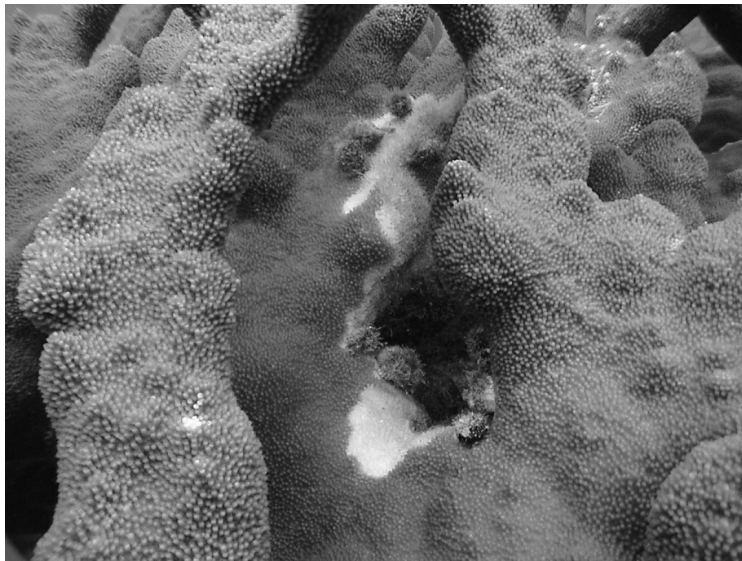




**STATUS OF CANDIDATE CORAL, *ACROPORA PALMATA*, AND ITS SNAIL  
PREDATOR IN THE UPPER FLORIDA KEYS NATIONAL MARINE SANCTUARY:  
1998-2001**

BY

Margaret W. Miller, Iliana B. Baums, Dana E. Williams, Alina M. Szmant



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## FOREWORD/ACKNOWLEDGMENTS

The goals of this project, begun in 1998, were initially to document patterns of distribution of the corallivorous snail, *Corallophila abbreviata*, on its two major coral host taxa, *Acropora palmata* and *Montastraea* spp. (*annularis* complex), in the Key Largo sector of the upper Florida Keys, and assess the impact these snails are having on the corals in no-take and reference sites. The approach was to survey as many reefs in the area as possible that had at least some live cover of *A. palmata*, the apparently preferred prey but least abundant of the two coral hosts. Snail abundance patterns were examined with regard to the population characteristics of their host corals such as colony size and condition. With the naming of *Acropora palmata* to the Candidate Species list in 1999, the survey gained a bit more focus on the status of the *A. palmata* colonies, themselves.

The original two years of funding came from NURC/UNCW, Grant #UNCW 9824 to Alina Szmant and Margaret Miller. The results of these first two years of survey work formed the basis of a Master's thesis for graduate student Iliana Baums and are currently being published in the peer-reviewed literature (Baums et al. (in revision, a); Baums et al. (in revision, b)). The project was not funded in 2000, but snail measurements and minimal coral counts were conducted at all six survey sites. Funding for the survey in 2001 and this compilation of results (those already in press with the more recent survey data from 2000 and 2001) was provided through NOAA-Fisheries Coral Reef Initiative funding for FY01 (under Margaret Miller, Task # 8L2AC1EA).

Many other individuals have assisted with the field work including John Barimo, Amanda Bourque, Charles Fasano, and Susan Colley. Substantial contributions by Robin and Andrew Bruckner in the design and initiation of the study are greatly appreciated.

## ABSTRACT:

Population surveys of elkhorn coral, *Acropora palmata*, and its corallivorous snail predator, *Coralliophila abbreviata*, were conducted annually in May from 1998 to 2001. At each survey, size and condition of each sampled coral colony was estimated as well as the number and size of its resident snails. *A. palmata* patches at six sites in the FKNMS were surveyed in all years; three no-take zones and three reference areas. A drastic decline in *A. palmata* populations was observed between May 1998 and May 1999, coinciding with a severe bleaching event and Hurricane Georges during summer/fall of 1998. All colonies in three patches (out of 10) sampled in 1998 suffered complete mortality by May 1999. Sampling at two sites in October 1998, after Hurricane Georges, confirmed that average sizes of standing colonies and of loose fragments had decreased while the abundance of fragments had increased. The total amount of live *A. palmata* (as measured by total # of colonies or by total “live area index” (see text)) extant at three sites where all colonies were sampled declined drastically from 1998 to 1999 and has shown only marginal recovery from 1999 to 2001. The density of *A. palmata* at all sites has surely declined during the study (mostly between 1998 and 1999), but the quantitative expression of this parameter is complicated by the decrease in areal extent of several patches and the fragmenting morphology/life history of the species. The average condition of remaining *A. palmata* colonies (estimated as % of colony surface with live tissue) declined slightly but significantly from 1998-99 but rebounded by 2001 to the 1998 level of ~60%. The incidence of white band disease (WBD) in these *A. palmata* patches has been consistently low throughout the study, below 6% for any given site survey with zero incidence observed in many site surveys. The average incidence of WBD observed in 2001 was 2% of colonies (n=6 sites).

*Coralliophila abbreviata* showed somewhat less dramatic dynamics during the study period. The average density of snails on *A. palmata* (#/*A. palmata* colony surveyed, n=6 sites) more than doubled from 1998-1999 but declined again between 2000 and 2001. Similar density trends were observed between no-take reserve and reference sites. Sites with low-density *A. palmata* patches (LD sites) had consistently more snails colony<sup>-1</sup> than sites with thickets. Meanwhile, the average size of snails on all hosts (*A. palmata* thickets, LD *A. palmata*, and *Montastraea* spp.) declined between 1998 and 1999. By 2001, average snail size on *Montastraea* spp. hosts had resumed 1998 levels, but, on *A. palmata*, remained smaller than the

initial survey. Snail size distributions appear to be site-specific, somewhat confounding analysis of higher-level factors such as stand structure or management scheme.

