siderastreidae and even within species in the genus

Table 4 *Psammocora stellata, Psammocora profundacella*

Species	Location	Months	No. months $year^{-1}$	Ova cm^{-2} $year^{-1}$
Psammocora stellata	Caño I, Costa Rica	Jul–Jan	≥7	≥18,418 ± 2,731
	Uva I, Panamá	Jan–Dec	12	12,835 ± 1,294
	Gulf of Panamá, Panamá	May–Dec	≥8	≥13,233 ± 1,414
	Galápagos Is.,	Nov–Jul	≥9	≥18,193 ± 2,568
Psammocora profundacella	Caño I, Costa Rica	Dec–Feb	≥3	≥12,175 ± 2,214
	Uva I, Panamá	Jan–Mar, Sep–Oct	5	20,338 ± 2,813
	Galápagos Is.,	Dec, Feb–May	≥6	≥16,473 ± 2,936

Annual fecundity estimates for all study localities based on number of months per year gonads contained mature gametes (attribute #8 + 25 % Appendices 12 and 13 × respective no. months $year^{-1}$). Mean ovum densities calculated by increasing number of polyps cm^{-2} by 25 % to compensate for use of non-processed tissue

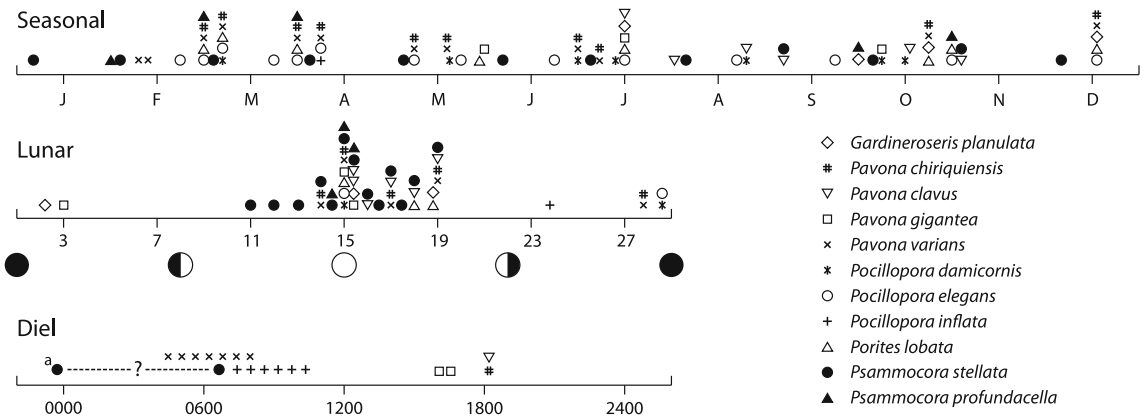

Fig. 9 Seasonal, lunar, and diel timing of 11 broadcast spawning zooxanthellate corals predominantly at Uva Island reef, Gulf of Chiriquí, Panamá. Data are from Stage IV gonadal presence in male and female colonies, and spawning observations (Glynn et al. 1991, 1994, 1996, 2000, 2011; Glynn 1999). Diel spawning times of *Pocillopora inflata* and *Pavona gigantea* were observed in Gulf of Panamá and Galápagos Islands, respectively. Spawning in *Psammocora stellata* may occur sometime from 2300 to 0700, based on mature ova observed in sealed bags when collected soon after sunrise

Siderastrea (Szmant 1986; Harrison and Wallace 1990; Baird et al. 2009a). In the Caribbean, the mode of reproduction has generally been attributed to colony morphology and environmental conditions (Szmant 1986). Large adult size and predictable environments were hypothesized to favor broadcast spawners whereas brooding species occurred more commonly in unstable habitats where high adult mortality is frequent. This pattern is consistent with *Porites* in some eastern Pacific areas where the large broadcast spawner *Porites lobata* typically occurs in predictable deeper reef zones, and *Porites panamensis,* a small brooding species, characteristically occupies shallow habitats subject to frequent disturbances such as bleaching and extreme low tidal exposures (Glynn 1976; Glynn et al. 1994). At Caño Island, however, *P. lobata* microatolls are abundant on shallow reef flats, and *P. panamensis* occurs from 2 to 15 m depth (Guzmán and Cortés 1989; Guzmán, personal communication). *Psammocora stellata* at Uva Island inhabits multiple reef zones including the deep (20 m) forereef rubble plain, while *Psammocora profundacella* more often occurs on basalt substrates along wave-exposed shores. In the Galápagos Islands and the Gulf of Panamá, *P. stellata* is also found in deeper reef habitats.

