

Article

Resource Partitioning by Corallivorous Snails on Bonaire (Southern Caribbean)

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Abstract: A biodiversity survey on three corallivorous snails (Mollusca: Gastropoda) was performed at 28 sites around the island of Bonaire to assess their distribution patterns and associated host corals. The snails and their hosts were identified and counted in three depth zones: 5–10, 10–20, and 20–30 m. The snails were *Coralliophila galea* and *C. salebroza* (Muricidae: Coralliophilinae), and *Cyphoma gibbosum* (Ovulidae: Simniinae). All three species were widespread around the island without apparent interspecific geographical variation. *Coralliophila galea* was found exclusively on scleractinian corals, *Coralliophila salebroza* almost exclusively on octocorals, and *Cyphoma gibbosum* only on octocorals. *Coralliophila salebroza* showed more dietary overlap with *Cyphoma gibbosum* than with *Coralliophila galea*. *Coralliophila galea* was the most commonly encountered species with the largest number of host species. Owing to its hosts distribution, this species also showed a greater maximum depth and a wider bathymetrical range than the other two snails. The other two snails were shallower and their depth ranges did not differ significantly. Host-coral size did not seem to have influence on the number of snails per host. Coral damage caused by the snails was visible but appeared to be low, causing no mortality in Bonaire, which suggests that the relation with their hosts is more parasitic than predatory. Because these three corallivores have occasionally been reported to occur as outbreaks in other Caribbean localities and may act as vectors in the dispersal of coral diseases, it is recommended that future studies should focus on their population dynamics.



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Keywords: *Coralliophila*; *Cyphoma*; Gastropoda; bipartite network; corals; corallivory; niche

1. Introduction

Coral reefs in the Atlantic, including those in the Caribbean Sea and the Gulf of Mexico, are relatively poor in species compared to those in the Indo-West Pacific [1,2]. This is also evident for corals. For example, the number of ca. 75 Atlantic scleractinian reef coral species is only 10% of the much larger number of ca. 750 Indo-Pacific species [3]. For various other groups of reef-dwelling corals, such as octocorals, similar comparisons are more difficult to make because of insufficient taxonomic knowledge and lack of biogeographic review studies.

Reef corals are host to many other groups of invertebrates, among which various species of gastropod molluscs [4,5]. Most of these snails are host-specific to a certain degree, either as corallivorous parasites or as predators [6]. In daylight, they can be observed roaming on the coral surface [7–9], hiding underneath their host corals [10,11], inside coral crevices [12,13], in between coral branches [14,15], or on the outer surface of branches by use of camouflage [16,17]. They belong to a number of families, such as Epitoniidae [18], Muricidae [19–21], Pediculariidae [22–24], Ovulidae [23,25,26], and Trinchysiidae [27–30]. Some other coral-associated gastropods live entirely or partly embedded in the coral skeleton, such as the *Leptoconchus* species of the family Muricidae [31,32]) and worm snails of the family Vermetidae [33,34].

Corallivorous snails have a reputation for causing damage to coral reefs [35–37] and have the potential to form aggregations that can manifest themselves as outbreaks [38–44]. The snails are also known to spread infectious coral diseases [45–49]. Therefore, monitoring of their abundance could be relevant during surveys of coral reef health, especially in tropical marine protected areas (MPAs).

A well-known example of such an MPA is Bonaire National Marine Park in the southern Caribbean (12°9' N, 68°16' W), which was established in 1979 and is important for the local diving industry [50]. Although Bonaire is known to harbor one of the best preserved coral reef ecosystems in the Caribbean Sea [51], the island itself is undergoing much urban development and its reefs are therefore under much anthropogenic stress [52–55].

Relatively few studies on Bonaire have a focus on its marine biodiversity and the role of coral-associated fauna therein. Therefore, an expedition was organized in 2019 to survey its coral reef biota [56]. Special attention was given to the role of interspecific relationships in benthic communities, mostly involving cnidarians that live in association with other invertebrates. This resulted in the discovery of various novel associations [34,57–64], two of which appeared to be harmful to corals. One of these two was about symbiotic worm snails and the other one about sabellid worms that lived partly embedded in the coral skeletons [34,60]. Here, we report on the abundance and co-occurrences of corallivorous snails because of the possible damage they may cause to their coral prey.

The most common corallivorous snails in the Caribbean are species of the genera *Coralliophila* (Muricidae) and *Cyphoma* (Ovulidae) [65]. These snails usually stay on the same coral that they eat and can be found on the outer surface of coral branches, underneath coral margins, and inside crevasses of massive corals [12,36,66,67]. There are a few records of *Coralliophila* aggregations that consume large portions of the host-coral's soft tissue [36,68]. In total, eight valid *Coralliophila* species are known to occur in the Caribbean [68], of which *C. galea* (previously also recorded as *C. abbreviata*) and *C. salebrosa* (previously recorded as *C. caribea*) [12,68], are most commonly recorded. *Coralliophila* species show weak genetic diversity between hosts, and there are some clear differences in shell morphology for specimens living on different hosts [12,69–71]. *Coralliophila* species feed with the help of a proboscis, which is inserted into the oral opening of coral polyps [72,73]. Many *Coralliophila* species are sessile for long periods of time, feeding off nearby corals without destroying the host-coral tissue [73,74].

Currently, 15 *Cyphoma* species are recognised in the Caribbean, of which *Cyphoma gibbosum* is by far the most common [23,75]. They are vividly coloured molluscs with different patterns on their mantle, which is key to their identification [26,75,76]. It is typically coloured light brown, with black ring-shaped markings. The number and size of these marks are variable, and occasionally different marks develop. The species is active during the day and snails are often seen foraging by SCUBA divers. *Cyphoma gibbosum* has been found to consume octocoral species of the families Gorgoniidae, Plexauridae, Briareidae, and, occasionally, Anthothelidae [7,26,77–79].

