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Host-dependent variation in density of corallivorous snails (*Coralliophila* spp.) at Curaçao, southern Caribbean

Gerrit Potkamp [1,2] · **Mark J. A. Vermeij** [2,3] · **Bert W. Hoeksema** [1,4]

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Abstract Snails of the genus *Coralliophila* (Muricidae: Coralliophilinae) are common in the Caribbean as corallivores that feed on a large range of host species. The present study concerns the distribution of two *Coralliophila* snails, *C. caribaea* and *C. galea*, at 5-m and 10-m depths at Curaçao (southern Caribbean), as associates of the common scleractinians *Orbicella annularis* and *Pseudodiploria strigosa*. *Coralliophila galea* was abundant on both host species, while *C. caribaea* was represented only by a single individual on a colony of *P. strigosa*. No significant differences in shell length were found between snails associated with *O. annularis* and *P. strigosa*. The distribution of *C. galea* on both host species deviated significantly from a random distribution. The snails were most abundant at 5-m depth, particularly on larger colonies of *O. annularis*, with > 60 % of large colonies colonized by snails, while snails were absent on small colonies. This distinction was not significant in *P. strigosa* at the same depth or in *O. annularis* at a depth of 10 m. The results suggest that host preference should be considered in assessments of reef health in connection to damage caused by *Coralliophila* spp.

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Introduction

Coral reefs are amongst the most biologically diverse ecosystems in the world, providing habitats for many marine species (Reaka-Kudla 1997; Rotjan and Lewis 2008; Netchy et al. 2016). Some of the reef-dwelling species, such as corallivorous snails, consume live coral, which may contribute to the decline in coral reefs (Rotjan and Lewis 2008).

Corallivorous gastropods of the genus *Coralliophila* (Muricidae: Coralliophilinae) can be found at depths ranging from shallow to deep in both the Atlantic and the Indo-Pacific (Oliverio et al. 2009). A total of four shallow-water reef-dwelling species of this genus are known from the Caribbean (Kosuge and Suzuki 1985; Rosenberg et al. 2009), another one from the northeastern Atlantic and the Mediterranean (Kružić et al. 2013), and ca. 20 species from the Indo-Pacific (Oliverio 2008). With these four *Coralliophila* species and a coral-predating heterobranch slug of the genus *Berthellina* (Vermeij 2010), the diversity of corallivorous snails in the Caribbean is low compared to that in the Indo-Pacific, which is consistent with earlier findings (Robertson 1970). In addition to the ca. 20 *Coralliophila* species mentioned above, various coral-eating gastropods have been reported from the Indo-Pacific, belonging to genera and families that are not known from the Caribbean, such as four coral-eating *Drupella* species (Muricidae: Ergalataxinae; Claremont et al. 2011), the nudibranch genus *Phestilla*, with five species (Ritson-Williams et al. 2003), and 17 corallivorous wentletrap snails of the family Epitoniidae (Gittenberger and Gittenberger 2005). For a better

understanding of the damage inflicted by corallivorous snails, information on their choice of prey is needed, which can be inferred from the host corals on which they have been found. Many known studies have investigated the diet of *Drupella* snails associated with Indo-Pacific scleractinians (Boucher 1986; Turner 1994; Cumming 1999; Morton et al. 2002; Shafir et al. 2008; Schoepf et al. 2010; Al-Horani et al. 2011; Hoeksema et al. 2013; Moerland et al. 2016) and *Cyphoma* snails (Ovulidae: Simniinae) associated with Caribbean octocorals (Lasker and Coffroth 1988; Lasker et al. 1988; Chiappone et al. 2003; Burkepile and Hay 2007; Reijnen et al. 2010; Schärer and Nemeth 2010; Lucas et al. 2014). Snails of those genera appear to be generalists regarding their choice of host, which is in part dependent on variable host availability (Lasker and Coffroth 1988; Moerland et al. 2016). Based on a number of local studies, shallow-water *Coralliophila* spp. in the Indo-Pacific appear to be predominantly associated with *Porites* corals (Fujioka and Yamazato 1983; Schuhmacher 1993; Al-Moghrabi 1997; Oren et al. 1998; Chen et al. 2004; Raymundo et al. 2016), whereas *Coralliophila* snails in the Caribbean have been recorded from a wide range of host corals (Van Benthem Jutting 1927; Miller 1981; Del Monaco et al. 2010; Williams et al. 2014; Potkamp 2016).

