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Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: Population structure of snails and corals

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Abstract Despite their potential importance in structuring reef communities, invertebrate corallivores and their population structures are poorly understood. We found distinct differences in the population structures (length-frequency distribution and sex ratio) of the corallivorous gastropod *Coralliophila abbreviata* residing on two coral-host taxa, *Montastraea* spp. and *Acropora palmata*, in the Florida Keys. In each of two survey years, around 50% of the *Montastraea* spp. colonies were infested, with a mean snail density of eight snails per infested colony (range 1–45), while around 20% of *A. palmata* colonies harbored three snails per infested colony (range 1–23). Variation in patterns of snail occurrence was also observed within a host taxon. *A. palmata* occurred in low- and high-density stands (0.4 and 1 colony m^{-2}, respectively, at the initial survey) at different sites. Hurricane Georges struck the area in September 1998. When resurveyed in 1999, density of colonies in low-density stands had decreased by 75% to 0.1 colonies m^{-2}. This decrease was accompanied by a doubling in the proportion of colonies infested with snails (from 19% to 46%) and an increase in snail density per infested colony (from 3.7 ± 3.3 SD to 5.4 ± 4.6 SD) as snails apparently concentrated on surviving *A. palmata*. In contrast, sites with high density *A. palmata* stands (thickets) retained colony densities of about ~1 colony m^{-2} among years, while snail infestation increased only from 9% to 14% of colonies surveyed and snail density essentially remained unchanged (from 2.7 ± 1.8 to 2.9 ± 1.9 snails per infested colony). Snails collected from *Montastraea* spp. were shorter than those from *A. palmata* in low-density stands and were longest on *A. palmata* in thickets. On both host taxa, female snails were longer than males. The sex ratio of snails on *Montastraea* spp. hosts was even (1:1), while that of snails on *A. palmata* was skewed (70% males). Factors that could explain observed differences in size structure and sex ratio between *Coralliophila* populations on the two coral host taxa include: differential susceptibility to predators, influence of host tissue nutritional quality and/or secondary metabolite content, and genetic differences (cryptic species). The host-specific characteristics of *C. abbreviata* populations imply that the impact of gastropods on reef communities will vary with the coral species composition.

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Introduction

Corallivores are recognized as an important factor in structuring reef communities (Moran 1986; Birkeland and Lucas 1990; Knowlton et al. 1990; Turner 1994; Carpenter 1997), yet information on their population structure is limited. In the Pacific, the muricid gastropod *Drupella* (reviewed by Turner 1994) and the crown-of-thorns sea star *Acanthaster* (reviewed in Moran 1986; Birkeland and Lucas 1990) are examples of corallivores that undergo population outbreaks with significant impacts on coral populations and communities (Glynn 1990). Improved knowledge of processes that affect corallivore population structure will aid in understanding corallivore impacts on coral reef communities. Anthropogenic effects on tropical reefs likely influence population structure of both corals and corallivores.

Of special concern is that overfishing of certain trophic groups may alter predation pressure on the corallivores and thus contribute to corallivore outbreaks and/or increases in corallivore size (McClanahan 1997).

Coralliophila abbreviata Lamarck is a Caribbean corallivorous gastropod that feeds on at least 14 species of scleractinian coral (Miller 1981). Several authors have reported small and localized tissue damage from *C. abbreviata* predation (e.g., Ward 1965; Robertson 1970). Ott and Lewis (1972) concluded that such predation did not cause extensive damage to the corals in Barbados, West Indies. However, more recent investigators, including Knowlton et al. (1981, 1990), Brawley and Adey (1982), Hayes (1990a, 1990b), and Bruckner et al. (1997), consider *C. abbreviata* a potent predator. Bruckner et al. (1997) reported a mean coral tissue consumption rate of 1.9 cm^2 $snail^{-1}$ day^{-1} (max = 6.5 cm^2 $snail^{-1}day^{-1}$) for snails feeding on *Acropora palmata*. At such feeding rates, *C. abbreviata* has the potential to have a major impact on its coral prey.

The most dramatic example of coral community shifts influenced by *C. abbreviata* predation followed Hurricane Allen in 1980. In Jamaica, *Acropora cervicornis* suffered a 100-fold decrease in density, and surviving coral consisted mostly of fragments, whereas the density of *C. abbreviata* remained at close to pre-storm levels (Knowlton et al. 1981, 1990). Live coral fragments were eaten by *C. abbreviata* before they could reattach themselves, arresting the recovery process of the staghorn corals.

Study approach

In the current study, population structure of *C. abbreviata* was examined on two prominent reef-building coral taxa in the Florida Keys, the massive growing *Montastraea "annularis"* species complex and the branching species *A. palmata,* that have marked differences in life history. *Montastraea* spp. (including *M. annularis* sensu strictu, *M. faveolata*, and *M. franksi* [Weil and Knowlton 1994] but not *M. cavernosa*) are slow growing (~0.8 cm $year^{-1}$ linear skeletal extension rate; Gladfelter et al. 1978) and form distinct colonies at the reefs surveyed in this study. *A. palmata* growth rates are rapid (5–10 cm $year^{-1}$; Bak 1976; Gladfelter et al. 1978), and it can form dense thickets under favorable conditions. These differences in host species growth characteristics provided an opportunity to investigate population structure of *C. abbreviata* under different food and habitat characteristics.