Since most *Coralliophila* and *Cyphoma* species are considered host generalists, the present study aims to study (1) which corallivorous snails are present on Bonaire, (2) how they differ in geographical and bathymetrical distributions, (3) and what are their host ranges and overlaps therein. Eventually, the results may show which coral taxa are potentially most in danger in the event of outbreaks.

2. Materials and Methods

Data collection. The field survey on Bonaire was performed between the 23rd of October and the 8th of November, 2019. Distribution data on *Coralliophila* and *Cyphoma* was collected during SCUBA diving in daytime at 28 different locations (one dive each) around the island (ESM Figure S1, Table S1). Most localities were at the leeward site of the island, where wave action is less strong than at the windward side. The roving diving (timed-swim) technique was employed based on fixed periods of observations [80]. One extra night dive was performed to study the foraging behaviour of the snails, which was not part of the

regular survey. During each dive, 20 min were spent per depth zone (5–10, 10–20, and 20–30 m) to record coral-snail associations by visual inspection. Whenever snails were found on a hard coral (Scleractinia), the number of individuals was counted visually and also determined by manually touching the host along and below its edges. Octocorals were only visually scanned for snails. Notes were made of the number of snail individuals, their identity, depth, host-coral identity, host-coral size, and presence/absence of apparent host-coral damage (visible as grazing wounds). The coral length was measured using a measuring tape. Notes were written on a home-made PVC slate and entered in the database after each dive. Pictures were taken of the snails and their hosts for the conformation of their identity. The camera was an Olympus tough TG5, with an underwater housing.

Specimen identification. *Coralliophila* species were identified based on the work by Potkamp et al. [12], who found three reef-dwelling species at the adjacent island of Curaçao. *Coralliophila galea* and *C. salebroso* can be distinguished based on the colouration of their shell aperture and operculum. *Coralliophila galea* has an orange-white shell aperture and orange operculum and *C. salebroso* has a purple-white shell aperture and a red-brown operculum (Figure 1a,b). *Coralliophila curacaoensis* is smaller and its shell is more angular than the other species; the colour of its operculum is intermediate between that of *C. galea* and *C. salebroso* [12]. For the identification of *Cyphoma* snails (Figure 1c), the work by Lorenz [76] was used, which differentiated between various colour morphs despite the apparent genetic heterogeneity, because in previous studies, different *Cyphoma* colour morphs showed variation in coral associations [76,81]. The coral identifications were carried out with the help of two publications: a printed field guide [82] and an online source that was published as electronic supplementary material [83]. Octocoral identification is often tedious and requires microscopic examination of skeletal sclerites [84]. Because the aim of this research was to find as many gastropod-coral associations as possible, we recorded octocoral hosts at species level when they could be easily identified in the field and otherwise at genus level.

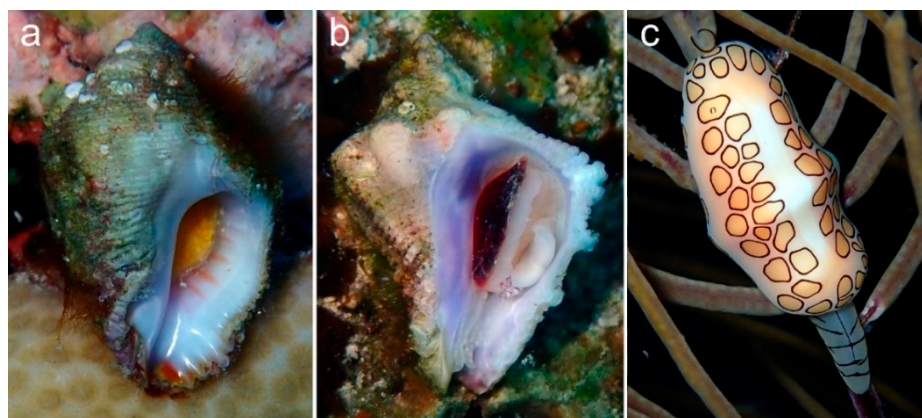


Figure 1. The three corallivorous snails encountered on Bonaire: (a) *Coralliophila galea*; (b) *Coralliophila salebroso*; (c) *Cyphoma gibbosum*.

Analysis. The results were analysed in R version 3.6.2 and 4.2.1 [85]. Differences in bathymetrical distributions were examined using ANOVA. A linear model was used to correlate coral sizes with the number of snail individuals found on a coral.

Bipartite network. For the snail–coral interactions, a bipartite network was composed using the R-package *bipartite* [86,87]. This network allows for comparisons between interacting species and is often used for interactions between predators and prey species [88,89]. The H_2' -factor was calculated with the function *H2fun* [90]. This value is an index of entropy, where 0 means that there is no specialization and interactions are completely random and 1 means that all species in a system are specialized. Non-randomness was tested with the function *wine*, which estimates the weighted interaction nestedness of a dataset.

Principle component analyses. Principle component analyses were performed using the numerical data collected with each observation: locality coordinates, depth, number of snails, and coral size. The analysis was done once to interspecifically compare the snail species, and again for every recorded snail species to compare associated coral species. A generalised mixed model (GLM) was then used to assess the significance of individual predictors in the dataset; the GLM used was a negative binomial GLM to avoid over-dispersion. This analysis was performed using the *glm.nb* function from the package “MASS” in R. The data were log-transposed.