These predatory snails are the subject of the present research and concern the two most commonly recorded *Coralliophila* species in the Caribbean (Miller 1981; Del Monaco et al. 2010; Potkamp 2016), i.e., *C. caribaea* Abbott 1958, and *C. galea* (Dillwyn, 1823). The latter has typically been misidentified as *C. abbreviata* (Lamarck, 1816) in the literature (Netchy et al. 2016; Potkamp 2016). Morphological descriptions of Caribbean *Coralliophila* species are given by Abbott (1958), Wells and Lalli (1977), and Potkamp (2016).

The impact of *C. galea* on coral assemblages was long thought to be minimal (Ott and Lewis 1972), but the effect of this snail on reef communities can be profound, and played a major role in the collapse of *Acropora cervicornis* (Lamarck, 1801) in Jamaica in 1980 after hurricane Allen (Knowlton et al. 1981, 1988, 1990; Hayes 1990a). Removal of life tissue by the snails is usually followed by algal colonization of the exposed skeleton, and such wounds appear to be difficult to heal (Brawley and Adey 1982). The host-related differences in population structure, metabolism and genetic structure of *C. galea* are well studied (Baums et al. 2003a, b; Johnston and Miller 2006; Johnston et al. 2012), but only a few studies deal with the distribution patterns of *C. galea* over various hosts or its prey preferences (Miller 1981; Rylaarsdam 1983; Hayes 1990a, b; Bruckner et al. 1997).

In the present study, the distribution of *Coralliophila* spp. over two abundant host corals, *Orbicella annularis* (Ellis and Solander, 1786) and *Pseudodiploria strigosa* (Dana, 1846), is investigated to examine how host colony size affects the distribution of snails and how these patterns vary over the studied hosts. In particular, *O. annularis* is well known as a common host for *Coralliophila* spp. (Wells and Lalli 1977; Miller 1981; Del Monaco et al. 2010). At Curaçao, it was the most common host coral species, whereas *P. strigosa* ranked second (Potkamp 2016). The elkhorn coral, *Acropora palmata* (Lamarck, 1816), is known as a common prey of *Coralliophila* snails (Baums et al. 2003a; Miller 2001; Johnston et al. 2012; Bright et al. 2016). However, its abundance in Curaçao has strongly declined over the last decades (Chamberland et al. 2015), which made it unsuitable as possible host in the present study. The present study also investigates the relation between host and snail shell size, as has been reported in previous studies on other host coral species (Bruckner et al. 1997; Baums et al. 2003a; Johnston and Miller 2006).

Material and methods

Surveys for this study were conducted 12–16 March 2015 during scuba diving on the reef at the Waterfactory (N12°06′, W068°57′), at the leeward side of the island of Curaçao, southern Caribbean. The distribution of *Coralliophila* spp. on *Orbicella annularis* was assessed at depths of 5 m and 10 m (±1 m) and on *Pseudodiploria strigosa* at a depth of 5 m (±1 m). An assessment of *P. strigosa* at 10 m was not feasible due to the low abundance of this coral species at this depth. The first 50 colonies of the host coral species encountered within the targeted depth range were examined for the number of associated snails. In the case of *P. strigosa*, a colony was defined as one spherical structure (Fig. 1a; Humann and DeLoach 2013: 140–141). For *O. annularis*, one colony was defined as a cluster of smaller columns that were still connected to one another at the base (Fig. 1b; Humann and DeLoach 2013: 128–129). The exact length and width of each of these three transects depended on the density of the targeted host species and the steepness of the reef slope.

The height and circumference of each coral colony were measured, the exact depth was noted, and colonies were photographed to prevent duplicate sampling from the same coral colonies. If present, all snails from the colony were collected in a single sampling bag per colony. At the end of each day of sampling, snails were stored in 70 % ethanol. Two *Coralliophila* species were encountered, *C. galea* and *C. caribaea*, which could be distinguished by the colour of their operculum (Abbott 1958). Snails were counted per colony. Shell length, defined as the length from the tip of the apex to the tip of the aperture, was measured with digital callipers.