The general goals of this study were to document patterns of distribution of *Coralliophila* on these two major coral host taxa, *A. palmata* and *Montastraea* spp., in the Key Largo sector of the upper Florida Keys and to assess the impact of their predation. *A. palmata* appears to be the preferred prey but is the less abundant of the two corals. The approach was to survey as many reefs as possible where *A. palmata* was present in some minimal abundance. Snail abundance and population characteristics were examined with regard to the population characteristics of their host corals.

The results of our study are presented in two parts. In the first paper, we address two questions: (1) Do snail population characteristics differ between coral hosts? and (2) Are snail population characteristics correlated with host population characteristics? In a second paper (Baums et al. 2003), we present snail growth and metabolic and feeding rates and examine these results with regard to the observed size and sex ratio patterns reported here, as well as use them to estimate the potential impact these snails can have on their coral hosts under the observed snail densities, size ranges, and feeding rates.

Materials and methods

Study sites

Six reefs in the Key Largo sector of the Florida Keys National Marine Sanctuary (FKNMS), Florida, USA (Fig. 1) with live *Acropora palmata* were surveyed for *Coralliophila abbreviata*. Three were no-take Sanctuary Protected Areas (SPAs; South Carysfort Reef, French Reef, and Molasses Reef), and three were fished (reference) sites (Horseshoe Reef, Little Grecian Reef, and

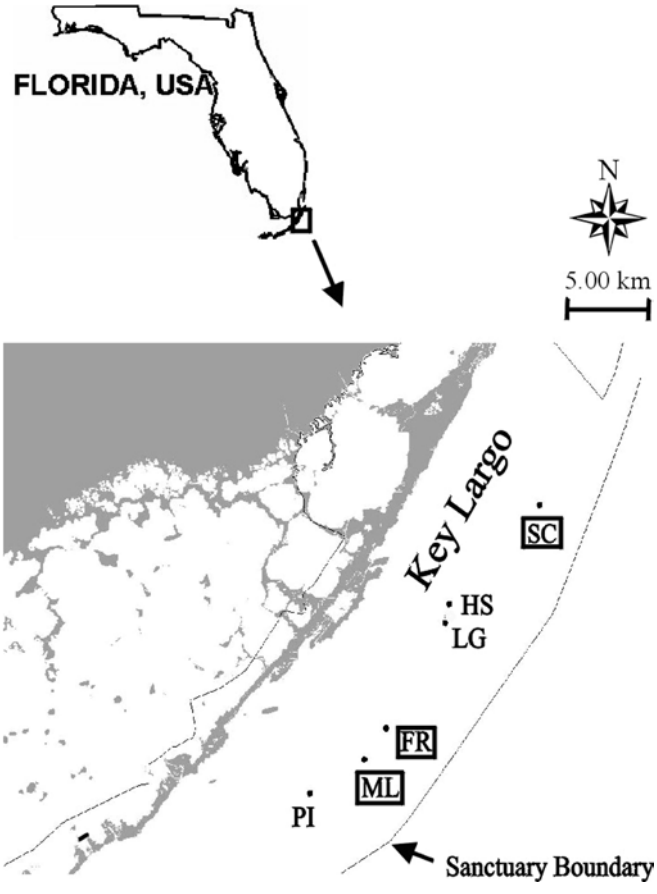

Fig. 1 Study sites in the northern sector of the Florida Keys National Marine Sanctuary, Fla., USA. No-take zones are *boxed*. *SC* South Carysfort Reef, *HS* Horseshoe Reef, *LG* Little Grecian Reef, *FR* French Reef, *ML* Molasses Reef, *PI* Pickles Reef

Pickles Reef). South Carysfort (N 25° 12.208; W 80° 13.594), Little Grecian (N 25° 07.114; W 80° 18.007), and Molasses (N 25° 00.752; W 80° 22.259) are more exposed and have high-relief spur and groove fore-reefs; French (N 25° 02.15; W 80° 21.25) and Pickles (N 25° 59.25; W 80° 24.86) are exposed but are low-relief relic reefs (Jaap 1984; Chiappone and Sullivan 1997). Horseshoe Reef (N 25° 07.106, W 80° 18.029) is similar to a large patch reef in its structure. Snails were sampled from subsets of these sites for the other measurements and experiments as described below.

Snail and coral surveys

In May 1998 and again in May 1999, populations of *C. abbreviata* were surveyed on two host coral taxa, *A. palmata* and *Montastraea* spp., in the 1–10 m depth range. In the interval between the two surveys, coral reefs in the Florida Keys experienced two significant disturbances: Hurricane Georges (September 1998) and a major bleaching event (August and September 1998). Live coral cover is low in the northern Florida Keys (generally $<20\%$ and often $<10\%$; Chiappone and Sullivan 1997), and because the snails are difficult to locate, we never found them on reef substrate away from live colonies. Because of this, we chose to survey snail populations on a per coral colony basis, as has been done in previous studies (Hayes 1990a; Bruckner et al. 1997). An *A. palmata* colony was defined as a continuous, upright skeleton with a stalk attached to the substrate. Unattached broken branches of *A. palmata* were classified as fragments.

A. palmata occurs primarily in patches on the reef flats and upper fore reef slopes in the Key Largo area. At the southern study sites, *A. palmata* patches were small and consisted of distinct, widely scattered colonies ("low-density stands"; see Results, Table 1 for patch sizes). At these sites, all colonies were sampled and the area occupied by the patch was measured. The northern sites had extensive, higher density patches, henceforth termed "thickets," in which individual colonies overlapped and colony boundaries were often difficult to distinguish; haphazard belt transects were used to subsample these patches. All attached colonies located within 2 m on either side of the transect tape were measured. Fragments were counted when over 50% of their total lengths were located within the belt transect.