GIS. The maps in this report were generated using ArcMap 10.5.1. For the distribution maps displaying snail abundance per site, a light grey map provided by Esri was used as a base layer. Total abundance of each species was displayed for each dive site. For the map displaying the dive sites, a world topographical map, also provided by Esri, was used (ESM Figure S1).

3. Results

Coralliophila snails were generally immobile on dead patches of coral along the edges of the host-coral colonies. During the day, only a few were found on top of living coral but these were not foraging. Foraging behaviour was only observed once, during a night dive that was not part of the regular survey. *Cyphoma gibbosum* was seen to be actively foraging in day light.

In total, 689 corallivorous gastropods were recorded, representing two *Coralliophila* species, *C. galea* and *C. salebrosa* (Figure 1a,b). A single *Coralliophila* specimen could not be identified. Only one *Cyphoma* species was represented, i.e., *Cyphoma gibbosum* (Figure 1c).

No *Coralliophila* grazing scars were found. Patches of dead coral were present in the crevices where the snails were settled but these were not new. *Cyphoma gibbosum* snails were usually found on wounds of a few centimetres long on octocoral branches where soft tissue was damaged or had disappeared. There are no quantitative data for this.

There was no indication of dissimilarity among the three species with regard to geographical distribution (Figure 2a–c). The southernmost locality, Red Slave (Bon.27), was the only site without *Coralliophila* records, but the nearest dive sites, Bon.07 and Bon.17, yielded 19 and 56 snails, respectively, with all three species represented (Figure 2a–c).

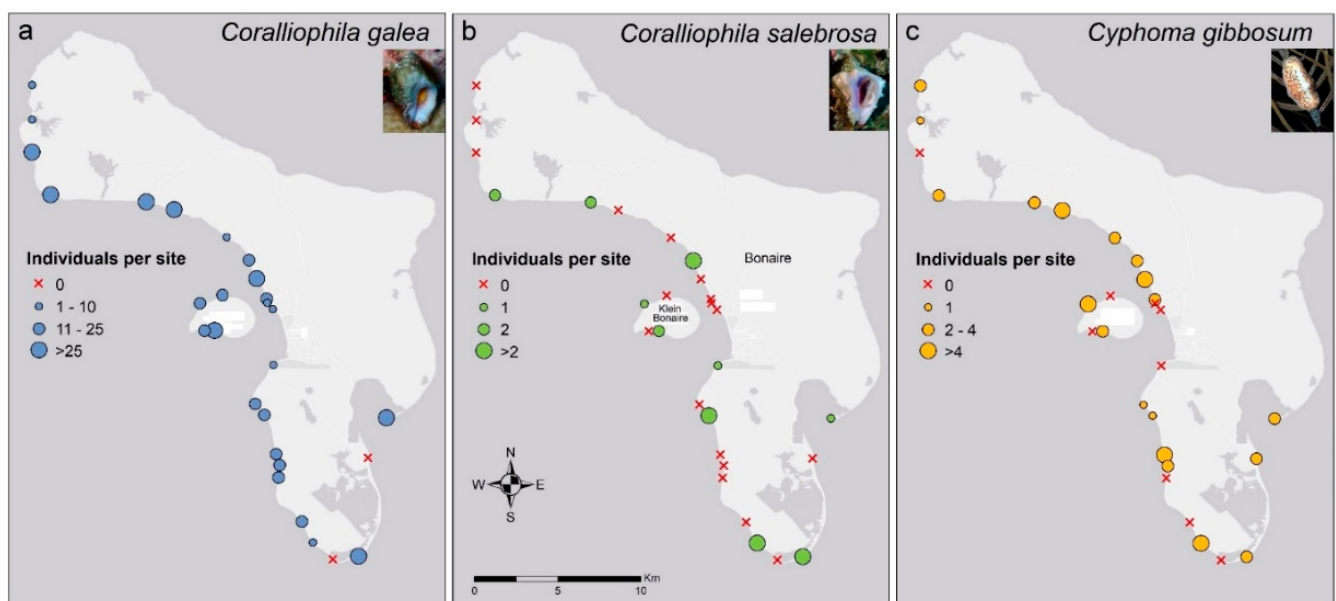


Figure 2. Distribution of three corallivorous snail species at 28 localities around Bonaire.

Coralliophila galea was the most commonly observed species, represented by 575 individuals on 101 scleractinian host corals at 26 out of 28 localities. Up to 36 snails

were encountered on a single coral. *Coralliophila salebroso* was rarer with 34 snails on 16 host corals (predominantly octocorals) at 10 localities. The highest number of snails on a single host was four. *Cyphoma gibbosum* was found exclusively on octocorals—79 individuals on 40 host corals at 20 localities. The highest number of individuals on a single coral was eight. As host corals, 10 scleractinian species, five octocoral species, and three octocoral genera were recorded (Table 1).

Table 1. Host corals of corallivorous gastropods on Bonaire. The total number of associated snails is shown with the number of host corals in brackets. *Coralliophila* sp. is an unidentified snail.