## INTRODUCTION

Geographically widespread (e.g. Aronson and Precht 2001) and locally intense (e.g. Miller et al. in press) declines in populations of the only two fast-growing reef-building corals in the Caribbean, the elkhorn coral *Acropora palmata* and the staghorn coral *Acropora cervicornis*, led to their designation in 1999 as Candidate Species under the US Endangered Species Act (Diaz-Soltero 1999). Aronson and Precht (2001) offer an extensive review of this regional decline and argue that white band disease was the primary culprit on the Caribbean-wide regional scale, with more localized losses being caused by hurricane damage. Jamaica was an area devastated by Hurricane Allen in 1980. *A. cervicornis* suffered a 100-fold decrease in density, whereas the densities of its predator, the gastropod *Coralliophila abbreviata* remained close to pre-storm levels (Knowlton et al. 1981, 1990). Live coral fragments, potentially able to reattach themselves and form new, healthy stands, were eaten by surviving *C. abbreviata* populations, arresting the recovery process of the staghorn corals.

As recently emphasized by the Florida Keys National Marine Sanctuary (FKNMS) Science Advisory Panel ([http://www.fknms.nos.noaa.gov/research\\_monitoring/sap2000.html](http://www.fknms.nos.noaa.gov/research_monitoring/sap2000.html)), declining coral populations in the Florida Keys demand attention to identifying causes and implementing management strategies aimed at arresting this decline. Given the documented decline in Acroporid coral abundance throughout the Sanctuary, the current study was begun in 1998 to monitor remnant *Acropora palmata* patches in the upper Keys and the status of resident corallivorous snails, *Coralliophila abbreviata*, as one of these causal threats. Snail feeding has been shown to remove an average of  $3.37 \text{ cm}^{-2} \text{ colony}^{-1} \text{ day}^{-1}$  of live *A. palmata* tissue on FKNMS reefs (Miller 2001).

## HYPOTHESES

The primary hypothesis that instigated the study was that snail impact on *A. palmata* had been enhanced over time due to fishery removal of predators of the snail. With no-take reserves established in FKNMS in 1997, the opportunity arose to compare snail populations in reserves where predation should resume and in reference sites. Similarly, we hypothesized that declining snail populations would result in *A. palmata*

enhancement (i.e., increased cover/density or less decline) in the reserves compared to reference sites. Thus, surveys were undertaken in both No-take reserves and in reference (fished) sites to examine the effect of different management regimes on snail populations (abundance and size structure) and on *A. palmata*. Corallivorous snails, *C. abbreviata*, are found on many other scleractinian corals, though they usually cause less obvious damage on these alternate hosts than on *A. palmata*. For comparison, snail populations were concurrently censused on an alternate host taxa, *Montastraea* spp. (*annularis* complex).

Some secondary hypotheses evolved during the study that will also be discussed in this report:

1. The structure of existing *Acropora palmata* stands (thickets vs. low density (LD) patches) differed between sites and has been shown to affect resident snail populations (Baums 2000, Baums et al. (in revision, a)). Coral cover can also differ regionally, so inherent site differences needed to be explored as a potential confounding factor when comparing management regime:
  - a. Does *A. palmata* live cover differ between sites?
  - b. Do snail populations (abundance and size structure) differ between hosts (LD or thicket *A. palmata* or *Montastraea* spp.)?
  - c. Do snail populations differ between sites (snails resident on *Montastraea* spp. were used as an ‘outgroup’ to evaluate site-dependent differences in snail populations not directly associated with *A. palmata* population status)?
2. After initial surveys in May 1998 a mass-bleaching event occurred in the Florida Keys (Causey et al. 2000, pers. obs.) and Hurricane Georges (category two) made landfall in Key West on September 25, 1998. Two sites were resurveyed in October of 1998 to document hurricane damage. Though these major disturbances may obscure our initial hypotheses, the 1999 through 2001 surveys present an opportunity to document post-disturbance trends in both coral and snail populations:
  - a. Did the 1998 bleaching/hurricane disturbance affect *A. palmata* cover?
  - b. Did the 1998 bleaching/hurricane disturbance affect snail populations?



3. Ultimately our initial hypotheses must be evaluated in the context of both a change in management regime and major disturbance:
  - a. Is ‘recovery’ (increased *A. palmata* cover, decreased snail abundance) from the 1998 disturbance enhanced in the reserves compared to the reference sites?

## METHODS

### Field Surveys:

The study sites were offshore bank reefs in the northern sector of the Florida Keys National Marine Sanctuary (FKNMS), Florida, USA (Fig 1, Table 1) where *A. palmata* populations were known to persist. *A. palmata* and their resident *Coralliophila abbreviata* populations were surveyed at 6 offshore sites, three no-take reserves, called Sanctuary Protected Areas (SPAs), and three reference (fished) sites.

Annual surveys of *A. palmata* patches at each site were undertaken in May each year from 1998 to 2001. At the southern study sites, *A. palmata* patches were small and of low density in which case all colonies were sampled and the area of the patch was measured (fully censused). These sites (French, Molasses, and Pickles) are subsequently referred to as “low density,” or LD, *A. palmata* stands (Fig. 1). The three northern sites had extensive patches of higher colony density which we termed “thickets” (Fig. 1). The large thickets at South Carysfort and Horseshoe were subsampled using haphazard belt transects. At Little Grecian, the thicket was small and so this patch was fully censused, like the LD sites. In all years but 2000, each standing colony was measured (length and width to nearest decimeter) and its condition assessed by estimating percent of colony surface with live tissue (% in five categories 0-10, 10-25, 25-50, 50-75, 75-100) as well as the presence of disease, damselfish, etc. From these measurements a live area index (LAI) was calculated (Length \* Width \* % live / 100) as a rough estimate of live coral cover (or size) for the irregular, arborescent colonies. Each colony was then searched for snails, *Coralliophila abbreviata*, which, when found, were counted, measured, and returned to the colony (n= 21-165 snails per site per year). Loose fragments were not measured but were classified as small/medium/large (<25cm/25-100cm/>100cm) counted, and searched for snails. Thus, fragments are included in the reported snail

parameters (e.g. snails per colony) but not in the parameters of *A. palmata* size and condition. In 2000, only snail counts and measurements were conducted, not *A. palmata* size and condition. An additional survey of *A. palmata* size and condition was conducted at two sites (Little Grecian and Horseshoe) in Oct 1998 to assess the impact of Hurricane Georges.