Colony dimensions (width and length to nearest decimeter) and estimated live cover (% in five categories: 0–10%, 10–25%, 25–50%, 50–75%, and 75–100%) of each colony were recorded for attached colonies only; loose fragments were not measured due to time constraints. *A. palmata* colonies often have a high percent of partial mortality, and thus colony size may not reflect the area of live coral available for snails to feed on. Therefore, a live-area index (LAI) was calculated (Length×Width×% live/100) as a rough estimate of live colony size or total amount of host tissue. Between 16 and 290 *A. palmata* colonies and fragments were surveyed at each site depending on abundance (Table 1).

Montastraea spp. colonies were haphazardly selected for survey by swimming across the reef in the vicinity of the *A. palmata* transects. Between 5 and 24 colonies were examined at each site (Table 1).

Colonies and fragments were searched to determine snail abundances, and the maximum length of each snail was measured with a vernier caliper (± 0.05 mm) and recorded. From this information we were able to calculate infestation levels (proportion of colonies with snails), snail density (number of snails per infested colony), and snail size distribution for each site. Snail density calculations are based on both colonies and fragments (as defined above).

An additional method to estimate relative infestation and snail density in *A. palmata* patches was employed in 1999 and compared with the "per colony" data obtained above. A 1-m^2 quadrat was placed on 20 haphazardly chosen *A. palmata* colonies at each of the survey patches (except Molasses Reef). The PVC quadrat had a 6×6 grid dividing the 1 m^2 into 36 sections. The type of substrate underneath each intersection of the grid was recorded as live coral, dead coral, algae, or non-coral substrate, along with the total number of snails counted within the quadrat. This information was used to compute infestation as the proportion of quadrats with snails and *A. palmata* snail density as number of snails m^{-2} coral.

Statistical analysis

Repeated-measures analysis of variance (ANOVA) was used to analyze possible differences between sites and survey years in *A. palmata* colony density (including fragments) after verification that ANOVA assumptions of normality and equal variances were met. The *Montastraea* spp. colonies sampled in the two survey years were two independent subsamples of the *Montastraea* spp. population at each survey site and thus did not require repeated-measures analysis.

Two-way ANOVA (on ln-transformed data) was used to test whether the mean LAI differed between years and/or low-density and thicket *A. palmata* stands. We wanted to accept the null hypothesis that there was no difference in colony size between sites or years in order to confirm that our results are not confounded by differences in colony size. Using a regular ANOVA is more conservative in this case than using a repeated-measures ANOVA since it reduces the chance of a type II error. LAI was compared between years only (i.e., one-way analysis) for *Montastraea* spp. using a ranked-sums test.

Two-way ANOVA was used to test for differences between hosts and survey years in snail infestation and snail length. Two-way ANOVA on ranks (a non-parametric test) was used to test for significant differences in snail density between thickets versus low-density stands and survey years (equal variance and normality tests failed). A ranked-sums test was used to test for differences in snail density per square meter of coral between thicket and low-density stands for the quadrat-based surveys.

Table 1 Summary of *Acropora palmata* (Ap) and *Montastraea* spp. population characteristics from surveys in May 1998 and May 1999. *A. palmata* densities include attached colonies and unattached fragments. Study sites abbreviated as in Fig. 1; *n.a.* Not available

Site	Protection status	Ap Stand structure	Reef area surveyed for *A. palmata* (m^2)		*A. palmata* density (colonies m^{-2})		No. *A. palmata* surveyed		No. *Montastraea* spp. surveyed	
			1998	1999	1998	1999	1998	1999	1998	1999
SC	SPA	Thicket	240	200	0.78	0.84	187	168	23	22
HS	Fished	Thicket	240	212	0.94	0.81	226	171	18	9
LG	Fished	Thicket	224	80	1.20	1.64	268	131	14	n.a
FR	SPA	Low-density	401	201	0.72	0.27	290	55	5	19
ML	SPA	Low-density	552	552	0.23	0.06	128	33	20	14
PI	Fished	Low-density	440	440	0.16	0.04	72	16	12	11
Total			2,097	1,685	0.56	0.33	1,171	574	89	75

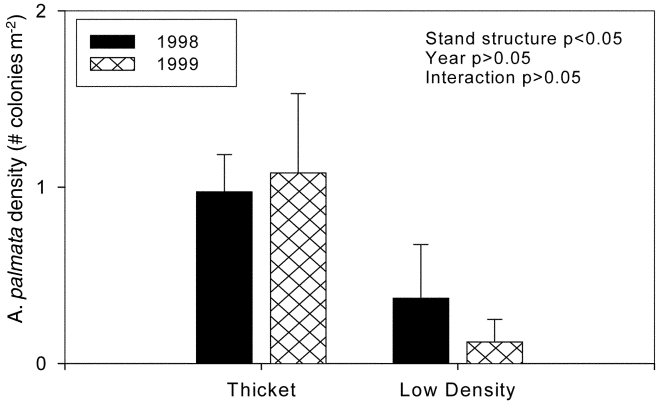

Fig. 2 Comparison of mean (+1 SD) *Acropora palmata* total colony density (attached colonies and fragments) between thickets and low-density stands for 2 years. Density is reported as the mean number of colonies m^{-2} of surveyed reef. Probability values are from two-way ANOVA. Thicket sites are SC, HS, and LG (Fig. 1, Table 1); low-density stand sites are FR, PI, and ML (Fig. 1, Table 1)