Host Coral Taxa	Snail Species			
	<i>Coralliophila galea</i>	<i>Coralliophila salebroso</i>	<i>Coralliophila</i> sp.	<i>Cyphoma gibbosum</i>
Scleractinia				
Acroporidae				
<i>Acropora palmata</i>	6 (1)			
Agariciidae				
<i>Agaricia agaricites</i>	14 (10)			
<i>Agaricia humilis</i>	1 (1)			
<i>Agaricia lamarcki</i>	2 (2)			
Meandrinidae				
<i>Eusmilia fastigiata</i>			1 (1)	
Merulinidae				
<i>Orbicella annularis</i>	500 (70)			
<i>Orbicella franksi</i>	18 (7)			
Montastraeidae				
<i>Montastraea cavernosa</i>	1 (1)			
Mussidae				
<i>Pseudodiploria strigosa</i>	9 (1)			
Pocilloporidae				
<i>Madracis auretenra</i>	24 (8)	1 (1)		
Octocorallia				
Gorgoniidae				
<i>Antillogorgia bipinnata</i>				12 (7)
<i>Antillogorgia</i> sp.		3 (1)		6 (4)
<i>Gorgonia ventalina</i>		3 (2)		3 (2)
Plexauridae				
<i>Eunicea flexuosa</i>				5 (3)
<i>Eunicea fusca</i>				2 (1)
<i>Eunicea</i> sp.		4 (3)		13 (6)
<i>Plexaura homomalla</i>		6 (2)		14 (4)
<i>Pseudoplexaura</i> sp.		17 (7)		24 (13)

A bipartite network visualised interactions between snails and their host corals with possible overlapping (Figure 3). The H_2' -value is the measurement of entropy, where a value of 0 implies no specialization and 1 implies extreme specialization [90]. With all coral and snail species, $H_2' = 0.833$, and for only the octocorals $H_2' = 0.123$. The model shows statistically dissimilar food utilisations on the analysed coral selection ($p < 0.01$).

Coralliophila galea was found in association with nine scleractinian coral species. It was most common on *Orbicella annularis*, represented by 85% records. *Madracis auretenra*, *Orbicella franksi*, and *Agaricia agaricites* were the only other host species with more than 10 *C. galea* records (Table 1). *Coralliophila salebroso* was almost exclusively found on octocorals. Only one individual was found on a scleractinian coral, *Madracis auretenra*. The recorded host species for *Cyphoma gibbosum* are all in the octocoral families Gorgoniidae and Plexauridae (Table 1). The diversity of octocoral hosts was higher than that of *Coralliophila salebroso*. It seemed to be absent at localities near Kralendijk, the only town on Bonaire. *Antillogorgia bipinnata*, which was common on Bonaire, was commonly found to host *Cyphoma gibbosum*, but not *Coralliophila salebroso*.

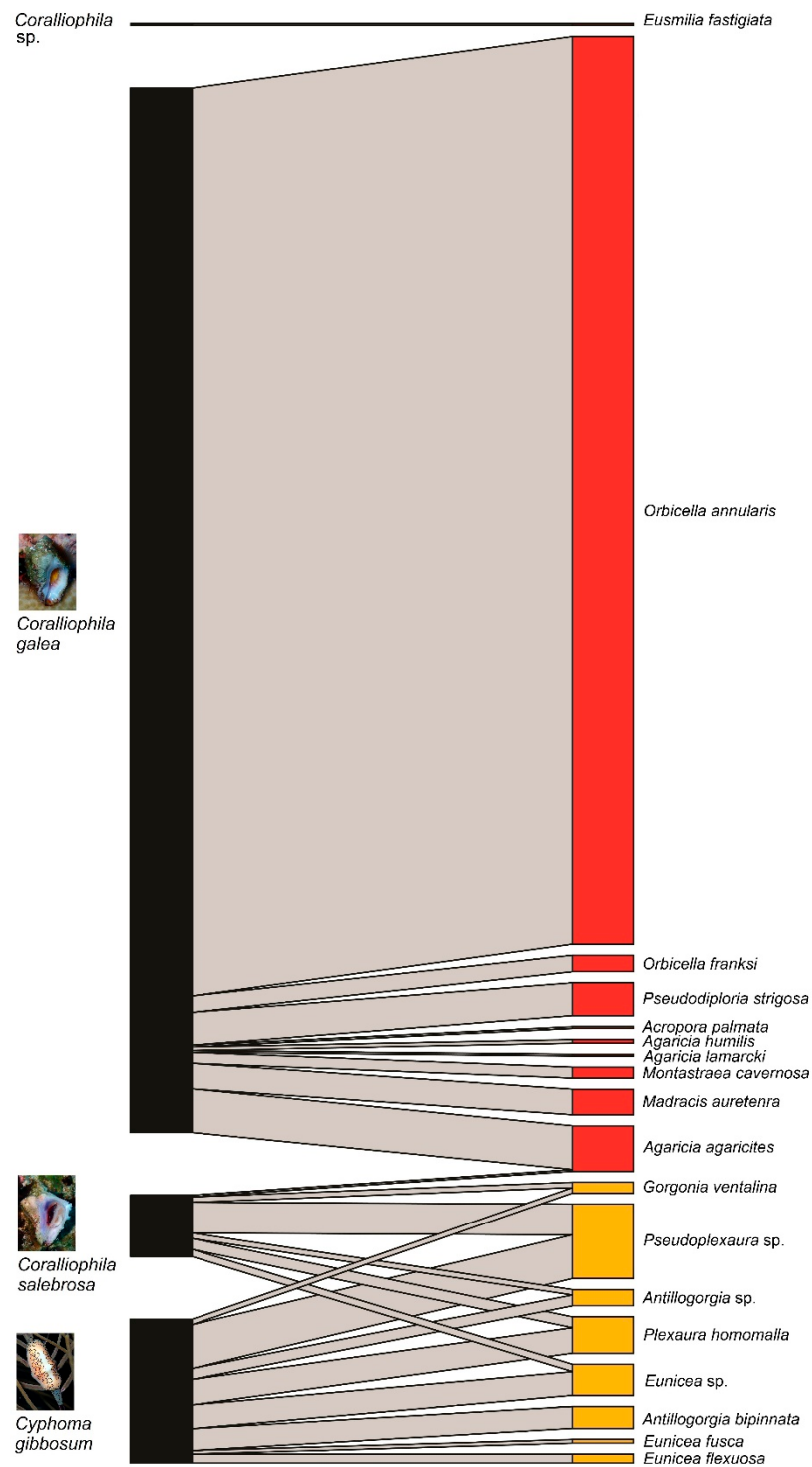


Figure 3. Bipartite network showing the associations between predator species (left side) and the host-coral species (right side: red = scleractinians; yellow = octocorals). The width of the grey lines represents the number of snails found per association. *Coralliophila* sp. is an unidentified snail.