Several *Montastraea* spp. colonies (n=5-24 colonies) were haphazardly chosen in the vicinity of the *A. palmata* patches at each site. These colonies were also measured to the nearest decimeter (length, width, height), live surface cover was estimated, and resident snail populations were surveyed (n=20-168) for comparison to *A. palmata* snail populations (Table 1).

### **Statistical Methods:**

#### ***Acropora palmata***

The effect of Hurricane Georges on the LAI of standing colonies (n=62-118) at Little Grecian and Horseshoe was tested by 2-way ANOVA (SITE and HURRICANE) on transformed ( $X'=\ln(X)$ ) data (to achieve normality and equal variances). Change over time (YEAR) in the total “amount” of *A. palmata* at the four fully censused sites (as both total number of colonies + fragments or as total LAI) was tested by Repeated Measures ANOVA on Ranks. Repeated Measures analysis was used in this case because the sites were considered replicates (n=4) and the same sites were sampled each year. The change in average condition (estimated % live surface) of all standing colonies (sites pooled, n=472-333) was tested by one-way ANOVA (YEAR) after verifying normality and equal variance assumptions.

The incidence of specific conditions of *A. palmata* colonies (i.e. Threespot Damselfish, or white band disease) was expressed as a proportion of colonies at each site. Overall snail prevalence on the *A. palmata* population was expressed as the mean number of snails per sampled colony. This parameter did not meet normality and equal variance assumptions and was not aided by standard transformations. Hence, temporal trends were tested by 1-way ANOVA on Ranks followed by Dunn’s pairwise post-hoc comparisons. Though there is not adequate site-replication to statistically test the effects

of LD versus thicket and reserve vs. reference sites with any sort of power, these group means were plotted for inspection.

### ***Coralliophila abbreviata***

The lengths of snails infesting different hosts (LD *A. palmata*, thicket *A. palmata* and *Montastraea* spp.), were compared between years (1998 through 2001) and between no-take reserve and reference sites. Length data were transformed ( $X' = X^{1/2}$ ) and analysis of variance (ANOVA) using general linear model (GLM, Statsoft Inc., 1995) was performed to evaluate the effects of host, year and reserve status on the mean length of snails on *A. palmata*. Pair-wise contrasts were considered significantly different when the least squares mean " 95% confidence interval did not overlap.

In this 'reserve' model both the reserve and host effects are potentially confounded by a 'site effect' caused by unbalanced design. Thus a 'site specific' model was also run to isolate site differences (sites: SC, LG, HS, ML, FR, PI), and included year and host factors to identify any significant interactions. Size frequency distributions were constructed using 1mm size intervals to visually compare the size-structure of the populations between hosts, years, and sites.

## RESULTS:

### ***Acropora palmata***

*Acropora palmata* suffered dramatic losses between the May 1998 and the May 1999 survey, coinciding with a severe bleaching incident associated with the 1997-98 ENSO event and the passage of Hurricane Georges along the Florida reef tract (25 Sept 1998). In the initial survey of May 1998, a total of nine isolated patches were sampled at the six sites. Two of these nine patches (22%) had undergone complete mortality by the May 1999 survey and are excluded from the data presented here. An additional reserve site (Grecian Rocks) where ~100 colonies were lost from additional between 1998 and 1999 is also excluded from the following presentation. These disappearing patches (one at French and one at Little Grecian, and the Grecian Rocks site) represents a loss of ~220 *A. palmata* colonies between 1998 and 1999.

Supplemental surveys of *A. palmata* at two thicket sites (LG and HS) in Oct. 1998 suggest that Hurricane George increased the proportion and abundance of small and medium fragments and decreased the size of standing colonies at both of these sites (Fig. 2). In contrast, very few fragments were found in qualitative observations (and subsequent surveys) at the LD sites suggesting that the thicket structure aided in retaining hurricane-generated fragments.

At all four fully-censused sites (PI, FR, ML, LG), the total “amount” of *A. palmata*, expressed either as total colony abundance or total LAI, showed drastic decline between 1998 and 1999 and has shown only marginal recovery from 1999 to 2000 (Fig. 3). Repeated measures ANOVA on ranks showed significant decline in total LAI over the three survey years ( $p=0.042$ ). However, total *A. palmata* abundance (standing colonies + fragments) at LG, the only thicket in this comparison, remained quite stable (Fig. 3A).

The average condition (estimated % live surface) of all *A. palmata* colonies declined slightly but significantly ( $p=0.034$ ) from 1998 to 1999, but had recovered by 2001 to the original level of ~ 60% (Fig. 4). The prevalence of specific conditions such as infestation by threespot damselfishes (*Stegastes planifrons*) or of white band disease (WBD) are shown in Fig. 5. WBD prevalence is <3% on average. Damselfishes occupied an average of 30-40% of *A. palmata* colonies throughout the study. No clear patterns in these parameters were evident between thicket vs. LD, nor reserve vs. reference sites.

### ***Coralliophila abbreviata***

Snail density (number of snails per surveyed colony, Fig. 6 A) increased significantly from 1998 to 1999 and from 1999 to 2000 (Dunn’s  $p<0.05$ ), then dropping in 2001 to a level intermediate between (and not different from) 1999 and 2000. No-take reserve sites and reference sites showed very similar trends. Thickets had consistently lower snail densities than LD sites (Fig 6B & C).

Snail lengths differed among coral hosts and years as well as between reserve and reference sites. All main effects (year, host, and reserve status) and interactions to the third degree were significant (Table 2).

### Host Effect

Inspection of the size structure of snail populations living on different hosts (Fig. 7) reveals predominantly smaller snails (15 to 20 mm quartile range in shell length) on *Montastraea* spp. compared to *A. palmata*. Further, within *A. palmata*, thicket stands hosted relatively larger snails (22 to 34 mm quartile range in shell length) than the LD stands (18-28 mm quartile range in shell length). Snail length was significantly different among the three host levels (ANOVA,  $p < 0.0001$ ). Snails from *Montastraea* spp. were significantly smaller (17.4 " 0.47; LS mean, 95% CI) than snails from LD *A. palmata* hosts (22.4 " 0.58), which were significantly smaller than snails from *A. palmata* thickets (28.5 " 0.51)(Figure 8).