Sex ratios

Snails were collected from both host taxa at Horseshoe, Pickles, and Little Grecian Reefs ($n = 170$; Fig. 1) and frozen until examination. Shell length was measured, the shell was removed, and the soft tissues were examined with a dissecting microscope. Sex was determined by the presence or absence of a penis, located above the left eyestalk. We compared the length distribution of males and females from each host taxon. A chi-square test was used to test for differences in sex ratio between snails from *A. palmata* and *Montastraea* spp. hosts. *C. abbreviata* is reported to be a protandrous hermaphrodite (Hayes 1989).

Results

Coral populations

Acropora palmata patches differed in size and colony density among sites. We arbitrarily defined thickets as patches supporting 0.75 or more colonies m^{-2}, while low-density stands had less than 0.3 colonies m^{-2} (Table 1, Fig. 2). South Carysfort, Horseshoe, and Little Grecian Reefs had contiguous and intermingled *A. palmata* colonies at high density and were classified as thickets. The patches on Pickles and Molasses Reefs were low-density stands. French Reef had a high live-colony density in the 1998 survey that decreased by the 1999 survey to levels characteristic of a low-density stand (Table 1). The differences in *A. palmata* density between thickets and low-density stands were significant for both years [2×2 repeated-measures ANOVA, Stand structure (thicket versus low-density stands) $P < 0.05$ and YEAR $P > 0.05$, interaction $P > 0.05$]. These differences became more pronounced by the summer of 1999, after Hurricane Georges and severe bleaching disturbances in 1998 (Table 1, Fig. 2). While the thickets maintained a stable average total colony density (attached colonies plus fragments) of $\sim$1 m^{-2}, colony density at the sites with low-density stands dropped from an average of 0.4 colony m^{-2} in 1998 to 0.1 colony m^{-2} in 1999 (Fig. 2). One out of three patches at French Reef and one out of two patches at Little Grecian Reef suffered complete coral mortality between the two surveys, resulting in smaller reef areas surveyed in 1999 (Table 1).

The mean LAI of *A. palmata* colonies, a rough estimate of live coral tissue per unit colony, did not differ significantly between low-density and thicket *A. palmata* stands ($P > 0.05$, Table 2). Hence, snail densities per colony can be compared between thicket and low-density stands. LAI decreased significantly from 1998 to 1999 ($P < 0.001$), and this decrease was greater for thicket colonies than for colonies in low-density stands (Stand structure×Year interaction $P < 0.001$, Table 2). This is likely due to the impact of Hurricane Georges, which broke colonies into smaller pieces that were retained in the thicket stands but lost from low-density stands. Total colony density (attached colonies plus

Table 2 Mean live area index (LAI = length×width×%live cover) of *Montastraea* spp. and *A. palmata* colonies (without fragments) surveyed in 1998 and 1999. *Montastraea* spp. did not differ in mean LAI between 1998 and 1999 (Wilcoxon signed rank test on square-root-transformed data $P > 0.05$, $n = 164$). *A. palmata* did differ in mean LAI between years ($P < 0.001$) but not between stand-structures (P = n.s.). However, the interaction was significant ($P < 0.001$). P-values for *A. palmata* are from a 2*2-way ANOVA onln-transformed data with the factors stand structure, year, and LAI as the response. Sites abbreviated as in Fig. 1; *n.a.* Not available

Stand structure	Site	*A. palmata*				*Montastraea* spp.			
		1998		1999		1998		1999	
		n	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD
Thickets	SC	130	3,053 ± 3,163	99	2,517 ± 3,431	23	10,150 ± 17,520	22	4,074 ± 4,230
	HS	106	11,036 ± 11,215	130	3,300 ± 3,469	18	5,789 ± 5,749	9	8,496 ± 8,185
	LG	72	5,545 ± 5,186	102	2,945 ± 2,833	14	3,921 ± 2,708	n.a.	n.a.
Low-density	FR	103	5,846 ± 6,464	45	4,795 ± 5,330	5	828 ± 969	19	3,139 ± 4,588
	ML	63	5,006 ± 7,785	25	3,092 ± 2,997	20	3,156 ± 6,806	14	226 ± 233
	PK	43	2,570 ± 3,650	15	2,361 ± 1,938	9	1,253 ± 694	11	3,697 ± 3,185
Total		517	5,791 ± 7,544	416	3,142 ± 3,544	89	5,293 ± 10,230	75	3,594 ± 4,900
Thickets		308	6,383 ± 8,110	331	2,956 ± 3,280				
Low-density		209	4,919 ± 6,543	85	3,865 ± 4,372				

fragments) did not decrease in the thickets after the storm (Table 1) because of the higher retention, but many of the surviving attached colonies suffered partial mortality, decreasing their LAI. Therefore, care must be taken in interpreting 1998–1999 differences in snail densities since the same number of snails per colony would represent a greater snail density per amount of live *A. palmata* tissue in 1999 then in 1998.