A principal component analysis (PCA) tested the significance of numerical variables on the observations. The data concerned depth, coral size, number of snails, and locality coordinates (Figure 4). The analysis was done for all snail species together (Figure 4a) and for each separate one (Figure 4b–d). The longitudinal and latitudinal coordinates have opposite correlations, because most localities are on a Northwest/Southeast line (Figure 2). The interspecific comparison does not show obvious ecological differences (Figure 4a). The

generalised mixed model shows that depth is the only significant predictor for the number of snails per observed association ($p < 0.001$; $z = -3.5$).

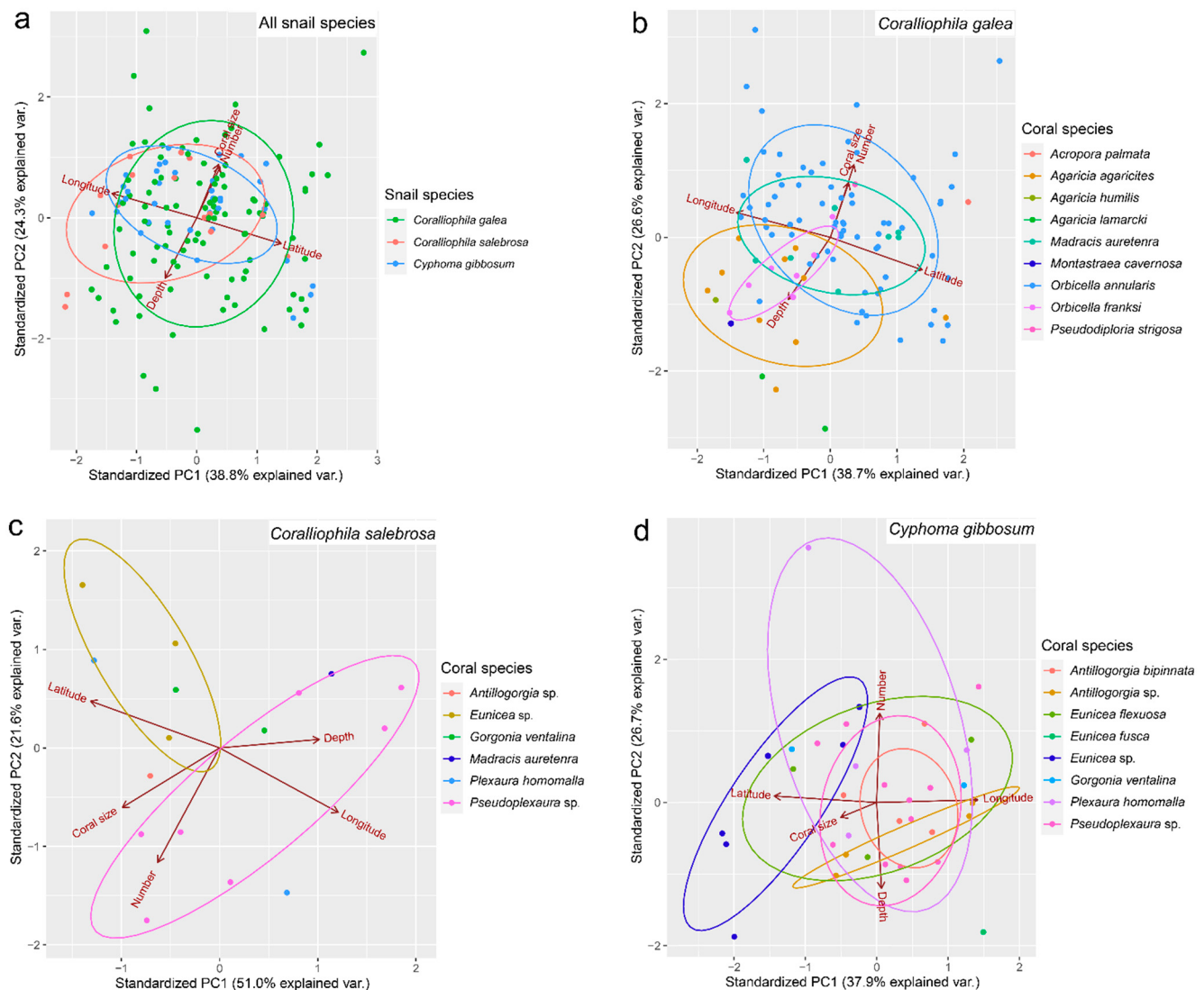


Figure 4. Interspecific relations of corallivorous snails and their host species by PCA. Each data point is an observation. Components: depth, coral size, number of snails, locality coordinates. (a) Snails species and environmental variables; (b–d) Snail species with their host corals.

For *Coralliophila salebrosa* and *Cyphoma gibbosum*, the number of data points is too low to show reliable correlations in the PCA. For *Coralliophila galea*, there seems to be a correlation between the number of snails and the size of the coral, which are negatively correlated with the depth of the observation. The number of snails per coral also seems to be negatively correlated with depth. *Agaricia agaricites* stands out as host with no more than two snail individuals per coral colony. Overall, this host was utilised at greater depths than all hosts together, with an average depth of 15 m.

