The false limpet Siphonaria gigas, *a simultaneous hermaphrodite, lives in pairs in rock fissures on the Pacific coast of Panama*

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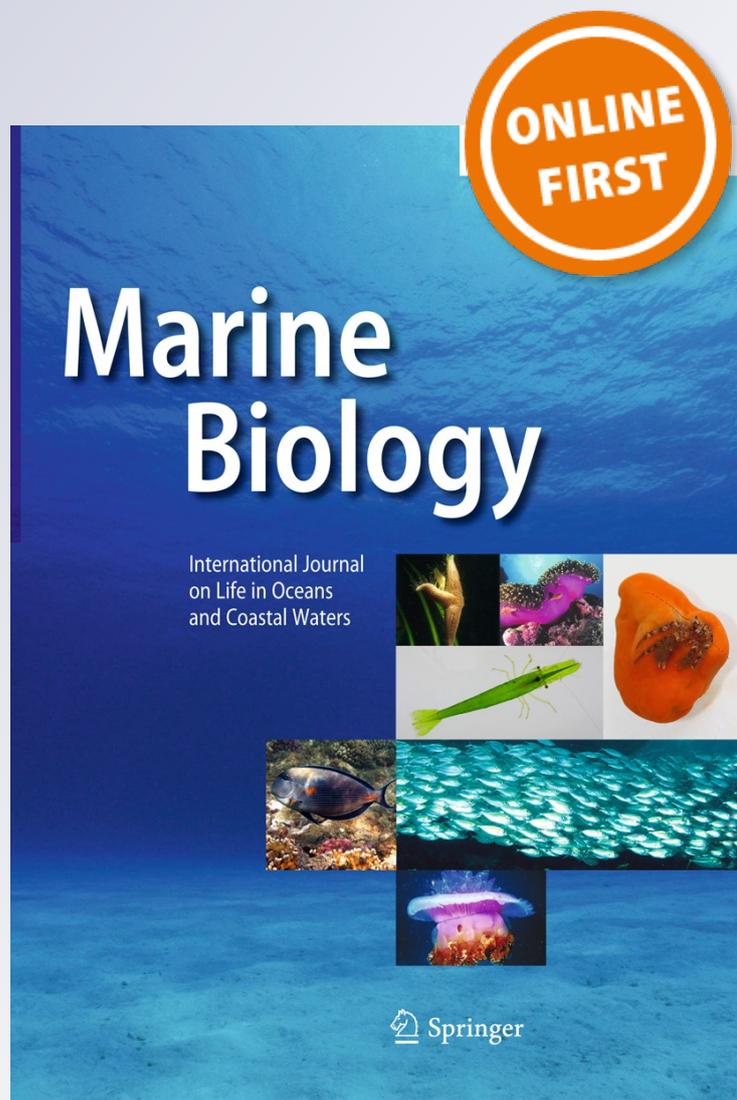**Roberto C. Lombardo · John H. Christy · Roberto Cipriani**

Abstract The pulmonate limpet *Siphonaria gigas*, a simultaneous hermaphrodite, lives in the mid- to upper-intertidal zone on rocky shores in the tropical Eastern Pacific. Samples along five transects taken in June–July, 2004, on Culebra Point (8°54′N to 79°31′W), Republic of Panama, showed that 71 % of the population occurred in fissures, a significant preference for this habitat. Of 200 adults in 27 fissures, 150 lived side by side in pairs with their shells touching or nearly so, a significant deviation from the number of pairs expected given a random arrangement. Pair frequency did not increase with limpet density suggesting pairing was not an incidental consequence of crowding. Pair living was unknown in the genus *Siphonaria*, and is very uncommon among simultaneous hermaphrodites. Reproductive synchrony and restrictions on movement due to predation and environmental stress may limit opportunities for encountering and mating with multiple partners favoring pair living in *S. gigas*.