Montastraea spp. colonies were not sampled on an areal basis; therefore, colony density is not known. The LAI of surveyed *Montastraea* spp. colonies did not differ between the two years (ranked-sums test $P > 0.05$, $n = 164$), indicating that the populations sampled were comparable in colony "size" (Table 2).

Snail populations

Infestation and snail density

About 50% of the surveyed *Montastraea* spp. colonies harbored snails each year (paired *t*-test, $P > 0.05$, Fig. 3A), while only 10% of all *A. palmata* colonies (including fragments) harbored snails in 1998, increasing to 20% of all surveyed *A. palmata* in 1999. We did not statistically compare proportional infestation levels between species due to differing colony morphologies. For *A. palmata*, low-density stands had higher infestation levels than thickets, and the proportional snail infestation was significantly higher in 1999 than in 1998 [two-way ANOVA, Stand structure (thicket versus low-density stands) $P < 0.05$, Year $P < 0.05$]. Though not statistically significant (interaction $P > 0.05$), there was a greater increase in infestation between years for low-density stands (19–46%) than for thickets (9–14%), corresponding to a greater decrease in colony density in low-density stands compared with thickets (Fig. 2). Snail infestation was inversely related to *A. palmata* density, i.e., sparser colonies had higher snail infestation levels (power regression, $r^2 = 0.70$ in 1998, $P < 0.001$, Fig. 3B). This relationship was more pronounced in 1999 ($r^2 = 0.91$ in 1999, $P < 0.001$, Fig. 3B) than in 1998, coincident with a decrease in colony density in low-density stands (Fig. 2).

Infested *A. palmata* colonies harbored an average of 3 snails, ranging from 1 to 23 snails per colony or fragment. The number of snails per infested *A. palmata* colony was higher in 1999 than in 1998 (despite smaller colony LAI, see above), and for both years was higher on low-density stand colonies (3.7 ± 3.3 SD in 1998 and 5.4 ± 4.6 SD in 1999) than on thicket colonies (2.7 ± 1.8 SD in 1998 and 2.9 ± 1.9 in 1999) (2×2 ANOVA on ranks, Stand structure $P < 0.001$, Year $P < 0.05$). The interaction term was non-significant ($P > 0.05$). The number of snails on infested *Montastraea* spp. colonies was highly variable, ranging from 1 to 45 with an average of 8 snails per infested colony (Fig. 4). Snail densities on *Montastraea* spp. did not vary significantly between survey years (ranked-sums test, $P > 0.05$).

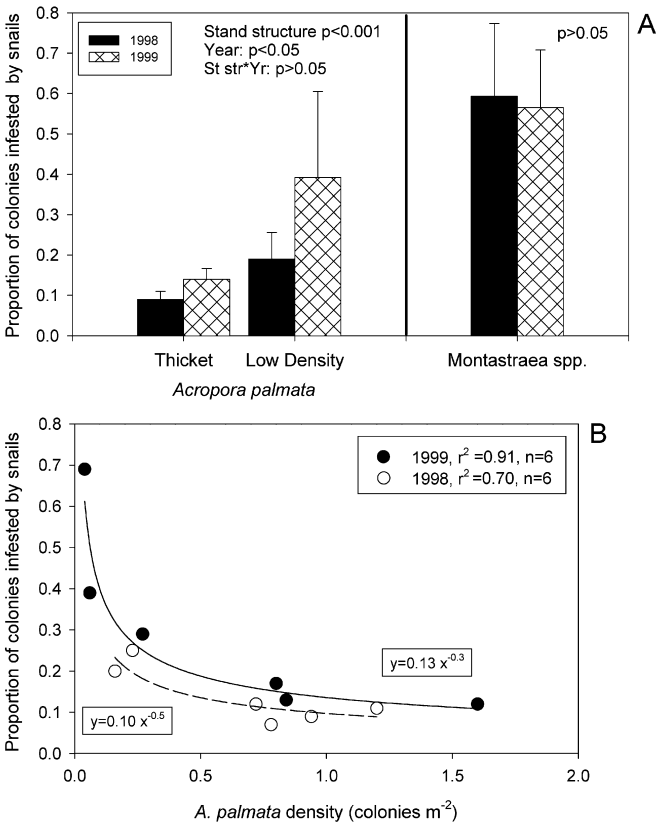

Fig. 3A Comparison of mean (+1 SD) proportion of total colonies infested (attached colonies and fragments) for *A. palmata* low-density stands and thickets (*P*-values from two-way ANOVA) and *Montastraea* spp. (*P*-values from paired *t*-test) in 1998 and 1999. **B** Relationship between total colony density (attached colonies and fragments) and proportional infestation of *A. palmata* for each year. r^2 values are for non-linear exponential regressions (for both regression lines $P < 0.001$)

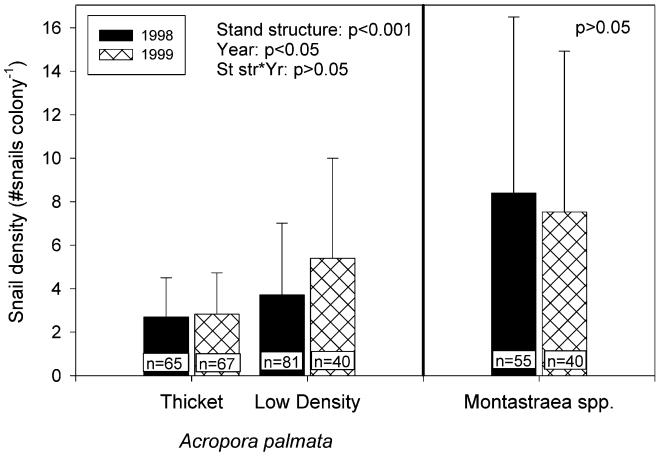

Fig. 4 Snail density on infested colonies (mean +1 SD). *P*-values for *A. palmata* are from two-way ANOVA on ranks, and *P*-values for *Montastraea* spp. are from a one-way ranked-sums test