There was a slight correlation between coral size and the number of snails (Figure 5), but this was not significant (*C. galea*: $R = 0.02$, $F = 2.14$, $p = 0.14$; *C. salebrosa*: $R = 0.08$, $F = 2.27$, $p = 0.15$; *C. gibbosum*: $R = 0.01$, $F = 0.50$, $p = 0.48$). The five observations with the highest number of snail individuals all concern *Coralliophila galea* on *Orbicella annularis* colonies between 60 and 80 cm in width. On average, there were slightly more individuals of *Coralliophila galea* on *Orbicella annularis* compared to the other coral species, but this difference was not significant. Hence, there is no evidence of a relationship between coral size and the number of corallivorous snails.

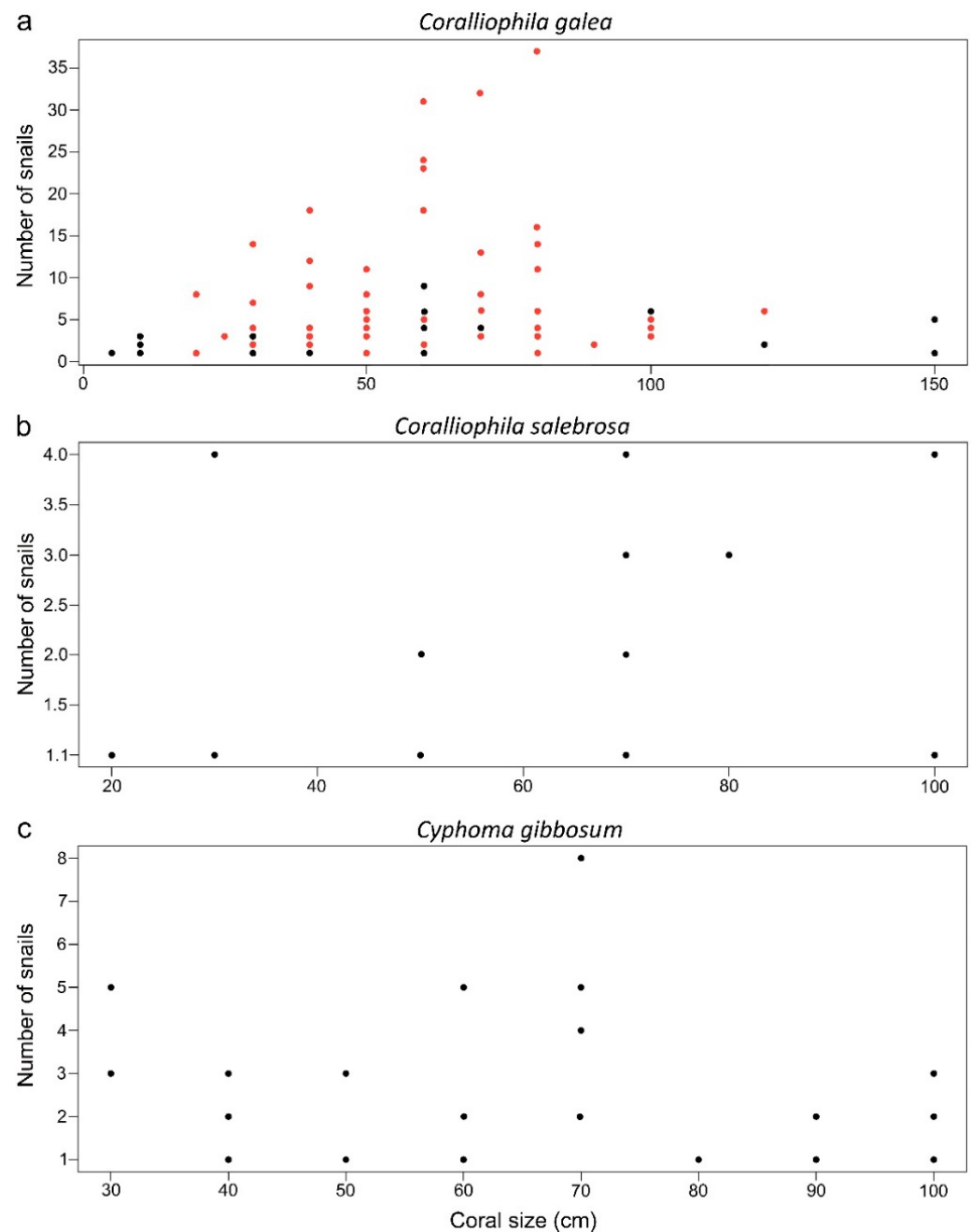


Figure 5. Linear regression of snail numbers and coral size for three snails species. Each dot represents an observation of a snail colony on a coral. For *Coralliophila galea*, the red points indicate observations on the coral species *Orbicella annularis*. The correlations are not significant.

There was variation in bathymetrical distribution among the snail species (Figure 6; ANOVA: $F = 5.27$; $p < 0.05$). *Coralliophila galea* was on average deeper than the other two species and it was much more common at depths over 20 m; among 25 recorded corallivorous snails, 22 were *Coralliophila galea*, two were *C. salebroso*, and one, *Coralliophila* sp., was unidentified. Differences in bathymetrical distributions between any two species were not significant. No coral damage was observed around *C. salebroso* snails. They were always found on the base of the host but within reach of some polyps.