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Introduction

The scale of non-random patterns of distribution and abundance of intertidal organisms frequently indicates the nature of the process responsible for them (Underwood and Chapman 1996). At the scale of meters to centimeters, vertical zonation and distributions across habitats are largely driven by the interplay between behavioral responses to environmental stress and species interactions (Menge and Sutherland 1987; Bertness and Callaway 1994; Tomanek and Helmuth 2002). The spatial arrangement of individuals is affected by impact from waves, temperature extremes during low tides (Underwood 1980; McQuaid and Branch 1984; Denny and Wethey 2001), predation and competition (Connell 1975; Menge and Sutherland 1987; Denadai et al. 2000; Turra and Denadai 2006), and social interactions including gregarious settlement (Burke 1986), territoriality (Shanks 2001), and competition for mates (Collin 1995). Here, we report habitat preferences and pair living in an intertidal invertebrate and suggest possible causes for this distinctive and highly unusual spatial pattern and mode of life.

The pulmonate false limpets in the family Siphonariidae are variously distributed over different heights in the mid-intertidal zone reflecting differences in their physiology, morphology, and behavior (Hodgson 1999). *Siphonaria gigas* occurs in the tropical Eastern Pacific from Mexico to Peru (Keen 1971). It is the most abundant molluscan grazer in the mid-intertidal zone on Pacific rocky shores of Panama (Levings and Garrity 1984). As is typical of most siphonariid limpets (Garrity and Levings 1983; Hodgson 1999), individual *S. gigas* occupy a particular area on the rock, called a home scar, to which the edges of their shells fit uniquely and precisely. They stay "on scar" during the day and when immersed by the tide at night, leaving to

forage only during nocturnal low tides, returning to their scar on the rising tide (Garrity 1984). *Siphonaria gigas* feeds on microalgae, which it scrapes from the rock surface using its protrusible buccal bulb and fine-toothed (~ 200 teeth row^{-1}) radula (Garrity and Levings 1983). "Off-scar" limpets are easy prey of both aquatic and terrestrial predators but when clamped tightly to the rock "on scar," they are very tenacious (Lowell 1987), and their predation rates are very low (Garrity and Levings 1983).

All siphonariids are hermaphrodites with internal fertilization (Hodgson 1999). Mating patterns are known only for *Siphonaria capensis* which gives or receives sperm, but not both, in a single mating (non-reciprocal copulation, Pal et al. 2006). In Panama, Levings and Garrity (1986) found that *S. gigas* mate most often (59/86 cases, 68 %) with their nearest neighbors which typically are so close that their shells touch. Twice monthly during neap low tides, individuals deposit one or more egg masses on steeply inclined rock surfaces (Fig. 1). Members of nearest-neighbor pairs may mate repeatedly during a single low tide (J. Christy, personal observation) and both limpets often lay eggs during the same reproductive period (Fig. 1) suggesting they copulate reciprocally (give and receive sperm) with their neighbor either in a single mating or in closely spaced sequential matings. *Siphonaria gigas* spermatophores are large measuring up to 20 mm in length (Berry 1977). Previous studies in Panama (Levings and Garrity 1984; Garrity 1984) indicate that predation on *S. gigas* by fish during high tides, and overheating and desiccation during diurnal low tides favor limpets that occupy scars on vertical surfaces (cooler, 50 % of all adults) and in fissures (cooler and protected, 20 % of adults) in the rock. *Siphonaria gigas* seldom occurs in tide pools. As a result of these limitations, *S. gigas* can encounter and mate with individuals other than their nearest neighbors primarily during nocturnal ebb tides when most limpets leave their scars to graze while the rock is wet and cool (Garrity 1984; R. Lombardo and J. Christy, personal observations).