Quadrat method

Overall snail infestation estimated by the quadrat method was high (45% of quadrats). The mean was lower in thickets compared with low-density stands (Table 3). Unfortunately, this difference could not be tested statistically because only two low-density stands were surveyed this way (insufficient *n*). *A. palmata* thickets harbored significantly fewer snails per m^2 of live coral (2.4 ± 3.7, $n = 59$) than the low-density stands (8.7 ± 11.1, $n = 35$) (ranked-sums test, $P < 0.05$; Table 3). Thus, population parameters expressed per live coral area follow the same pattern among sites and stand structures as when expressed "per colony."

Snail size and sex ratio

Coralliophila abbreviata ranged in length from 5.8 mm to 53.6 mm (Fig. 5). Snails were larger on *Acropora palmata* than on *Montastraea* spp. and, within *A. palmata* populations, significantly larger in thickets than in low-density stands for each survey year (Fig. 5, Kruskal Wallis ANOVA, $P < 0.001$; all Dunn's post-hoc pairwise comparisons $P < 0.05$; each year analyzed separately).

Sex ratios of snails differed between the two host taxa (χ^2 test, $P < 0.05$). *A. palmata* snails had a sex ratio of approximately three males ($n = 76$) per one female ($n = 21$). The *Montastraea* spp. snail population had a sex ratio close to one (males $n = 35$, females $n = 38$) despite smaller lengths. The length distribution of male and female *C. abbreviata* differed between the two host taxa (Fig. 6). On average, female snails were larger than males on both host taxa, with both males and females larger on *A. palmata* compared to on *Montastraea* spp. (two-way ANOVA on ranks, $P < 0.001$ for Sex and Host, interaction $P > 0.05$, Fig. 6).

Discussion

This study establishes baseline data on the population structure of a potentially important coral predator in the Florida Keys, the gastropod *Coralliophila abbreviata,* and the coral hosts it feeds on. Results suggest that snail population parameters are host specific. Thus, coral species composition and abundance appear to influence *C. abbreviata* population characteristics, and these host factors should be taken into consideration when assessing the impact of snail predation on reef community structure. These findings also raise management questions regarding the need to manage the snail in order to manage and protect *Acropora palmata.*

Comparison of snail populations on *Montastraea* spp. and *A. palmata*

Infestation and snail density

Snail infestation of *A. palmata* populations increased from 10% to 20% of colonies between survey years, largely due to an increase in the proportion of infested solitary colonies (Fig. 3A). Proportional infestation of acroporid colonies has been in the 10–20% range over the geographical extent of the Caribbean region over the past few decades (Panama 10% for *A. cervicornis*, Hayes 1990a; Jamaica 7.8–10.5% for *A. cervicornis*, Knowlton et al. 1990; Puerto Rico 18% for *A. palmata*, Bruckner et al. 1997). In contrast, *Montastraea* spp. colonies had a considerably higher incidence of snails in the Florida Keys: 56% and 53% of colonies in 1998 and 1999, respectively. This compares favorably with 64% of *Montastraea annularis* colonies reported to harbor *C. abbreviata* in Panama (Hayes 1990a).

The density of *C. abbreviata* residing on different coral hosts may be self-regulating. Hayes (1990b) reported a field experiment in which snail aggregations on *A. cervicornis* colonies were augmented with additional individuals, but aggregation size returned to original size over time. Additionally, snail densities (per infested colony) are quite similar in reports from across the Caribbean. Mean snail densities on *A. palmata* were 3.2 in the Florida Keys (range 1–23; this study), 3.7 in Puerto Rico (Bruckner et al. 1997), and 2.8 on *A. cervicornis* in Panama (range 2–14; Hayes 1990a). Average snail densities on *Montastraea* spp. are also geographically consistent with 8 per infested colony in the Florida Keys (range 1–45; this study) and 7.7 on *Montastraea annularis* in Panama (range 3–36; Hayes 1990a).

Snail size and population sex ratios

C. abbreviata is thought to be a protandrous hermaphrodite (Hayes 1989), suggesting that snail size and sex

Table 3 Population estimates of snails on *A. palmata* from the quadrat surveys. Values are means ±1SD. Mean snail density is expressed per quadrat and per m^2 of live coral (all quadrats included)

Stand structure	Site	*n*	% Quadrats with snails	No. snails m^{-2} total area	No.snails m^{-2} live coral
Thickets	SC	20	35	1.20 ± 2.19	2.53 ± 4.57
	HS	20	53	0.95 ± 1.61	1.98 ± 3.07
	LG	19	35	1.16 ± 1.5	2.58 ± 3.38
Low-density	FR	19	47	2.37 ± 2.73	7.79 ± 10.4
	PI	17	53	2.06 ± 2.68	9.68 ± 10.05
Total		95	45 ± 9	1.53 ± 2.21	4.76 ± 7.98
Thickets		59	41 ± 10	1.01 ± 1.77	2.36 ± 3.68
Low-density		35	50 ± 4	2.22 ± 2.67	8.69 ± 11.09