### Year Effect

The size structure of the snail populations found on each host also changed between 1998 and 2001. Most notably, the frequency of larger snails on LD *A. palmata* (>22mm length) decreased between 1998 and 1999 (Fig. 9).

*A. palmata* snails were significantly smaller in 2001 than 1998 while *Montastraea* spp. snails were not (significant host \* year interaction; Fig. 10). When all hosts are considered together, mean snail length was significantly different between years (ANOVA,  $p < 0.0001$ ).

### Reserve Effect

Snail populations sampled from within reserves were significantly larger (24.1 " 0.38) than those from reference sites (21.4 " 0.47) (ANOVA,  $p < 0.0001$ ). The interaction between year, host, and reserve status (Fig. 11) was also significant (ANOVA,  $p = 0.0019$ ) and indicates that for all hosts, the reserve site snails were significantly larger than the reference site snails in 1998, but not significantly different from each other in 2001. This trend appears most significant for the *A. palmata* thicket snails.

### Site Effects

In a second ANOVA model which treated sites separately, significant differences were found between sites (ANOVA Table 3,  $p < 0.00001$ ) and for the interactions Site \* Year (ANOVA,  $p = 0.00005$ ) and Year \* Host ( $p = 0.009$ ). Interestingly, there was no significant interaction between site and host, indicating that similar relative trends were seen among sites regardless of the host (Fig. 12), and that the pattern of snail size among hosts (i.e., thicket *A. palmata* > LD *A. palmata* > *Montastraea* spp.) was consistent across sites.

The size structure of the population reflects the host and site trends (Fig. 13), but also shows that the larger mean length of snails on LD *A. palmata* at FR is due to a relatively high number of large individuals (rather than a shift in mode length), uncharacteristic of snails inhabiting LD *A. palmata* stands.

### DISCUSSION:

Previous work, along with our initial survey indicated that *Acropora palmata* populations in the Florida Keys were likely in a remnant state at the beginning of the current study (Dustan and Halas 1987, Jaap et al. 1988, Porter and Meier 1992). It is clear that *A. palmata* populations in the upper Florida Keys have undergone further decline since 1998, likely the combined result of the 1998 severe bleaching episode and Hurricane Georges. Several measured parameters as well as informal observations suggest that some recovery from this major disturbance has occurred between 1999 and 2001. For example, the average estimated proportion of live surface for standing colonies had resumed its 1998 level by 2001 (Fig. 4). Also, snail densities appear to have peaked and begun to decline by 2001 (Fig. 6). Observations of individual *A. palmata* branches at Little Grecian and Horseshoe reefs from which small tissue samples had been collected for population genetic analysis showed vigorous growth during summer 2001 (Miller & Baums, pers. obs.).

In contrast, the more comprehensive parameters which we calculated to represent the total amount of *A. palmata* at the fully censused sites do not show this clear recovery pattern. The total number of *A. palmata* colonies (including fragments) and the total LAI

at the three LD stand sites do not show any recognizable recovery since a precipitous 98-99 drop (Fig. 3). In contrast, Little Grecian, the only thicket site that was fully censused, did not show much decline in either total LAI nor total number of *A. palmata* colonies. This contrast may be attributable to differential retention of hurricane-generated fragments between thickets and LD stands. Fragment retention after Hurricane Georges (Fig. 2) likely resulted in the stability of total *A. palmata* at Little Grecian (Fig 3) and, perhaps, other thicket sites, whereas at LD sites, hurricane-generated fragments appeared to have been completely exported from the site (Miller, pers. obs.). This stability of *A. palmata* at Little Grecian also suggests that bleaching mortality was a secondary factor with hurricane disturbance being the dominant cause of *A. palmata* loss.

Corallivorous snails also showed significant temporal trends in density (# colony<sup>-1</sup>) and length frequency, seemingly in direct or indirect (i.e. to changes in host coral population structure) response to the 1998 disturbances (hurricane and/or bleaching). Increase in density between 1998 and 1999 was likely due to loss of available habitat (*A. palmata* live area), though abundance has subsequently shown a gradual return toward 1998 levels. The decline in mean snail size from 1998 to 1999 may have moderated their damage to depressed *A. palmata* populations that would be expected to accrue from increased snail abundance.

Host coral species and stand density are consistent predictors of snail population characteristics across sites. Comparisons of snail populations at no-take reserve sites versus reference sites did not support the predictions of our original hypothesis that there would be increased predation on snails in no-take reserves, at least in the time frame of the current study.

Snail damage on *A. palmata* colonies is difficult to quantify and was not measured systematically throughout the current study. However, average snail aggregations of 2-3 individuals consumed 3.37 cm<sup>2</sup> d<sup>-1</sup> of *A. palmata* tissue on colonies within the surveyed populations at French and Pickles (Miller 2001). Hence, the overall densities (snails per colony averaged across all colonies, infested and uninfested) of 0.5 in 1998 to a high of almost 1.5 in 2000 represent a substantial threat to remnant populations of *A. palmata* (i.e. the loss of over 1 cm<sup>2</sup> of live tissue per colony per day). This chronic loss of *A. palmata* live area to predation is compounding what can clearly be dramatic losses to acute

disturbances such as bleaching or hurricane damage.

Overall, during the study period, substantial loss of *A. palmata* has occurred in the upper FKNMS and no meaningful recovery in abundance is evident.



## FIGURE LEGENDS

**Figure 1.** Map (A) showing the study sites in the Key Largo area of the Florida Keys National Marine Sanctuary. Site abbreviations as in Table 1, and those inside a box indicate no-take reserve status. Photos illustrate a thicket stand of *Acropora palmata* characteristic of the three northern sites (B) and an isolated colony from a low-density (LD) stand characteristic of the three southern sites (C).

**Figure 2.** *A. palmata* fragments and standing colonies surveyed at two thicket sites (240 m<sup>2</sup> at Horseshoe and 80m<sup>2</sup> at Little Grecian) before (May 1998) and after (October 1998) Hurricane Georges. Mean (+ 1SE) Live Area Index (LAI, see METHODS) for standing colonies (A; p-values from two-way ANOVA on ln-transformed data) and abundance of fragments in different size classes (B) found in May and Oct. 98.