On a rocky shore on Culebra Point, Republic of Panama, many *S. gigas* appeared to live in pairs with ample, habitable, but unoccupied space between them (Fig. 1). Levings and Garrity (1986) also noted that limpets at this site often lived close to each other but they did not recognize this pattern as possibly indicating pair living. The objectives of this study were to re-sample the distribution of *S. gigas* on the rocky shore at Culebra Point, describe the spatial distribution of individuals, and determine whether pairs of limpets are more common than expected by chance.
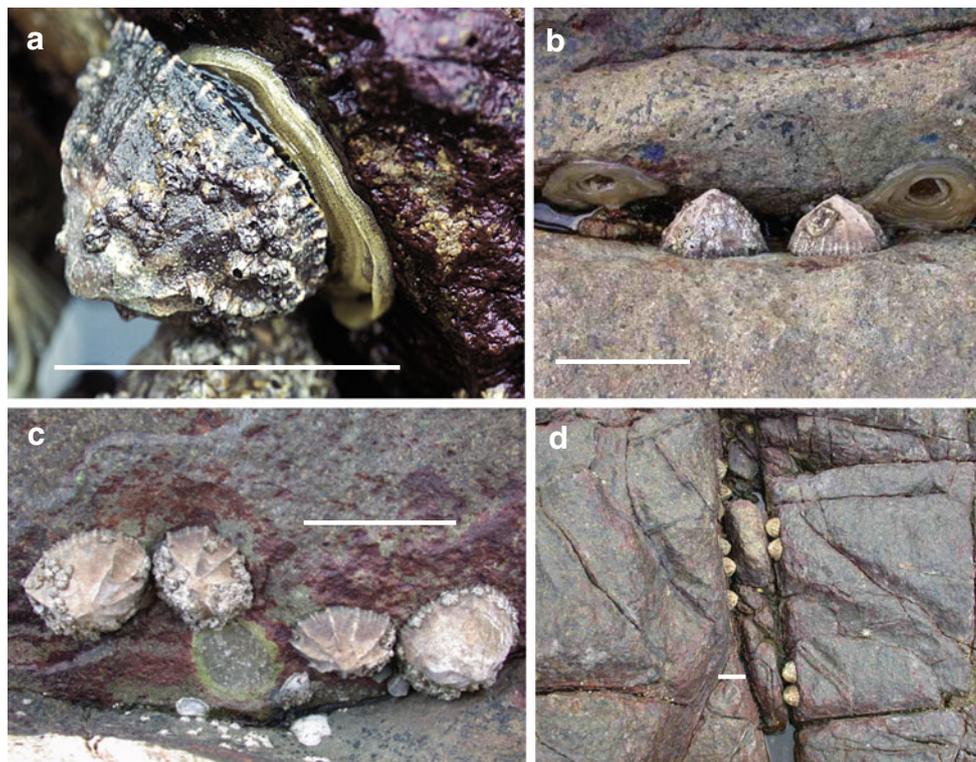

Fig. 1 *Siphonaria gigas*, their egg masses, and evidence of pair living. **a** Limpet completing its egg mass, **b** pair of limpets and their egg masses, **c** two pairs, shells touching; unoccupied scar suggests pair on left formed recently, **d** multiple pairs with ample unoccupied space between them. *White bars* indicate approximately 5 cm (photographs by J. H. Christy)

Methods

Study site

This study was carried out during diurnal low tides in June and July, 2004, on the intertidal rocky shore of Culebra Point (8°54′N to 79°31′W) located on the east side of the channel leading to the Pacific entrance to the Panama Canal. Tides are semidiurnal, with a mean range of 3.9 m and an average spring tide range of 5.0 m. The site has boulder fields low on the shore and massive rock outcrops with abundant fissures and tide pools in the mid- to upper-intertidal zone. The rock is basalt with a microporous weathered surface providing substratum for several species of crustose and coralline algae, gastropods, barnacles, and grapsid and xanthid crabs (Levings and Garrity 1984).