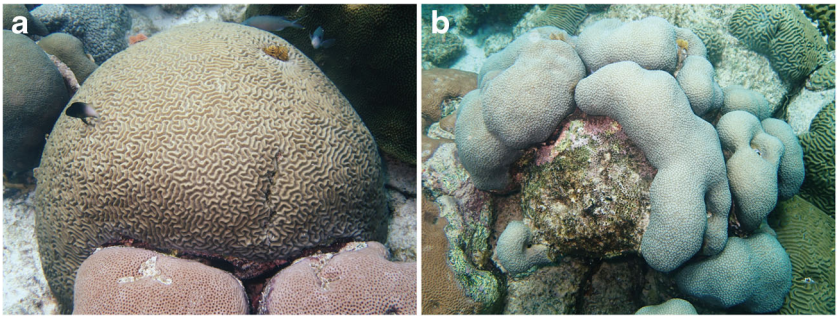

Fig. 1 Examples of corals at Curaçao used in the present study. **a** *Pseudodiploria strigosa* representing a spherical colony shape. **b** *Orbicella annularis* consisting of lobes and columns

Statistics

Distributions of snails on host colonies were compared to calculate random distributions, in which all colonies have an equal chance of being colonized by snails. To calculate a random distribution, the total number of snails found on each host species (*O. annularis*, $n = 197$; *P. strigosa*, $n = 32$) was randomly distributed 100 times over the number of searched colonies (*O. annularis*, $n = 100$; *P. strigosa*, $n = 50$). Colonies were ordinally ranked based on the number of associated snails for each separate host species, where ranking number 1 was assigned to the colony with the most associated snails. The calculated distributions were averaged to obtain a random distribution per host species. Both the observed and calculated random distributions of snails were fitted against the following equation:

$$n = a \times e^{-r \times b}$$

where n is the number of snails per colony, and r is the rank of a colony based on the number of associated snails. For both species, the random distribution was compared to the observed distribution by comparing the performance of a pooled model, where parameter values were estimated for a combined data set of both the observed and random distribution, vs. a separate model where the parameter values were estimated separately for the observed and random distributions. Both models were compared using analysis of variance (ANOVA). If the difference between the random and observed distribution was significant, parameter values were compared using Welch's t test.

Differences in the colonization frequency of snails (presence or absence) were tested using Fisher's exact test. For pairwise post hoc comparisons, p values were adjusted using a Bonferroni correction to reduce the chances of obtaining false-positive results. Colonies were arbitrarily divided into three size classes based on their circumference. Colony height was not used, as a relatively strong positive relation was found between height and circumference for both host species (*O. annularis*: $R^2 = 0.65$; $p < 0.0001$; *P. strigosa*: $R^2 = 0.49$; $p < 0.0001$). *Orbicella annularis* corals with a circumference ≤ 35 cm were classified as small ($n = 33$), with a circumference > 35 cm and ≤ 70 cm as medium ($n = 34$), and circumference > 70 cm as large ($n = 33$). *Pseudodiploria strigosa* corals with a circumference ≤ 70 cm were classified as small ($n = 16$), with a circumference > 70 cm and ≤ 120 cm as medium ($n = 16$), and a circumference > 120 cm as large ($n = 18$). Poisson regressions based on quasi-likelihood models were used to model snail counts as a function of colony circumference. Analysis of covariance (ANCOVA) models were constructed to test for differences in shell length. For these, only the shells of *C. galea* were used.

Results

A total of 229 snails were found on 38 of 150 searched colonies (Table 1). Of these 229 snails, eight individuals were lost during collection. All snails were identified as *C. galea*, with the exception of one snail on a colony of *P. strigosa*, which was identified as *C. caribaea*. No colony was found with both *C. galea* and *C. caribaea*. Snails usually occurred in clusters of ca. 5–10 individuals at the edge of living coral tissue, on *O. annularis* mostly between the columns making up the colony (Fig. 2).