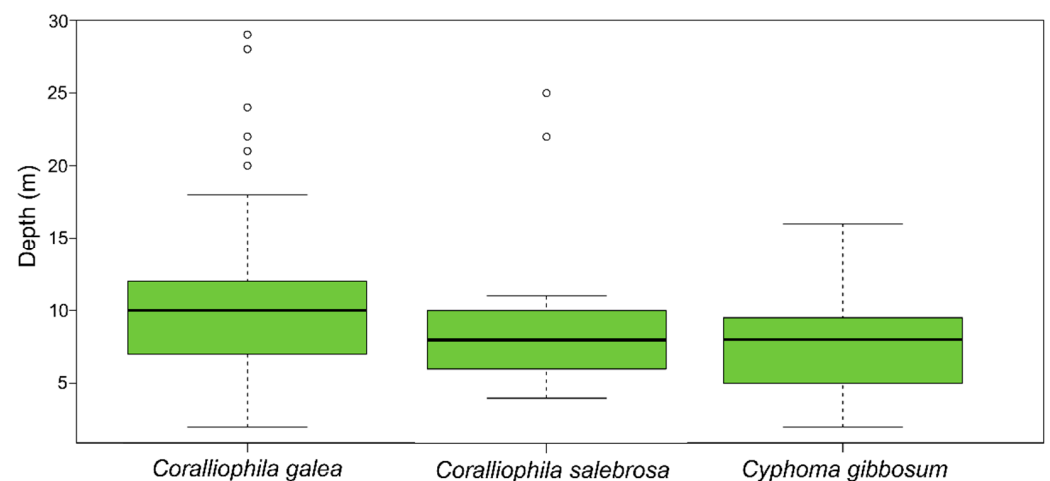


Figure 6. Box plot comparing the depth distributions for the different snail species. Interspecific variation is significant (ANOVA: $F = 5.27$; $p < 0.05$) but differences between any two species are not.

Coralliophila galea was the only species found abundantly below a depth of 10 m. The host utilization varies among the three depth ranges (Figure 7). In the shallowest zone (0–10 m), the most utilised coral species was *Orbicella annularis* with 90% of the encountered snails. No apparent feeding scars were seen on *O. annularis*. *Orbicella franksi* was not noted as a host at that depth. At 10–20 m depth, almost all snails were found on *O. annularis*, whereas *O. franksi* was the second-most common host. No *O. annularis* was observed at deeper than 20 m. Three observations of *Coralliophila galea* concerned *O. franksi*, with densities of one, two and five snails per coral, all at a depth of 21 m.

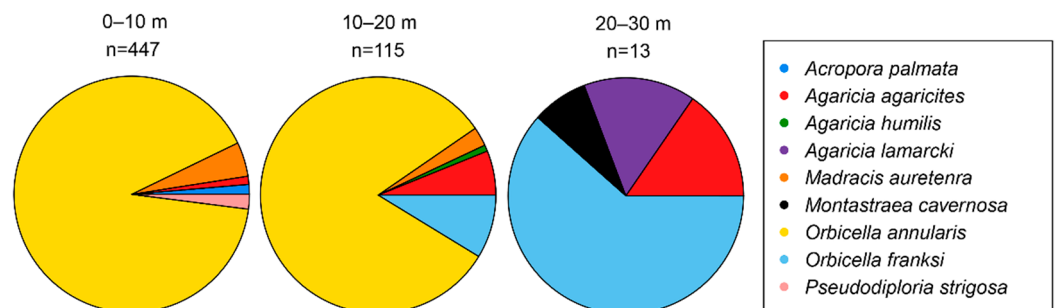


Figure 7. Host utilization by *Coralliophila galea* in three depth ranges.

4. Discussion

Our survey of the distribution and diet of corallivorous gastropods on Bonaire indicated interspecific overlaps in resource use. There were no signs of coral mortality because of predation. It appears that there is no shortage of food for the snails, which eventually might cause interspecific competition among them. There are reports from other Caribbean areas that mention severe coral mortality because of corallivorous snails [36,91]. The lack of mortality can be linked to the low densities of the three snail species.

Coralliophila galea was the most common species and found at the widest depth range, from 2 to 29 m, which approached the maximum survey depth. Since Bonaire's coral reefs extend beyond 50 m depth [51,92] and many of the same host coral species may occur there as those at 30 m [93], it is likely that *C. galea* occurs at a greater depth than the presently recorded maximum depth. All encountered host associations for *C. galea* were also found in Curaçao [12]. *Orbicella annularis* was by far the most common host of *Coralliophila galea*, which also agrees with results found on Curaçao [94]. Studies in other Caribbean localities also reported this association as common [95,96]. *Orbicella annularis* can be distinguished from other *Orbicella* species by its tendency to form columns with

wide space in between them, allowing for settlement of *Coralliophila* clusters [82]. Coral colonies of this species have many depressions in their surface without live tissue, which provide an optimal resting place for parasitic snails. At 20–30 m depth, no *C. galea* were recorded on *O. annularis*, which was found to be relatively rare in this depth range at nearby Curaçao [97]. The depth distribution and differences in host occupation across depths can therefore be explained by host availability, even though this was not recorded in the present study.

In the present study, no apparent recent feeding scars were seen on *Orbicella annularis*. *Coralliophila galea* may appear to be immobile for days or there may be some movement in time spans of several weeks without any increase in size of the scars presumably because they predominantly feed by probing polyps without killing them [12,75]. However, they may become lethal to their hosts when they reach high densities [35,36,68]. A single *Coralliophila galea* individual was observed on top of a living *Acropora palmata* causing much damage, suggesting that this coral may be susceptible to attacks by the snail, which is consistent with observations in other Caribbean areas [98–100].