Distribution across habitat types

Five transects, each 90 m long and extending beyond the lower and upper limits of the vertical distribution of *S. gigas*, were surveyed. The lower ends included boulders near the low tide line and the upper ends reached the massive basalt outcrop in the upper-intertidal zone. The transects were positioned to sample the range of habitat types on the rocky shore without regard to local variation in the abundance of limpets. We sampled the occurrence of *S. gigas* along each transect using a frame measuring 0.5 m on a side and enclosing an area of 0.25 m². The frame was placed at the lowest end of each transect and at intervals of 2 m along the full length of the transect (45 samples transect^{-1}). All *S. gigas* within each frame were counted and their shell lengths (SL) were measured with a caliper to the nearest 0.1 mm through the longer anterior–posterior axis of the shell.

The substratum inside each 0.25-m² frame was classified as relatively flat rock surface of any slope, fissure, tide pool, barnacle patch, or boulder on sand. The classification of the habitat in a frame seldom was ambiguous. Heterogeneous rock surface with multiple depressions, cracks, or surfaces that abutted at angles of about 90° or less was classified as "fissure." Areas with standing water at low tide that occupied >50 % of the space inside a frame were considered "tide pools." When there were two possible classifications (e.g., barnacles adjacent to a fissure) and limpets were present in one habitat (e.g., the fissure), the classification of the microhabitat in which the limpets occurred was chosen.

Distribution in fissures

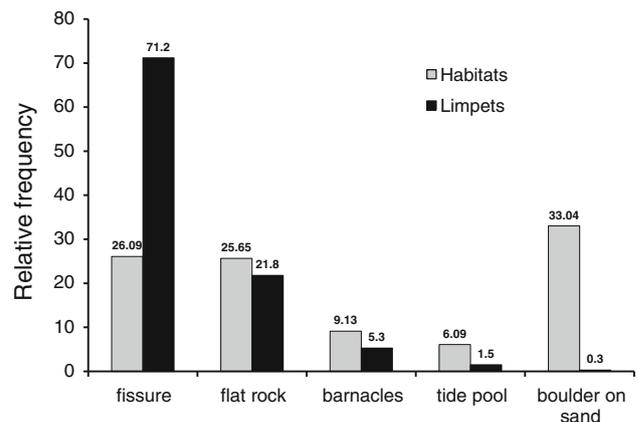Garrity (1984) found *S. gigas* most often (70 % of the population) on vertical surfaces and in fissures at Culebra.

Fig. 2 Observed (*black bars*) and expected (*gray bars*) relative frequencies (×100) of *S. gigas* in five habitats. Expected relative frequencies calculated from relative frequencies of 225, 0.25 m² quadrats classified into five habitat types

Our preliminary observations and re-sampling of the distribution showed this still to be the case (see Results). We therefore analyzed the spatial distribution of limpets along lines formed by fissures. Twenty-seven well-populated fissures in the upper range of the distribution of *S. gigas* were selected. We marked each fissure with a numbered aluminum tag on a screw anchored in the rock. Fissures terminated abruptly at each end, and we measured the length of each. The fissures included v-shaped cracks, some just wide enough to accommodate an adult limpet (Fig. 1d), as well as seams formed where nearly vertical rock surfaces abutted horizontal ones (Fig. 1c). In the latter case, limpets usually were positioned on the vertical face along or just above the seams. All *S. gigas* in the fissures were individually marked by gluing (epoxy putty) a numbered plastic tag on the upper part of their shells. Limpets in each fissure were counted and their position from one end of the fissure was measured to the nearest millimeter. In the few cases, where a limpet was positioned slightly above a seam (Fig. 1c), its location was projected down to the seam. Pairs were recognized as adjacent limpets that were so close that their shells touched or nearly so. Using a caliper and in some cases, a divider with articulating legs, we measured the SL to the nearest 0.1 mm of each limpet.