For both *O. annularis* and *P. strigosa*, the observed distribution of *Coralliophila* snails differed from a random distribution ($F = 2644.2$; $p < 0.0001$ and $F = 72.0$; $p < 0.0001$, respectively). Both parameters a and b were

Table 1 Numbers of coral colonies of *Pseudodiploria strigosa* (5 m depth) and *Orbicella annularis* (5 and 10 m depth) with snails and the total numbers of *Coralliophila galea* and *C. caribaea* individuals found per transect

	P. strigosa	*O. annularis*	
Depth (m)	5	5	10
Number of colonies	50	50	50
Colonies with snails	10	24	4
C. galea	31	190	7
C. caribaea	1	0	0

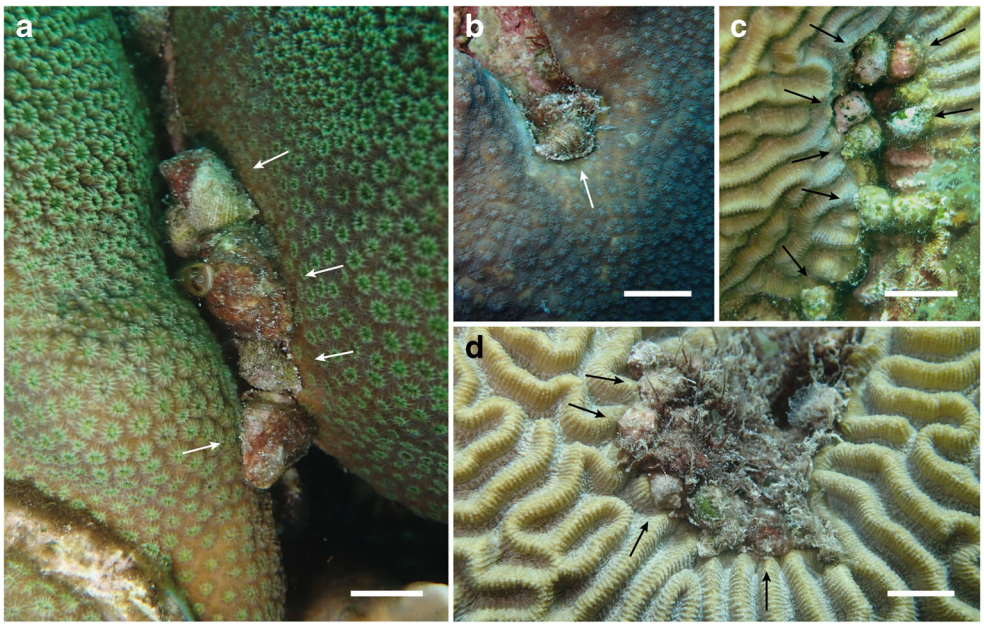

Fig. 2 **a** Cluster of *Coralliophila galea* snails wedged in between two columns of an *Orbicella annularis* colony. **b** A few *C. galea* individuals in a crevice on the surface of an *O. annularis* colony. **c**, **d** Clusters of *C. galea* inside crevices of *Pseudodiploria strigosa* colonies. *Scale bars*: ~ 1 cm

significantly different in the observed distribution compared to the random distribution in both *O. annularis* ($t = 67.4$; $p < 0.0001$ and $t = 51.3$; $p < 0.0001$, respectively) and in *P. strigosa* ($t = 11.2$; $p < 0.0001$ and $t = 7.8$; $p < 0.0001$, respectively [Table 2]). A higher proportion of snails was associated with only a small proportion of colonies (i.e., parameter *a* is higher in the model of the observed distribution compared to the random distribution): for *O. annularis*, 54 % of collected snails were found on only 5 % of searched colonies; for *P. strigosa*, 63 % of collected snails were found on 8 % of searched colonies (observed distribution in Fig. 3). A higher proportion of colonies had no greater number of associated snails than would be expected at random. This also follows from the higher parameter *b* in the model of the observed compared to the random distribution (Table 2; Fig. 3) and indicates that the snails show a clumped rather than random distribution over the available colonies.

The proportion of coral colonies with snails differed significantly among the three transects ($p < 0.0001$; Fig. 4). *O. annularis* at 5-m depth had the highest proportion of snail-colonized colonies, with 24 of 50 colonies observed with snails, which is significantly more than both *O. annularis* at 10 m (4 of 50 colonies with snails, $p < 0.0001$) and *P. strigosa* at 5 m (10 of 50 colonies with snails, $p = 0.017$).