**Figure 3.** Total “amount” of *A. palmata* at the four sites where *A. palmata* patches were fully censused. A) *A. palmata* abundance and B) sum of LAI for all standing colonies (p-value for Repeated Measures ANOVA on Ranks).

**Figure 4.** Mean (+ 1SE) estimated condition (live surface area of each colony) of all surveyed *A. palmata* colonies. P-value from one-way ANOVA; n is given in each bar.

**Figure 5.** Proportion of sampled corals at each site observed to display threespot damselfish (*Stegastes planifrons*, df) occupation (A) and white band disease (WBD, B). The red symbols with error bars represent the mean of all the sites and 1 standard error (n=6 sites).

**Figure 6.** *Coralliophila abbreviata* density expressed as number of snails per surveyed coral. Panel A) shows means for colonies at individual sites with the overall mean (SE) in red (n=395-947 colonies). Years with the same letter designation do not differ statistically by Dunn’s post-hoc pairwise comparisons following Kruskal-Wallis ANOVA. The other panels show the same site means averaged (SE) according to stand

structure (B) and reserve status (C) of the sites (n=3 sites).

**Figure 7.** Size-frequency distribution of snails resident on *A. palmata* low density (LD) and thicket stands, and *Montastraea* spp. colonies from all sites censused between 1998 and 2001. Median ( $\diamond$ ) length and inter-quartile range (|—|) shown on figure along with total number of snails measured.

**Figure 8.** Square-root transformed length of snails (least squares mean  $\pm$  95% confidence interval) found resident on different host corals (low density (LD) and thicket *A. palmata* stands, and *Montastraea* spp.) from all sites censused between 1998 and 2001.

**Figure 9.** Size-frequency distributions of snail populations by year and host. Number of snails measured shown on figure. Note different scales on the y-axes.

**Figure 10.** Two-way interaction between the effects of year and host (pooled all sites) on the length (square root-transformed) of snails (least squares mean  $\pm$  95% confidence interval). See Table 2 for significance levels and Figure 9 for number of snails measured.

**Figure 11.** Three-way interaction (Table 2) between the effects of year, host and reserve on the length of snails (square-root transformed).

**Figure 12.** Two way interaction between the effects of site and host (pooled years) on the length (square root transformed) of snails (least squares mean  $\pm$  95% confidence interval). Circled sites are those located within no-take reserves. See Table 3 for significance levels and Figure 14 for number of snails measured.

**Figure 13.** Size-frequency distributions of snail populations by host and site (pooled years 1998 through 2001). Number of snails measured shown on figure.

**Table 1.** Study sites and summary of *A. palmata* and *Montastraea* spp. surveys. Initial *A. palmata* area denotes the reef area surveyed in 1998 (band transects in thickets and rough area estimated for area occupied by low density (LD) patches). All the low density stands had regressed in area substantially by 1999. SC=South Carysfort Reef, HS=Horseshoe Reef, LG=Little Grecian Reef, FR=French Reef, ML=Molasses Reef, PI=Pickles Reef. Na=not applicable. Reserve sites are within no-take Sanctuary Preservation Areas (SPA's) while the Reference sites are fished. *Montastraea* spp. snail surveys were discontinued at Little Grecian after the first year because a large collection of *Montastraea* spp. snails was made at this site for laboratory studies in Jan 1999.

Site	Reserve Status	<i>A. palmata</i> Stand Structure	Initial <i>A. palmata</i> Area Surveyed (m <sup>2</sup> )	# <i>Montastraea</i> Colonies Surveyed			
				1998	1999	2000	2001
SC	Reserve	Thicket	240	24	22	19	15
HS	Reference	Thicket	240	18	9	9	13
LG	Reference	Thicket	80	14	NA	NA	NA
FR	Reserve	LD	308	5	19	40	20
ML	Reserve	LD	552	21	14	22	18
PI	Reference	LD	440	9	11	20	15

**Table 2.** Full ‘reserve’ model ANOVA table for year, host (3 levels: LD *A. palmata*, thicket *A. palmata*, or *Montastraea* spp.) and reserve (no-take reserve or reference) effects on snail length (square root transformed).

Factor	SS	df	MS	F	p
Year	43.0	3	14.35	34.90	<0.0001
Reserve	32.0	1	32.01	77.86	<0.0001
Host	415.9	2	207.94	505.77	<0.0001
Year*Reserve	5.0	3	1.68	4.09	0.0066
Year*Host	9.2	6	1.53	3.73	0.0011
Reserve*Host	3.3	2	1.64	3.99	0.0186
Year*Reserve*Host	8.6	6	1.43	3.48	0.0020
Error	1256.4	3056	0.41		

**Table 3.** Full ‘site specific’ model ANOVA table for year, host (three levels) and site (six levels) effects on snail length (square root transformed).

Factor	SS	df	MS	F	p
Year	49.1	3	16.37	41.38	<0.0001
Site	52.7	5	10.54	26.65	<0.0001
Host	309.2	2	154.60	390.73	<0.0001
Year*Site	18.4	15	1.22	3.09	<0.0001
Year*Host	6.8	6	1.13	2.85	0.0091
Site*Host	3.6	4	0.89	2.25	0.0612
Year*Site*Host	13.0	8	1.63	4.12	<0.0001
Error	1201.2	3036	0.40		