Analysis for pairing

A test was conducted to determine whether the number of pairs of limpets we observed in a fissure (OP) was larger than the number expected if pairs formed at random (RP). One-dimensional arrays were used to model the space available to the limpets in a fissure. The number of elements in the array in each fissure was the number of positions that could be occupied by limpets along the axis of that fissure. This number was estimated as the ratio of

the length of the fissure and the average SL of the limpets found in the fissure, rounded to the closest and largest integer value. Arrays were populated (in simulation) by randomly occupying the positions available in a fissure with the number of limpets in that fissure. Limpets were not allowed to co-occupy a position. The number of randomly formed pairs (RP) was the number of adjacent positions that were occupied in a given simulation. We tested for significant pairing by calculating the number of times (T) the observed number of pairs (OP) exceeded the number of pairs expected had the pairs formed at random (RP) after *n* simulations. The *P* value for a one-tailed test was estimated as $1 - T/n$, which was compared with values of $\alpha = 0.05$. Hence, *P* values $\leq \alpha$ indicated that the OP in a particular fissure was significantly larger than the RP. Simulations were repeated until *P* values did not change through the third decimal place for at least 1,000 iterations, usually $>5 \times 10^4$ runs.

Our model was spatially discrete and assumed that: (a) limpets had the same probability of occupying any unoccupied position (as defined above) within a fissure, (b) the average SL was different between limpets from different fissures, and (c) limpets could not move between fissures. However, we do not know how often limpets in one fissure move to another nor how far they may move. To permit such movement and to relax assumptions (b), and (c) simulations were also run with an array as long as the sum of the lengths of all 27 fissures, using the average SL of all limpets in the 27 fissures.

Results

Distribution across types of habitat

Habitats and *Siphonaria gigas* were sampled along 450 m in 225, 0.25 m² quadrats totaling 56.25 m². The 340 limpets we encountered did not occur in the five microhabitat types in proportion to their abundance on the shore ($X_4^2 = 392.616$, $P < 0.0001$, Fig. 2). About 71 % of the limpets occurred in fissures (X_1^2 (Yates correction) = 353.916, $P < 0.0001$), 22 % on flat rock (X_1^2 (Yates) = 2.414, $P = 0.106$), 5 % on barnacles (X_1^2 (Yates) = 5.546, $P = 0.014$), 2 % in tide pools (X_1^2 (Yates) = 12.194, $P = 0.0003$), and 0.3 % (one individual) on boulders (X_1^2 (Yates) = 162.574, $P < 0.0001$). Hence limpets preferred fissures and avoided all other habitats except flat rock which they occupied in proportion to its availability.

The size distribution of *S. gigas* across habitats was strongly skewed to the right with most individuals <2.4 cm in SL and far fewer larger individuals of 3.4–6.8 cm in SL (Fig. 3). There was a significant difference in the sizes of individuals in fissures, on flat rock and in barnacle patches
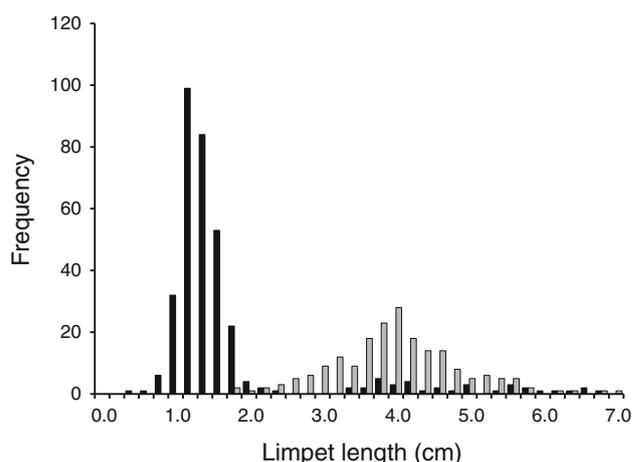

Fig. 3 Size frequency distributions of 340 *S. gigas* limpets in 56.25 m² across five habitats along five transects (*black bars*), and of 200 limpets in 27 fissures in upper-intertidal zone (*gray bars*)

(ANOVA, $F_{(2, 331)} = 7.067$, $P = 0.00098$). Whereas limpets of all sizes lived in fissures, few smaller individuals lived on barnacle patches and exposed flat surfaces, increasing the average size of limpets in these less protected habitats ($X \pm SE$ SL: fissures, 1.48 ± 0.067 cm, $N = 242$; flat rock, 1.99 ± 0.136 cm, $N = 74$; barnacle patch, 1.95 ± 0.375 cm, $N = 18$).