Colony size might be a factor in explaining the observed differences in proportion of snail-colonized colonies. Colony circumference differed significantly between *O. annularis* at 10 m and *O. annularis* at 5 m ($F = 14.9$; $p = 0.0002$, circumference transformed with a natural logarithm to achieve normality and homogeneity of variance; Fig. 5). With all transects pooled, there were indeed significant differences between colony size classes in the proportion of colonies with snails ($p = 0.0004$). Small colonies had significantly fewer snails associated with them than either medium ($p = 0.049$) or large colonies ($p = 0.0003$). However, when considering different host species and depth on their own, this trend is only significant in colonies of *Orbicella annularis* at 5 m ($p = 0.001$). Here again, a higher proportion of small colonies were found with snails than on medium ($p = 0.028$) or large colonies ($p = 0.001$; Fig. 6b). Differences in proportion of colonies with snails between different colonies size classes were not significant in either *O. annularis* at 10 m or *P. strigosa* at 5 m ($p = 0.346$ and $p = 1.0$, respectively; Fig. 6a, c).

Table 2 Estimated parameter values and standard errors of parameters *a* and *b* of the exponential function fitted to the observed and calculated random distributions of snails on host colonies of *Orbicella annularis* and *Pseudodiploria strigosa*

		Parameter *a*		Parameter *b*	
Host species	Distribution	Estimated	Standard error	Estimated	Standard error
P. strigosa	Observed	7.65	0.37	0.195	0.012
	Random	2.91	0.21	0.082	0.008
O. annularis	Observed	32.37	0.38	0.153	0.002
	Random	5.30	0.14	0.024	0.001

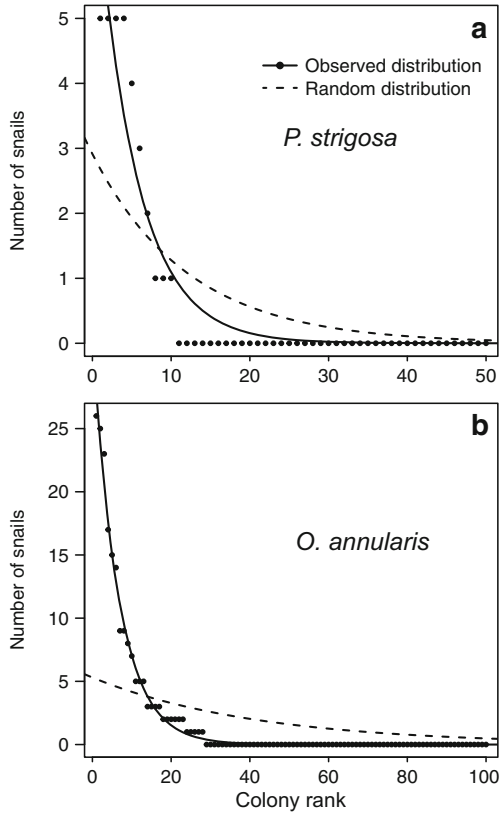

Fig. 3 Comparison of observed distribution with calculated random distribution for snails on *Pseudodiploria strigosa* (**a**) and *Orbicella annularis* (**b**). Individual observations are plotted as *dots*; *curves* represent the fitted models. For estimated parameter values, see Table 2

Colony size might also play a role in the number of snails that can be sustained on a singly colony. On *O. annularis* colonies (both 5-m and 10-m transects pooled), larger colonies sustained significantly more snails than smaller colonies ($p < 0.0001$; Fig. 7a). No significant relation was found between *P. strigosa* colony size and number of snails on a single colony ($p = 0.288$; Fig. 7b), which implies that larger colonies

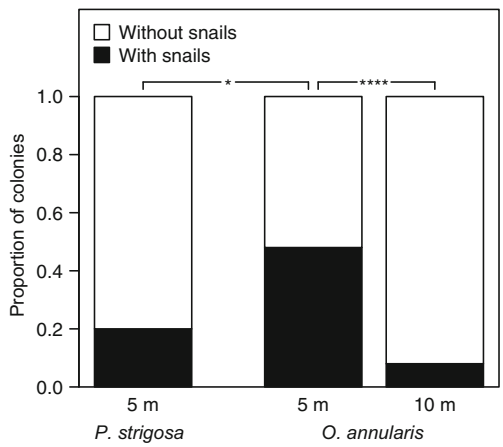

Fig. 4 Proportion of colonized host colonies of *Pseudodiploria strigosa* at a depth of 5 m, and *Orbicella annularis* at depths of 5 and 10 m. Significant differences: *$p < 0.05$; ****$p < 0.0001$