Both *Psammocora* species conform to the protracted seasonal reproductive patterns previously reported for zooxanthellate corals in the equatorial eastern Pacific (Fig. 9, e.g., Glynn et al. 2011). In thermally stable environments (Caño and Uva Islands), seasonal reproductive activity is mostly protracted throughout the year. In environments subject to seasonal upwelling (Gulf of Panamá), or marked annual variations in temperature (Galápagos Islands), reproductive activity was most pronounced during warm periods. This pattern of gamete development over extended reproductive periods, perhaps simply a response to sea temperature variation, may enhance survival in disturbed environments (Glynn et al. 1991, 1994, 1996, 2000, 2011; Colley et al. 2006).

After considerable effort over many years, neither species of *Psammocora* was observed spawning under natural conditions. The documented negative results reported here, however, should serve to narrow the timing of spawning that will hopefully be determined in future studies. The presence of mature male and female gametes at all lunar phases at all study sites (but one) suggests that spawning may be diffuse and not closely linked to any particular lunar phase. *Psammocora profundacella* at Uva Island was the one exception with mature gametes clustered over a 7-day period near full moon (lunar days 14–20). It is also possible, however, that this pattern is an artifact due to limited sampling.

Multispecific synchronous spawning has not been observed in the eastern Pacific, adding to the diversity of biogeographic reproductive patterns reported in coral assemblages (Guest et al. 2005; Baird et al. 2009a; Harrison 2011). Even though mature gametes in several species, suggestive of impending spawning, were clustered between lunar days 15 and 19 (Fig. 9), no simultaneous group spawning was ever observed. The closest approach to spawning synchrony in the eastern Pacific occurs in *Pavona varians* and *Pavona chiriquiensis*, which spawn during full moon, but 12 h out of phase (Glynn et al. 2000). This pattern of temporal reproductive isolation of 11 broadcast spawning species is similar to that reported for the northern-most Red Sea (Shlesinger and Loya 1985; Shlesinger et al. 1998). More recent studies in Kenya (Mangubhai and Harrison 2009), Japan, and the Great Barrier Reef (Baird et al. 2009b) have added to our knowledge of latitudinal differences in reproductive behavior and called into question the prevalence of mass spawning events. Patterns of seasonal spawning duration and synchrony have been shown to vary geographically; the equatorial eastern tropical Pacific exhibits a complete lack of synchrony and a greatly extended spawning season as compared to other regions of the world.

Ongoing studies at higher latitudes in the Gulf of Tehuantepec, México, a seasonally upwelling environment, report a relatively narrow reproductive period of 4 months for two broadcasting species—*Pocillopora damicornis, Pavona gigantea*—and one brooding species—*Porites panamensis* (Rodríguez-Troncoso et al. 2011). Egg maturation occurred in the two broadcast spawning species in August, about 4 months after upwelling when annual sea temperature peaks. During the very strong 1997–1998 ENSO in the non-upwelling Gulf of Chiriquí, the numbers of reproductive colonies of *P. damicornis* were significantly less than in non-ENSO years (Colley et al. 2006). However, *Psammocora stellata* collections contained female and male reproductive colonies in the Galápagos cool season in 1987, during a moderately strong El Niño event. These results underline the importance of site-specific environmental differences (e.g., seasonal temperature variability and tidal amplitude), interannual variability of oceanographic conditions (e.g., ENSO and Pacific Decadal Oscillation), and geographic population difference in determining gametogenesis and spawning.