Distribution in fissures

A total of 200 *Siphonaria gigas* were found in 27 fissures in the upper-intertidal zone. They were large adults (Fig. 3), and 150 (75 %) lived in pairs with their shells touching or nearly so. Paired *S. gigas* ($X \pm SE = 3.62 \pm 0.054$ cm SL, $N = 150$) tended to be similar in size (paired *t* test, $t_{74} = -1.169$, $P = 0.246$; Pearson's correlation, $r = 0.459$, $N = 75$, $P < 0.01$, Fig. 4) while singletons ($X \pm SE = 4.79 \pm 0.124$ cm SL, $N = 49$) were significantly larger (unpaired two-sample *t* test, $t_{197} = 9.983$, $P < 0.0001$, Fig. 5). Singletons often were next to a vacant scar, which could be discerned by the lighter color of the rock, suggesting they were surviving members of previous pairs.

When we ran simulations for each fissure using the average SL of the limpets in each fissure, we found that OP occurred more often than expected by chance in 12 of 26 fissures (Table 1; eliminating one fissure with but one limpet). Combining all fissures, as if they were a single continuous linear habitat and using the SL of all limpets in the fissures ($X = 3.911$ cm), the analysis revealed highly significant pairing ($P < 0.00001$; Table 1). Given the available living space in fissures, *S. gigas* lived in pairs more often than expected by chance. In addition, the OP in a fissure relative to the maximum possible number of pairs
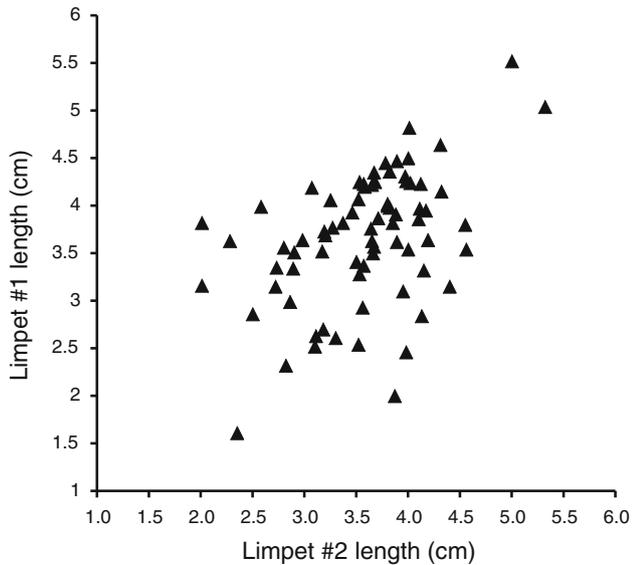
Fig. 4 Sizes of paired *S. gigas*. Limpets in pairs were arbitrarily designated number 1 or 2 and sizes of these individuals were plotted against each other
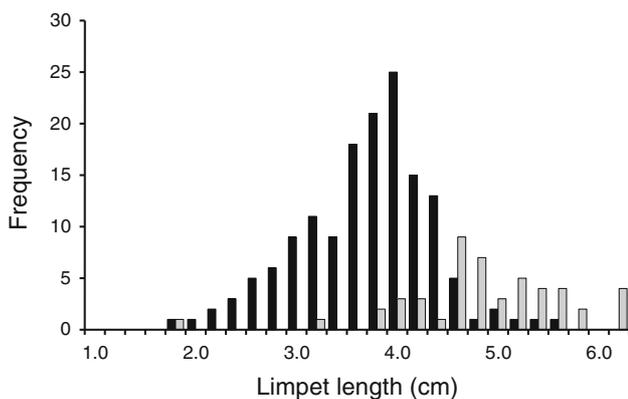

Fig. 5 Size-frequency distributions of 150 paired *S. gigas* limpets in 27 fissures (*black bars*) and 49 unpaired "singleton" limpets (*gray bars* length of one of 50 singletons not measured) in same fissures

in the same fissure was negatively correlated with limpet density, as measured by the ratio of the OP to the maximum number of limpets per fissure (Pearson's correlation, $r = -0.167$, $N = 26$, $P < 0.001$). Hence, pairing was not an incidental consequence of crowding.