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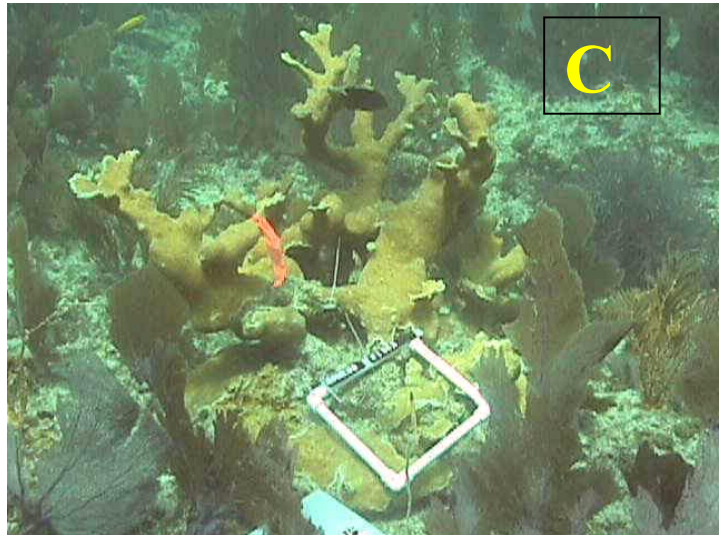
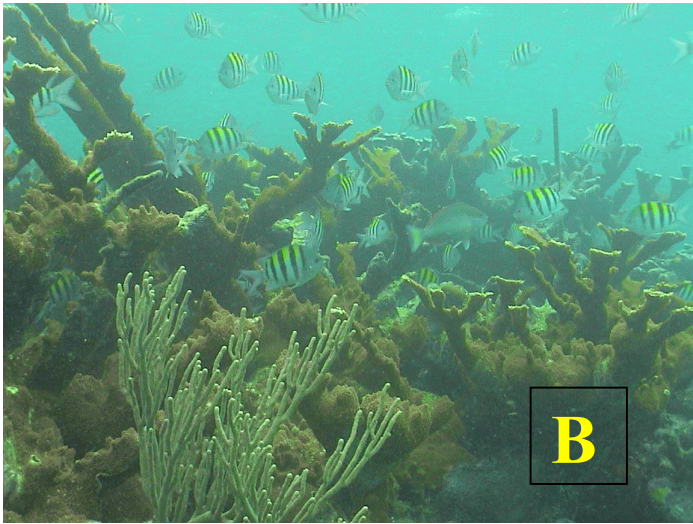
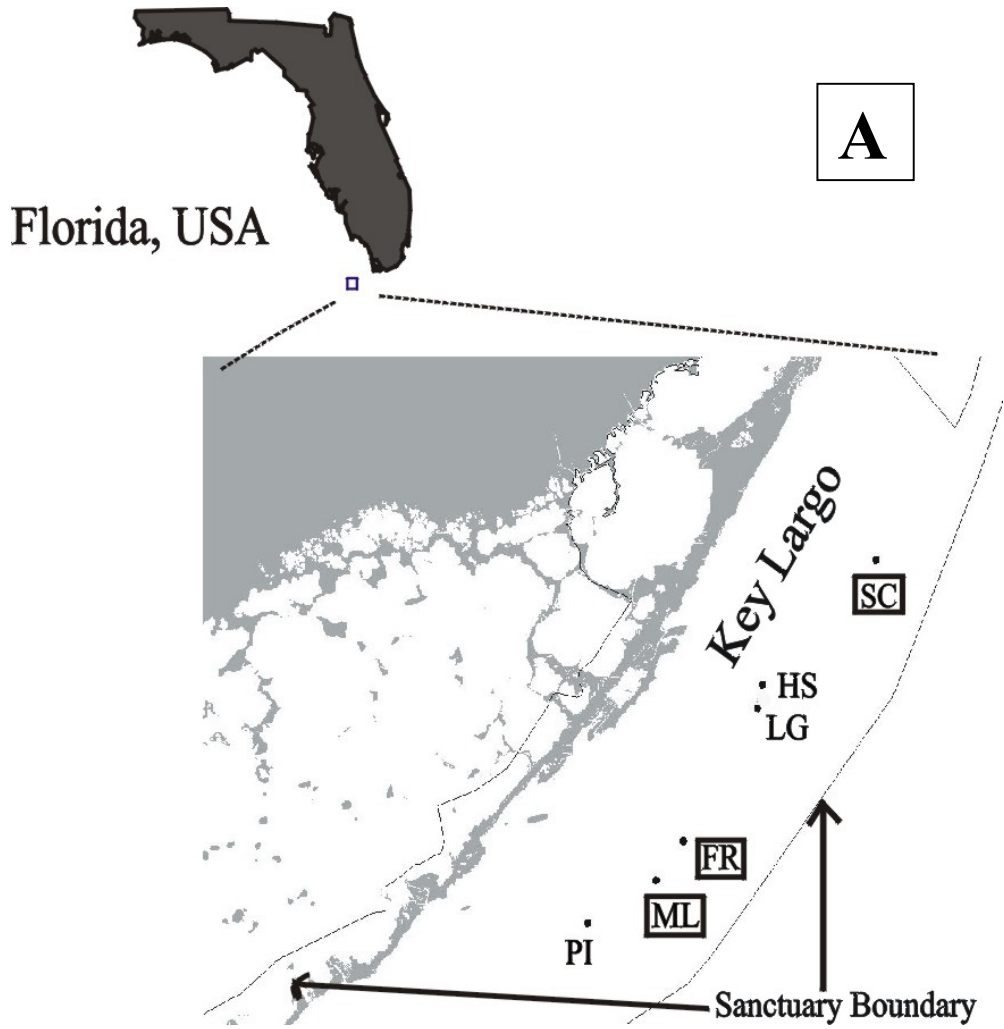