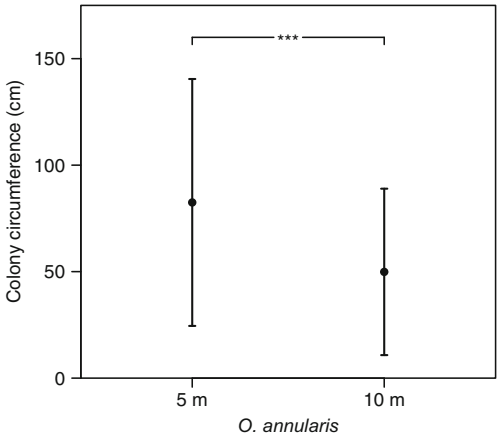

Fig. 5 Mean circumference of all sampled colonies of *Orbicella annularis* at depths of 5 and 10 m. *Error bars* show standard deviations. Significant differences: ***$p < 0.001$

of *P. strigosa* do not have a greater number of snails feeding on them.

The shell length of *C. galea* ranged from 6.2 to 24.6 mm, plus one outlier at 32.2 mm (associated with a colony of *P. strigosa*); the single *C. caribaea* had a shell length of 15.5 mm. Snails associated with *O. annularis* at both depths were pooled, as only a few snails were found on *O. annularis* at 10 m. An ANCOVA model was constructed for *C. galea* shell length, including the following factors: host species, an interaction effect between colony circumference and host species, and an interaction between number of associated snails per colony and host species (neither the colony circumference nor number of associated snails was included in the model as a single factor on its own, as differences, for example, in colony morphology may not allow for direct comparisons of these factors between host species). Of these factors, only host species contributed significantly to shell length ($F = 5.7$; $p = 0.018$; neither the interaction between number of associated snails and host species ($F = 2.8$; $p = 0.062$) nor the interaction between colony circumference ($F = 0.9$; $p = 0.425$) was significant. However, the one outlier contributed disproportionally to the significance of the host species factor. Without the outlier, host species was no longer significant ($F = 2.7$; $p = 0.105$). Therefore, no differences in shell length could be confidently detected within the data set (Fig. 8).

Discussion

Coralliophila galea was most abundant on both common coral host species, *Orbicella annularis* and *Pseudodiploria strigosa*, whereas *C. caribaea* was represented by only a single specimen on the latter. The same pattern, in which *C. galea* was more common on the same hosts compared to *C. caribaea*, was observed on other reefs along the coast of Curaçao (GP, personal observation), as well as in other

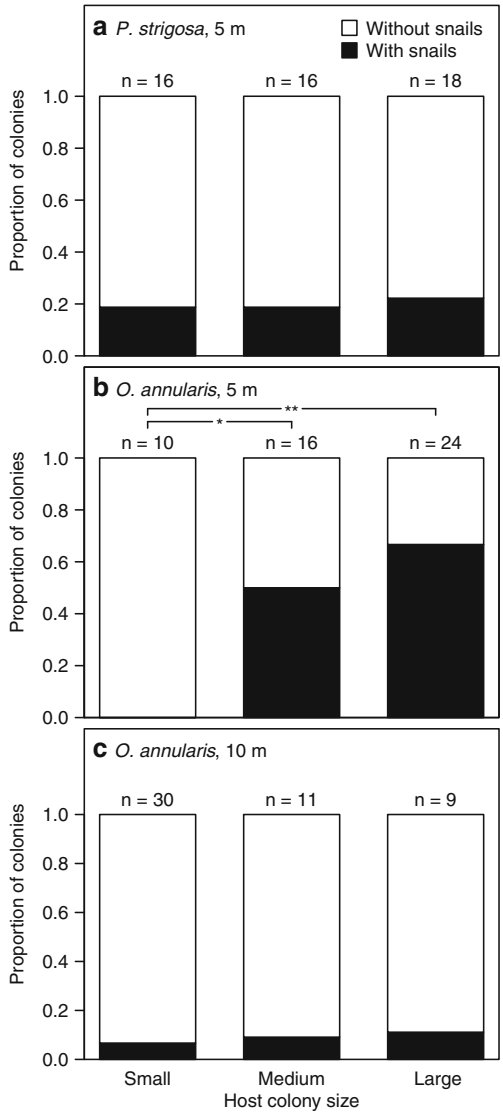

Fig. 6 Proportion of colonized host colonies of *Pseudodiploria strigosa* at a depth of 5 m (**a**) and *Orbicella annularis* at depths of 5 m (**b**) and 10 m (**c**), separated by colony size class. Significant differences: *$p < 0.05$; ****$p < 0.0001$