Discussion

Siphonaria gigas was non-randomly distributed across the available habitat types in the rocky-intertidal zone at Culebra Point. Only one limpet was found on a boulder and few in tide pools and on barnacle-covered rock. Although fissures made up just over 26 % of the available habitat, about 71 % of the limpets occurred in fissures and about

22 % on exposed flat rock. These results are very similar to those obtained by Garrity (1984) at this site over 30 years ago. Then, as now, limpets occurred disproportionately in fissures and they avoided barnacle patches and tide pools. Garrity (1984) suggested that this distribution across habitats results from limpets avoiding hot, desiccating locations and our observations support this assessment. We often observed that limpets raised their shells during daytime low tides to cool themselves and reduce the area of contact between their foot and the rock, a behavior shown by Garrity (1984) to reduce heat stress. Fissures not only provide local refuge for adults from heat and desiccation, but also they provide much better protection for eggs from predation by fish during high tide (Levings and Garrity 1986) and possibly from desiccation.

Habitat preferences for fissures and other protected sites are common among limpets and important for survival (Gray and Hodgson Gray and Hodgson 2004) and are known in other species of siphonariids from warm temperate regions. *Siphonaria japonica* and *S. thersites* retreat under algae during low tide. *Siphonaria maura, S. capensis*, and *Kerguelenella lateralis* prefer tide pools (Hodgson 1999). As in *S. gigas*, these preferences may allow limpets to escape heat stress. *Siphonaria gigas* may avoid small tide pools because they become very hot, and they may avoid cooler larger ones because they contain fish predators (Palmer Palmer 1979; R. Lombardo and J. Christy, personal observations).

We found two size classes of *S. gigas* on the rocks at Culebra Point. Large reproductively active individuals were found almost exclusively in higher fissures, whereas smaller non-reproductive individuals occurred in fissures lower on the shore. Branch (1985) suggested that the balance in water loss and recovery rates is more likely to determine vertical zonation patterns than any other factor alone. This might be the case in our study because adult siphonariids can retain more extravisceral water than can juveniles (Marshall and McQuaid 1992) and this allows them to live where evaporative cooling is critical for survival (Turra and Denadai 2006).

Large breeding adult *S. gigas* from fissures in the upper range of the distribution showed a statistically significant tendency to live in pairs with their shells touching. Individuals uniquely fit the rock surface on their home scar to which they almost always return after foraging. Consequently, pairs persist for months (Levings and Garrity 1986) and some for at least five years (J Christy, personal observations). Individuals often, but not always, mate within their pair (Levings and Garrity 1986; R. Lombardo and J. Christy, personal observations) suggesting pair living in *S. gigas* constitutes social but not strict genetic monogamy. Social monogamy has not been described for any other species of *Siphonaria* (Hodgson 1999) and

Table 1 Analysis to determine whether observed numbers of pairs of *S. gigas* in fissures at Culebra Point (8°54′N to 79°31′W), Republic of Panama were more common than expected by chance