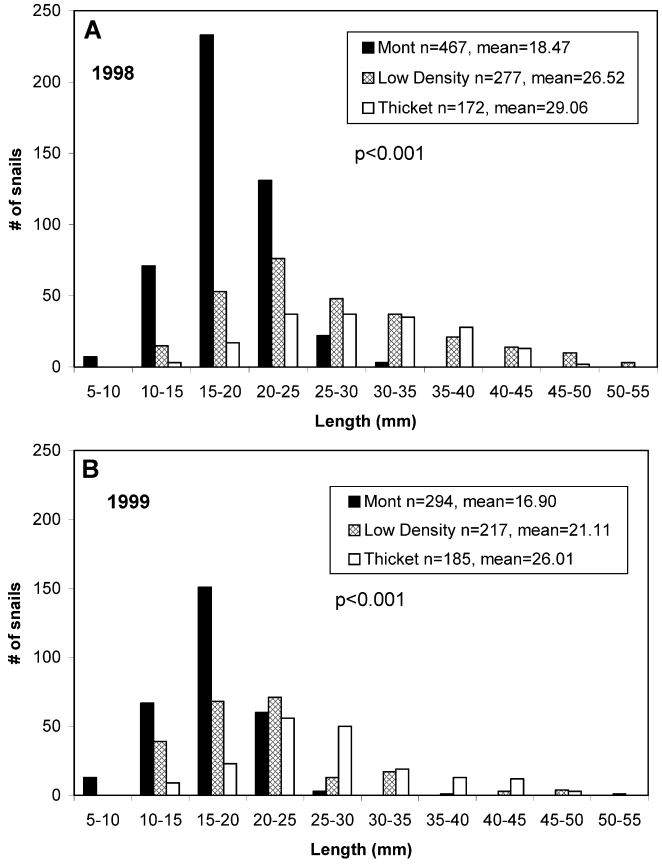

Fig. 5 Comparison of length distributions of *Coralliophila abbreviata* on *Montastraea annularis* (=Mont), low-density *A. palmata* populations, and high-density *A. palmata* thickets in 1998 (**A**) and 1999 (**B**). Probability values are from Wilcoxon/Kruskal-Wallis one-way ANOVA comparing the three host types within each year. Dunn's pairwise post-hoc analyses show that all three host types differ from each other ($P < 0.05$) each year

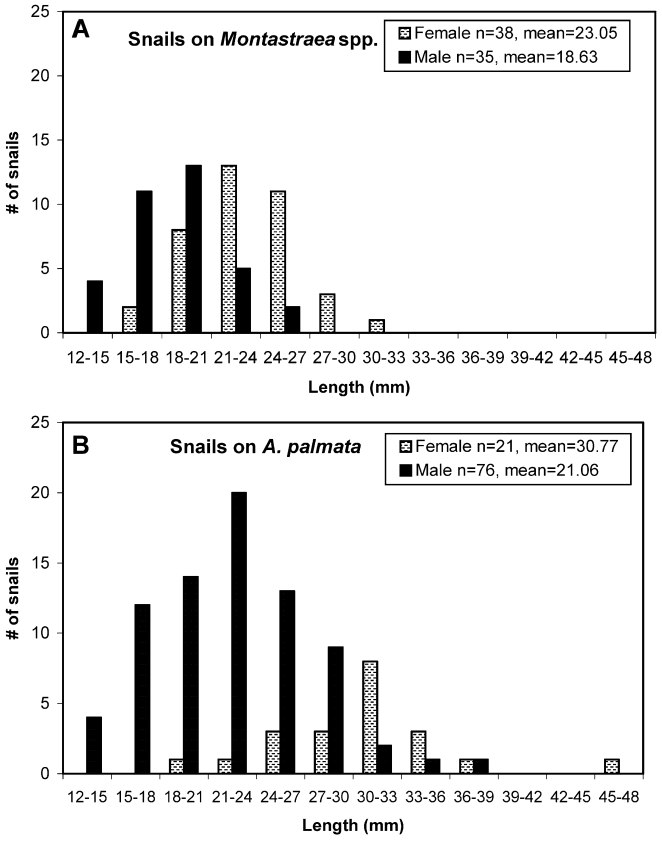

Fig. 6 Length distributions of male and female *C. abbreviata* for snails found on *Montastraea* spp. and on *A. palmata*. A two-way ANOVA on ranks was significant for the factors Sex ($P < 0.001$) and Host ($P < 0.001$) but not for the interaction ($P > 0.05$). Dunn's pairwise post-hoc analysis shows that all levels of host and sex differ from each other ($P < 0.05$)

are intricately linked. Thus, female *C. abbreviata* should be larger on average than males, and populations with differing size distributions would be expected to show different sex ratios: populations made up of smaller individuals would have a lower proportion of females. We found, however, that on *A. palmata*, the coral host with larger-sized snails, only 30% of the snails were females, whereas there were equal numbers of males and females in the populations of smaller sized snails residing on *Montastraea* spp. (Fig. 6). Hence, our data do not support a straightforward ontogenetic sex change. Either snail size at sex change is influenced by the coral host inhabited by the snail or some other environmental or social factor, or *C. abbreviata* is not a protandrous hermaphrodite in Florida. Social factors such as proximity and size of the nearest (snail) neighbor might play a role in the sex-changing behavior of *C. abbreviata*. In fact, male *Coralliophila violacea*, inhabiting poritid corals in the Red Sea, are reported to change sex over a wide range of ages, possibly influenced by the presence/absence and size of conspecific female neighbors (Chen et al. 1998; Chen and Soong 2002). A third alternative, namely that *C. abbreviata* is a complex of two cryptic sibling species, is discussed in Baums et al. 2003.