Coralliophila salebrosa was almost exclusively found in association with octocorals, whereas on Curaçao, this species was also found on 12 different scleractinian corals [12] and an additional scleractinian host species was recently recorded from Brazil [101]. Our results are in line with previous studies on host preference of this species [102,103]. The search effort by Potkamp et al. [12] on Curaçao was not specified, but their study took place in less than two months and was comparable to the effort of the present study.

No damage to the corals was observed around the snails of *Coralliophila salebrosa*. Its feeding mechanism has not been studied as much as that of *C. galea*, but it is similar to that and of other congeners, causing minimal damage [6,12,75,101,104,105]. Therefore, the effects are less visible as no scar of removed tissue can be observed, although severe damage may occur when the snails occur in large aggregations [36,68]. Since our observations were done during the day, it is possible that the location where *Coralliophila* snails were observed was not exactly the same as where they graze, but studies suggest that they generally do not move much for long periods of time [74,75].

Coralliophila curacaoensis, originally described from Curaçao, was not found during the present survey. This species is only known from two host species, *Madracis auretenra* and *M. decactis*, and two localities, Curaçao in the southern Caribbean and Martinique in the eastern Caribbean [12,68]. It is impossible to prove that *C. curacaoensis* is absent on Bonaire, but we can assume that it is at best very rare. Although Bonaire and Curaçao are only 40 km apart, their marine faunas are not entirely the same as observed in comparisons of anthozoan faunas [64,106].

We encountered 79 individuals of *Cyphoma gibbosum*, which is the most common reported ovulid species throughout the Caribbean. All encountered individuals were normally coloured, with round black ring-shaped markings (Figure 1c). It was most abundant around 10 m deep, which is also the depth where most gorgonian prey species are present. The predation marks on the corals were clearly visible but since snail densities were fairly low (Figure 2c). The current numbers of snails are therefore not expected to have an effect on the coral populations.

The absence of other Ovulidae observations during the survey can be related to their rarity. Earlier, two other species have been recorded as Bonaire, namely *Cyphoma signatum* and *C. cassidyae* [76]. Both of these species/morphs are rarely encountered [76,107]. *Cyphoma signatum* is usually found on *Plexaurella* spp., whereas *C. cassidyae* is probably polyphagous [76,81]. Other authors consider the three species to be synonymous [26,72].

The prey preference of *Cyphoma gibbosum* varies across different areas in the Caribbean. For example, whereas *Pseudoplexaura* corals were commonly predated by the snail in Puerto Rico [7], they were rarely predated in Florida [78]. Some species are never eaten by *Cyphoma* species; the reason for this is unclear but could be related to anti-predatory toxins. Octocorals have developed allelochemicals to protect against predation, and *C. gibbosum* has developed detoxifying enzymes to neutralise these chemical toxins [108]. Some have

suggested that octocorals avoided by *C. gibbosum* may have other secondary metabolites that the snails cannot break down [78]. Local outbreaks are known to cause considerable damage to octocoral populations [41,109].

The three corallivores of the present study were encountered on a range of food sources, which differed strongly between the species (Figures 5 and 6). The difference in utilisation of coral species was found to be statistically significant, also when only comparing the two predators on octocorals. This shows that in an area where multiple related food taxa are available to a generalist predator, food preferences arise, which may prevent competition between species. The process by which natural selection drives competing species into different patterns of resource use or different niches is called niche partitioning [110]. These differences may perhaps be caused by differences in secondary metabolites produced by the prey species, their sclerite size, or nutritional value [26].

The size of the coral was not a significant predictor in the number of snails found on a coral. Potkamp et al. [94] found that larger colonies were more likely to contain *Coralliophila* snails, and that the snails were generally absent on small coral colonies. This was most obvious at 5 m depth, where small colonies with a diameter of <35 cm did not contain snails. The smallest diameter of *Orbicella annularis* on which we recorded *Coralliophila* snails was 20 cm, so this is likely to be similar in Bonaire.

The aim of this survey was to obtain quantitative data on corallivorous snails. Due to the limited time, corals without snails were not identified and measured, so that we could spend more time looking for snails and get more data on host preference. A downside to this approach is that we cannot quantify snail densities and their effects, and because we have not recorded coral densities, we cannot relate snail numbers per host to the density of that host. For example, octocorals were more common on reef flats than on reef slopes, and consequently, corallivorous species associating with gorgonians are also expected to be more common in shallower waters. Nonetheless, the present study provides a baseline on knowledge of corallivorous molluscs on Bonaire, which may assist in future management strategies [111].

5. Conclusions

This study on corallivorous snails contributes to the knowledge on marine diversity of Bonaire's coral reefs. Even though the three snail species of this study showed much overlap in their spatial distributions, there was modest similarity in their diets and there were no signs of much damage or even mortality among the corals. The snails did not show outbreaks and the reefs of Bonaire appeared not to be threatened by their presence. An earlier study on the adjacent island of Curacao showed much more overlap in dietary overlap. The lack of *Cyphoma gibbosum* records around the capital Kralendijk suggests that this species could be negatively affected by the anthropogenic disturbances here [112]. Subsequent research needs to investigate whether species richness near Kralendijk is also less for other taxa. It seems that coral reefs of Bonaire are currently not under much stress from corallivorous molluscs. Because these species have occasionally been reported to occur as outbreaks in other Caribbean localities and may act as vectors in the dispersal of coral diseases, it is recommended that future studies should focus on their population dynamics.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010034/s1>, Figure S1 Location of the 28 study sites. Table S1 Locality names and coordinates. Tables S2–S4 Raw data.

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