Fissure	Fissure length (cm)	Limpet fissure^{-1}	Average shell length (cm)	Pairs fissure^{-1}	Singleton fissure^{-1}	P value fissure^{-1}
1	200	3	3.253	1	1	0.097
2	140	3	5.080	1	1	0.211
3	170	2	3.962	1	0	0.047*
4	280	6	3.560	2	2	0.030*
5	158	2	5.118	1	0	0.066
6	263	6	4.716	3	0	0.010*
7	134	9	4.407	4	1	0.020*
8	420	9	4.783	4	1	<0.001*
9	670	22	5.344	11	0	<0.001*
10	700	14	4.438	6	2	<0.001*
11	264	6	4.537	2	2	0.050*
12	90	3	5.080	1	1	0.313
13	210	5	5.570	2	1	0.040*
14	200	3	4.690	1	1	0.135
15	150	8	5.083	2	4	0.519
16	110	12	4.073	4	4	0.517
17	66	3	4.489	0	3	1.000
18	330	15	4.870	4	7	0.194
19	170	6	5.509	0	6	1.000
20	250	19	4.948	7	5	0.051
21	170	11	5.330	5	1	0.012*
22	180	10	5.646	5	0	0.001*
23	110	5	5.760	2	1	0.157
24	110	6	4.800	1	4	0.817
25	80	4	3.892	2	0	0.029*
26	70	7	3.678	3	1	0.119
27	220	1	4.505	0	1	1.000
Single array	5915	200	3.911	75	50	<0.001*

P values based on $>5 \times 10^4$ simulations fissure^{-1}

* *P* values ≤0.05 indicate significant pairing

appears to be uncommon among other hermaphrodites (Petersen 2006; Wong and Michiels 2011).

Monogamous mating patterns are thought to result from spatio-temporal and ecological constraints on mate availability (Emlen and Oring 1977; Charnov 1982). In hermaphrodites, social monogamy is favored under low population density (Petersen 2006), high predation risk, reduced habitat availability (Baeza 2010), and conflict over food resources, a conflict that decreases with decreasing group size (Wong and Michiels 2011). In the case of *S. gigas*, physical stress (Garrity 1984) and predation risk (Garrity and Levings 1983) appear to limit mobility severely and hence the rate that individuals encounter potential mates, resulting in strong selection for pair formation. Paring reduces the costs of finding mates in unpredictable or stressful environments (Charnov 1982; Sogabe et al. 2007).

Pair living ought to affect sex allocation because sperm donors are expected to produce just enough sperm to fertilize their partner's eggs while maximizing the amount of resources available for egg production (Charnov 1982). This may be especially important for *S. gigas* because intense egg predation by fish should additionally favor the female bias in sex allocation set up by pair living. In addition, as males, monogamous hermaphrodites benefit from decreased sperm competition (Wong and Michiels 2011). *Siphonaria* spp. store sperm (Hodgson 1999), which would decrease the fertilization rate of sperm transferred in extra-pair matings, further favoring pair fidelity (Emlen and Oring 1977; Charnov 1982).

Individuals in pairs of *S. gigas* tended to be similar in size. Size-assortative mating has been described for *S. capensis* and has been ascribed primarily to the association of limpets of similar size at small spatial scales with a lesser contribution of mate choice and mating constraints among available local partners (Pal et al. 2006). Each of these processes could contribute to the formation of pairs of similar size in *S. gigas* as well. In addition, given the evident longevity of *S. gigas* pairs, we suggest that relative differences in growth rates between small and large

individuals that formed pairs would, in time, reduce any difference in size. The similarity in size of paired individuals should minimize any conflict between them in allocation to male and female functions (Angeloni et al. 2002) and further stabilize pairs. The ecological and social environment of *S. gigas* clearly favors pair living. However, we have observed extra-pair matings indicating that that social monogamy in this limpet does not lead to strict genetic monogamy. Some of these matings involved a pair member and a nearby singleton, an individual less likely to contain stored sperm. *Siphonaria gigas* produce a very large spermatophore, a trait consistent with sperm competition, suggesting either that extra-pair matings are common or that selection favors male investment in infrequent matings with singletons. This unusual siphonariid provides an excellent opportunity to explore further the ecological, social, and genetic factors that favor pair living, opportunistic cheating, and the tension between the two in a socially monogamous species.

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