Fig. 1

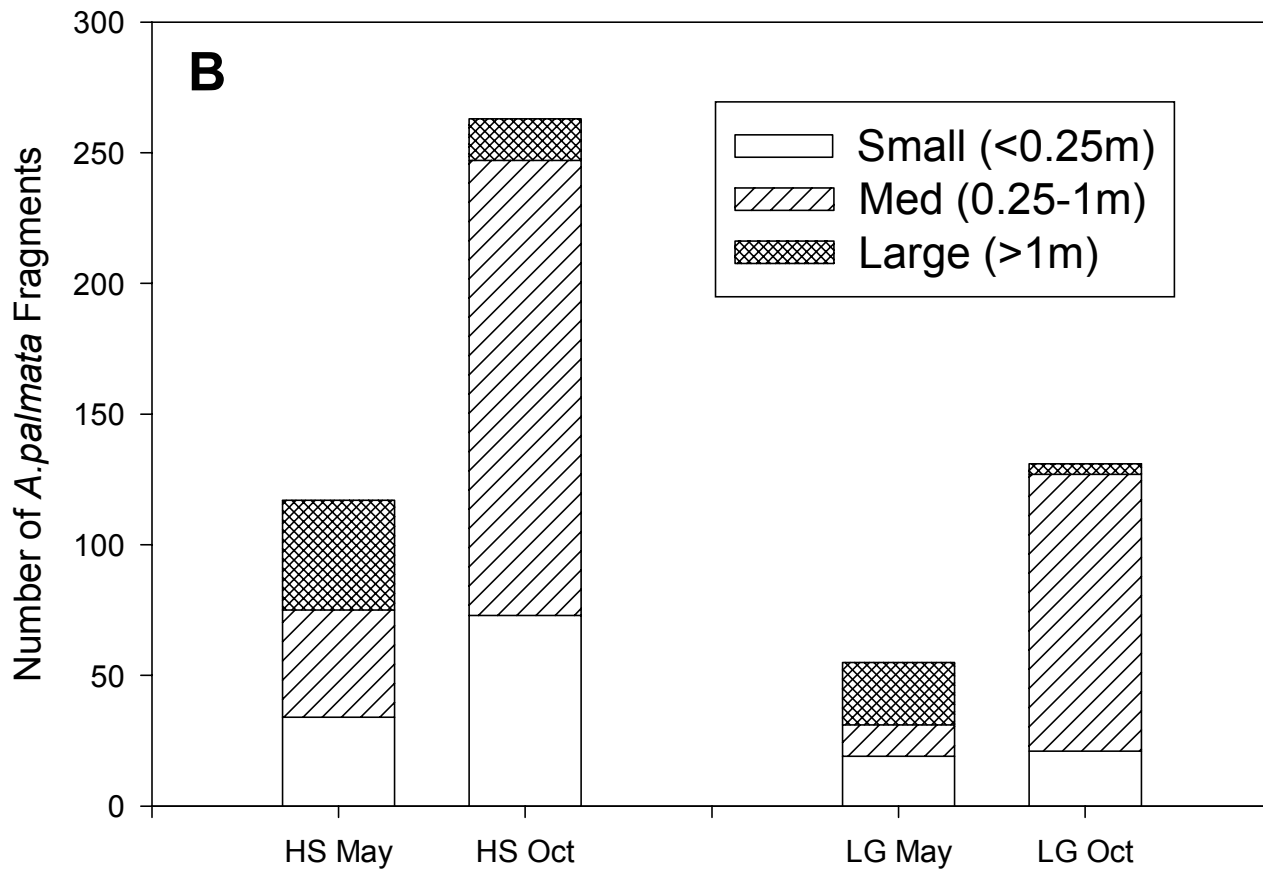
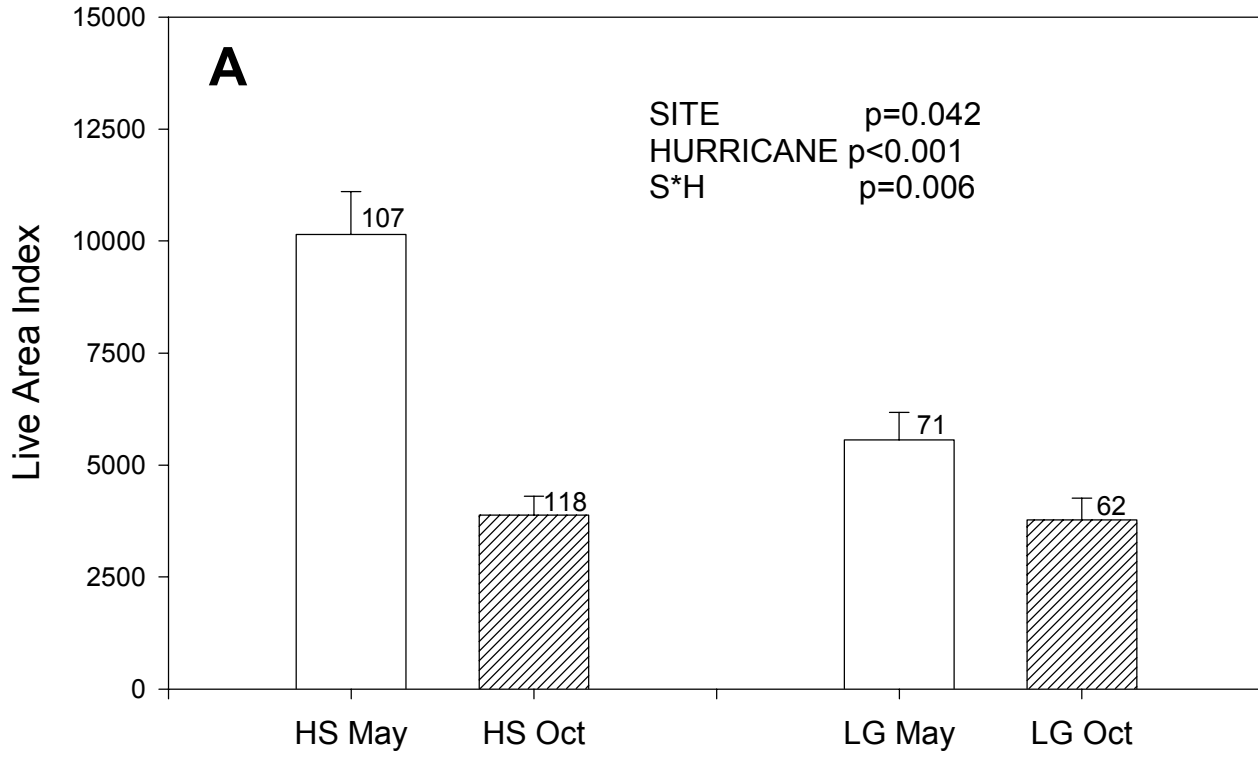