Psammocora spp. appear to possess four adaptive characters that would facilitate recovery following ENSO-related mortality: (1) relative resistance to bleaching/mortality, especially below 10–12 m depth, (2) persistence of surviving deep source populations that can potentially promote recruitment into decimated shallow reef habitats, (3) prolonged seasonal reproductive periods and high fecundities, (4) asexual reproduction. Compared to most zooxanthellate corals, *Psammocora stellata* experienced

less bleaching/mortality in Panamá (Glynn 1983, 1984) and the Galápagos Islands (Robinson 1985) during the severe 1982–1983 ENSO warming event, and in Costa Rica (Jiménez et al. 2001) and México (Carriquiry et al. 2001) during the equally strong 1997–1998 ENSO. Bezy et al. (2006) have offered evidence of the relative resistance of *Psammocora* spp. to stress and remarked on their ability to recolonize disturbed areas in Costa Rica. This also was observed at Gorgona Island, Colombia, following the 1982–1983 ENSO (Guzmán and López 1991). Deep (10–25 m) occurring colonies in the Galápagos Islands bleached but suffered minimal mortality and regained normal pigmentation in 5–6 months following the disturbance event (Glynn 1990; Feingold 1996). This depth-related survivorship pattern also was observed in Baja California (Reyes-Bonilla 2001). Both *Psammocora* species are highly fecund with annual ova production ranging from 1.2×10^4 to 1.8×10^4 cm^{-2} at all localities. These values greatly exceed all Indo-Pacific and Caribbean species listed in Harrison and Wallace (1990) and are similar to those reported for other eastern Pacific poritid and agariciid species (Glynn et al. 1994, 1996, 2000, 2011). Finally, fragmentation resulting from pufferfish corallivory could increase asexual reproduction (Guzmán and López 1991; Feingold 1996).

The relative contributions of sexual and asexual reproduction to the post-disturbance recovery of *Psammocora* populations are unknown. The small sizes and mobile habit of eastern Pacific *Psammocora,* especially *P. stellata,* make it difficult to distinguish between sexual and asexual (fragmentation) recruitment (Glynn 1974). Some studies, however, are suggestive of an important role of sexual larval recruitment from surviving deep populations. In Costa Rica (Caño Island), *P. stellata* was more abundant in deep compared with shallow habitats, and Guzmán and Cortés (2001) noted that sexual recruitment was responsible for increases in abundance at Caño Island after the 1992 ENSO disturbance. Jiménez and Cortés (2003) also observed high mortality of shallow-occurring *P. stellata* at Costa Rican mainland sites and suggested that recovery would depend on the recruitment of sexual propagules from deep populations. A slow but steady increase in *P. stellata* on the shallow Uva reef, primarily on rubble substrates previously lacking this species, occurred after the 1997–1998 ENSO. Less than 100-m downslope, at 12–18 m on the forereef, was a large population of *P. stellata* that survived both ENSO events and likely served as a source population. The recovery of shallow (2–3 m) *P. stellata* patches within Devil's Crown in the Galápagos Islands also appears to be due to settlement of larvae originating from nearby (15–25 m) upstream source populations at 15 to 25 m depth (Feingold 1996, 2001). A molecular genetic analysis aimed at establishing the degree of connectivity between deep and shallow corals should help to clarify this question. Additionally, determination of relatedness of colonies at various spatial scales would help pinpoint if population increases are primarily due to asexual or sexual reproduction or some combination of the two processes.

The reproductive biology of equatorial eastern Pacific scleractinian coral communities is different from most other regions of the world. Although only a few species have been seen releasing gametes, most are broadcast spawners, but do not form bundles except possibly for the Pocilloporidae. Each species has its own seasonality that can vary with locale. To date, only two species are proven brooders, two species are simultaneous hermaphrodites (Pocilloporidae), four species are sequential cosexual hermaphrodites (Agariciidae), and five species display stable gonochorism including one agariciid (*Pavona clavus*), two species of *Psammocora* (this study), one poritid (*Porites lobata*), and one fungiid (*Diaseris distorta*) (Glynn et al. 1991, 1994, 1996, 2000, 2008, 2011; Colley et al. 2000). Recent molecular genetic studies indicate that coral sexual traits in several taxa demonstrate strong phylogenetic relationships. For example, the two brooding species, *Tubastraea coccinea* (azooxanthellate) and *Porites panamensis* (zooxanthellate, endemic), are sister-group species in clades II and III; *Pavona* and *Porites* are members of the Complexa clade; and *Psammocora* and *Diaseris* are members of clade XI (Fukami et al. 2008; Kitahara et al. 2010; Huang 2012). Therefore, it follows that reproductive mode and gamete development may be more closely related to phylogeny than to environmental conditions. Temperature stability and its variation may, however, be an important factor in the success or completion of gamete cycling, and due to upwelling and ENSO effects, may show a varied pattern in at least some species on a yearly basis.

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