The relationship between snail size and host, with acroporids harboring larger snails than the *Montastraea annularis* species complex, appears to be consistent across Caribbean studies, with only slight differences in mean and maximum sizes of snails living on the two coral taxa reported for Barbados (Wells and Lalli 1977), Panama (Hayes 1990a), Puerto Rico (Bruckner et al. 1997), and Florida (this study; see also Hayes 1989).

Change of habitat with snail size has been reported for thaidid snails (Koch and Wolff 1996), and our observations of differences in snail size distribution between host taxa could be interpreted as an ontogenetic host-shift of young snails feeding on *Montastraea* spp. and moving to *A. palmata* colonies as they reach larger size. However, several lines of evidence suggest that this is not likely to be the case. First, small snails (<12 mm length) were present on *A. palmata*. Second, we found mature females on *Montastraea* spp. as indicated by the presence of egg cases (~46%, $n = 38$). Third, since *C. abbreviata* is thought to be a protandrous hermaphrodite, the presence of both sexes on each host, together with the host-specific difference in size range for males

and females, provides a strong contraindication of generalized ontogenetic snail migration between the two coral host taxa. While we do not suggest that movement of snails between host species does not occur, available evidence indicates that host switching is not common.

Influence of coral density on *C. abbreviata* populations

This study demonstrates that coral density influences *C. abbreviata* population characteristics, as evidenced by the inverse relationship between infestation of *A. palmata* colonies and coral density (Fig. 3A) and the differences in snail size distributions between thickets and low-density stands (Fig. 5). We did not obtain coral density estimates for *Montastraea* spp., but Ott and Lewis (1972) report a slight positive correlation between the densities of *Coralliophila* and the percent cover of *Montastraea* spp. ($r = 0.603$, $P < 0.01$) in Barbados, West Indies.

The severe disturbances in 1998 led to substantial coral population declines, especially in low-density *A. palmata* stands. We hypothesize, based on a 75% decrease in *A. palmata* density within low-density stands, accompanied by a 50% increase in snail infestation and a 30% increase in snail density, that snails were concentrated on the remaining coral colonies in low-density stands in 1999. The fact that the change in snail population characteristics in less-affected thickets was minimal further substantiates that *A. palmata* density may have a strong influence on its snail predator. Bruckner et al. (1997) showed high snail density in low-density *A. palmata* stands that were remnants of prior, high-density thickets. Knowlton et al. (1990) suggested a concentration of *C. abbreviata* on the remaining fragments of *A. cervicornis* generated by hurricane Allen in Jamaica.

Mechanisms regulating *Coralliophila* populations

Extensive human fisheries activities on Florida Keys reefs (Ault et al. 1998) have disrupted the complex trophic structure of reef communities. It is plausible that this disruption has resulted in an increase in snail density due to release from top-down control. Top-down control of corallivore population density and host impact has been reported for a coral-feeding nudibranch in Hawaii (Gochfeld and Aeby 1997). McClanahan (1997) found a weak correlation between *Drupella* density and an index of predation intensity across fished and reserve sites in Kenya. Data on predators of *C. abbreviata* are limited. The snapping shrimp, *Synalpheus fritzmuelleri*, is reported to feed on *C. abbreviata* in the Florida Keys (Goldberg 1971), and the Caribbean spiny lobster (*Panulirus argus*) feeds on *C. abbreviata* under laboratory conditions (personal observation). Additional suspected predators include puffer fish, hogfish, filefish, and octopi.

We hypothesize that differential predation on snails on the two host taxa might account for some of the observed snail population differences (see Trussel 1996 and references therein). The differing morphologies of the two coral host taxa (arborescent thicket versus large mounds) may provide differing shelter quality for snails and/or their predators. Indirect evidence based on the proportion of observed snails with shell scars is consistent with this hypothesis in that snails from *A. palmata* thickets have a higher incidence of shell scars (43% of snails on *A. palmata*, $n = 97$) than do those from *Montastraea* spp. (20.2% of snails on *Montastraea* spp., $n = 84$) (χ^2 test $P < 0.05$; Baums et al., unpublished data). However, shell scar incidence, indicating an unsuccessful predation attempt (Zipser and Vermeij 1978), may or may not be correlated with predation rates.

Implications for reef community structure

A. palmata has been on the decline over the past two decades in the Florida Keys (Jaap et al. 1988; Porter and Meier 1992) (Fig. 2) and throughout the Caribbean (Aronson and Precht 2001) to the extent that the U.S. is considering Endangered Species designation (Bruckner and Hourigan 2002). It might be expected that snail populations will adjust to decreased coral prey abundance by either a reduction in snail density (numeric response) or a shift in prey preference (functional response) as reported for the corallivorous gastropod *Drupella cornus* (Abevsirigunawardana and Ekaratne 2000). Should snail populations fail to respond to decreasing *Acropora* prey levels, snail predation could contribute to further loss of *A. palmata* from its dominant role in community and habitat structure and to curtailment of its resilience to other environmental stresses.

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