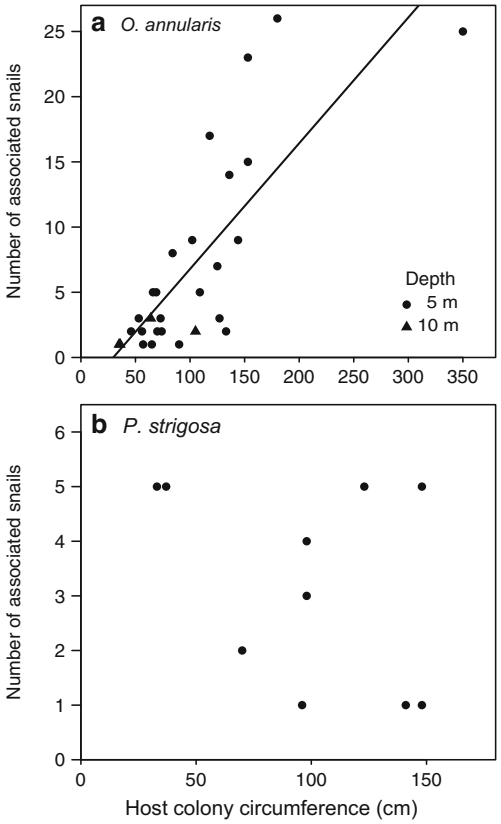

Fig. 7 Relation between the number of snails per host colony and the host colony circumference for both *Orbicella annularis* (**a**) and *Pseudodiploria strigosa* (**b**). Only the regression for *O. annularis* is shown ($p < 0.0001$); the regression for *P. strigosa* was not significant

Caribbean localities (Miller 1981; Del Monaco et al. 2010). Therefore, the predation impact of *C. caribaea* on both *O. annularis* and *P. strigosa* can be considered negligible. There is no indication of competition between the two *Coralliophila* spp. for these two host coral species, and it is unclear how the apparent partitioning in prey selection between the two snail species is maintained (Miller 1981).

In the present study, 25 % of all searched colonies were found to have associated *Coralliophila* snails, whereas a Puerto Rican study reported that 9 % of coral colonies belonging to seven species were observed with snails (Bruckner et al. 1997). The variation in occupancy appears to be host-related, since in Panama, 64 % of *Orbicella* colonies, 13 % of *Agaricia tenuifolia* Dana, 1848, and 10 % of *Acropora cervicornis* were found with snails (Hayes 1990b). The observed difference in *Coralliophila* colonization between *O. annularis* and *P. strigosa* in the present study may depend on the colony morphology of the hosts and on their depth. Corals of both species form massive colonies, but these differ in height and complexity. Among coral colonies of similar circumference, those of *O. annularis* show a lobate shape, with much space between the columns and

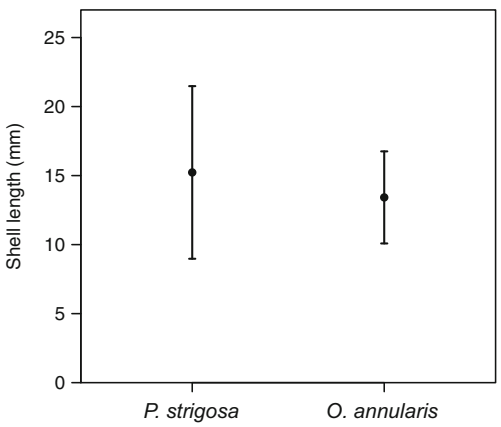

Fig. 8 Shell length of *Coralliophila galea* on *Pseudodiploria strigosa* and *Orbicella annularis*. *Error bars* show the standard deviations

relatively high total surface area, whereas those of *P. strigosa* are more dome-shaped, with less surface area. Lobate and columnar corals possess a relatively long borderline between living and dead coral tissue around the columns where *Coralliophila* snails are usually found. Little information is available regarding the dominant position of *Coralliophila* snails on their hosts, but there appears to be a preference for the fringes around the base of coral colonies (Miller 1981), while the present study and various others (Ward 1965; Ott and Lewis 1972) point to the boundary between dead and live coral tissue.

The distribution of snails was not random over the available hosts colonies for either of the studied host species. The number of snails per host was positively related to host coral size, which is consistent with research on corallivorous *Drupella* snails in the Indo-Pacific (Cumming 2009; Schoepf et al. 2010; Moerland et al. 2016). Intuitively, larger host colonies (with increasing age) have more likely become colonized by snails over time than smaller and younger host colonies, and also offer more available space for larger snail aggregations.

The extent to which snails are able to actively choose their prey is an important factor when considering distribution patterns. Experiments by Rylaarsdam (1983) and Hayes (1990a) showed that adult snails may have some preference for certain host species. Additionally, microcosm experiments showed that snails, after being displaced from colonies of *A. palmata*, returned to colonies of the same species, ignoring colonies of other host species (Brawley and Adey 1982). These findings suggest that snails are able to actively select their host colony, at least during the adult stage. No data are available on whether active selection of prey is already present during the larval stage or during egg deposition as seen in parasitic snails of the family Epitoniidae (Gittenberger and Hoeksema 2013) and corallivorous snails of the genera *Pseudosimnia* (Priori et al. 2015) and *Drupella* (Sam et al. 2016).

Differences in predation pressure may also explain variation in the number of snails per host species. Snails on colonies with a dome shape (*P. strigosa*) may be more exposed to attacks from their own predators than those in between the columns of a lobate coral colony (*O. annularis*), which may offer shelter (Fig. 2a). Unfortunately, information on predators feeding on *Coralliophila* spp. is limited to anecdotal evidence. Possible predators of *C. galea* include a snapping shrimp, a carnivorous snail, the Caribbean spiny lobster, puffer fish, hogfish, filefish and octopuses (Goldberg 1971; Baums et al. 2003a; Sharp and Delgado 2015).

No connections were observed between shell length and snail group size or host colony circumference. Such a connection might indicate the existence of intraspecific competition between snails, as larger groups of snails or snails on smaller colonies might have less food. A negative correlation between body size and population size is well known in land snails (e.g., Williamson et al. 1976; Cameron and Carter 1979). Host-specific size clustering of *Coralliophila galea* has been observed for different host species (Hayes 1990b; Bruckner et al. 1997; Baums et al. 2003a; Johnston and Miller 2006). However, no significant differences in shell length were found between snails associated with *O. annularis* and *P. strigosa*. In the present study, the sample sizes of colonies with specific size classes were unbalanced for the two *O. annularis* transects (Fig. 6). As this may affect the power of the statistical tests, future studies investigating the effect of host colony size on snail distribution, specifically sampling certain colony size classes, could overcome this problem, and may help provide a better understanding of the relationship between these two variables.

Most previous research on corallivorous gastropods on Caribbean reefs have focused on a few hosts such as *Acropora* spp. and *Orbicella* spp. (Miller 2001; Baums et al. 2003a, b; Johnston and Miller 2006; Bright et al. 2016), or have grouped many host species together (Bruckner et al. 1997). However, the host range on which Caribbean *Coralliophila* spp. can be found is large, spanning multiple orders within the class Anthozoa (Miller 1981). The present results indicate that patterns of distribution differ between two host coral species, and therefore that patterns found for one host species cannot be extrapolated to a whole reef coral assemblage.

To better understand how corallivory by *Coralliophila* spp. affects Caribbean coral faunas, it will be important for future surveys to cover a wide range of host species, including less common ones. It is also relevant to include the second most common *Coralliophila* species in the Caribbean, i.e., *C. caribaea*. The effect of *C. caribaea* on *O. annularis* and *P. strigosa* was negligible in the present study, but *C. caribaea* is common, for example, on *Porites* spp. and various octocoral species (Miller 1981; Del Monaco et al. 2010). Octocorals are an important part of Caribbean reef communities (Sánchez et al. 1998; Abeytia et al. 2013; Velásquez and Sánchez 2015; Edmunds et al. 2016). Future research on *Coralliophila* spp. as predators should therefore also focus more on octocorals as prey, which will provide a more comprehensive understanding of the impact of corallivory on coral assemblages.

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