Fig. 2



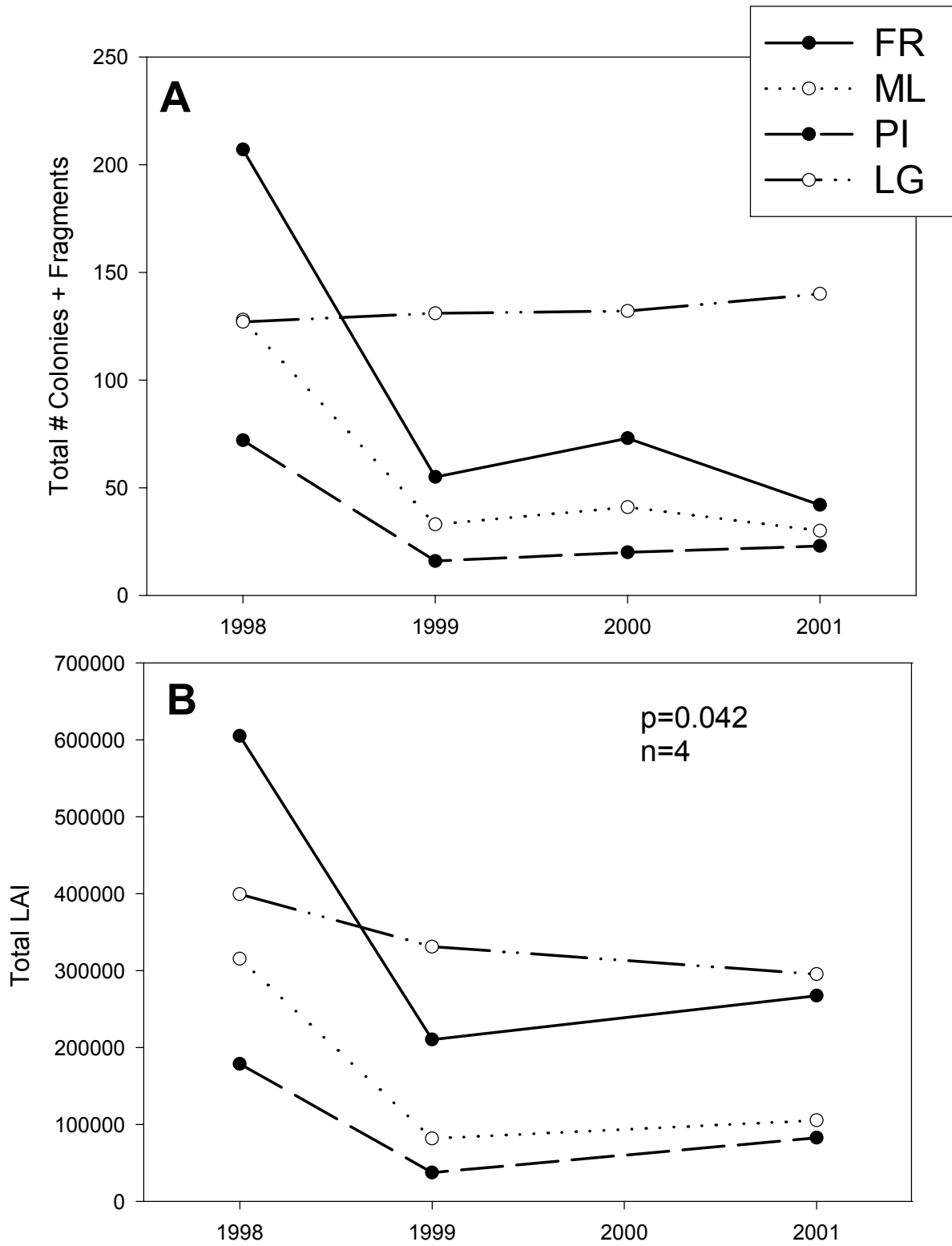


Fig.3

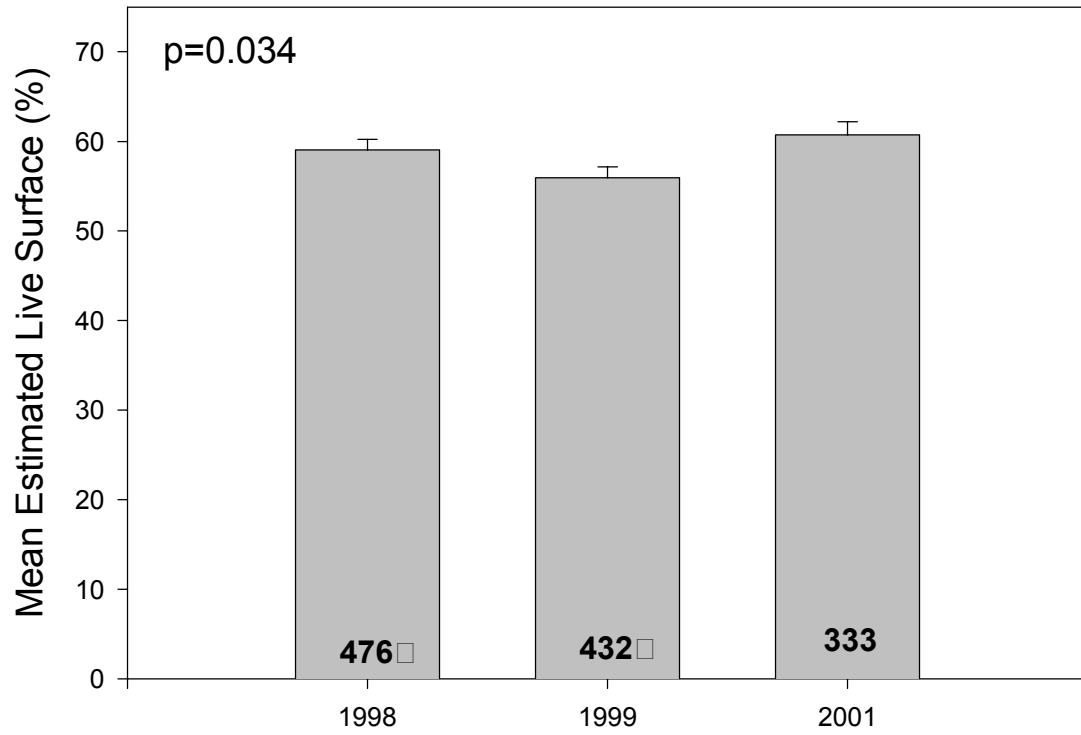


Fig 4

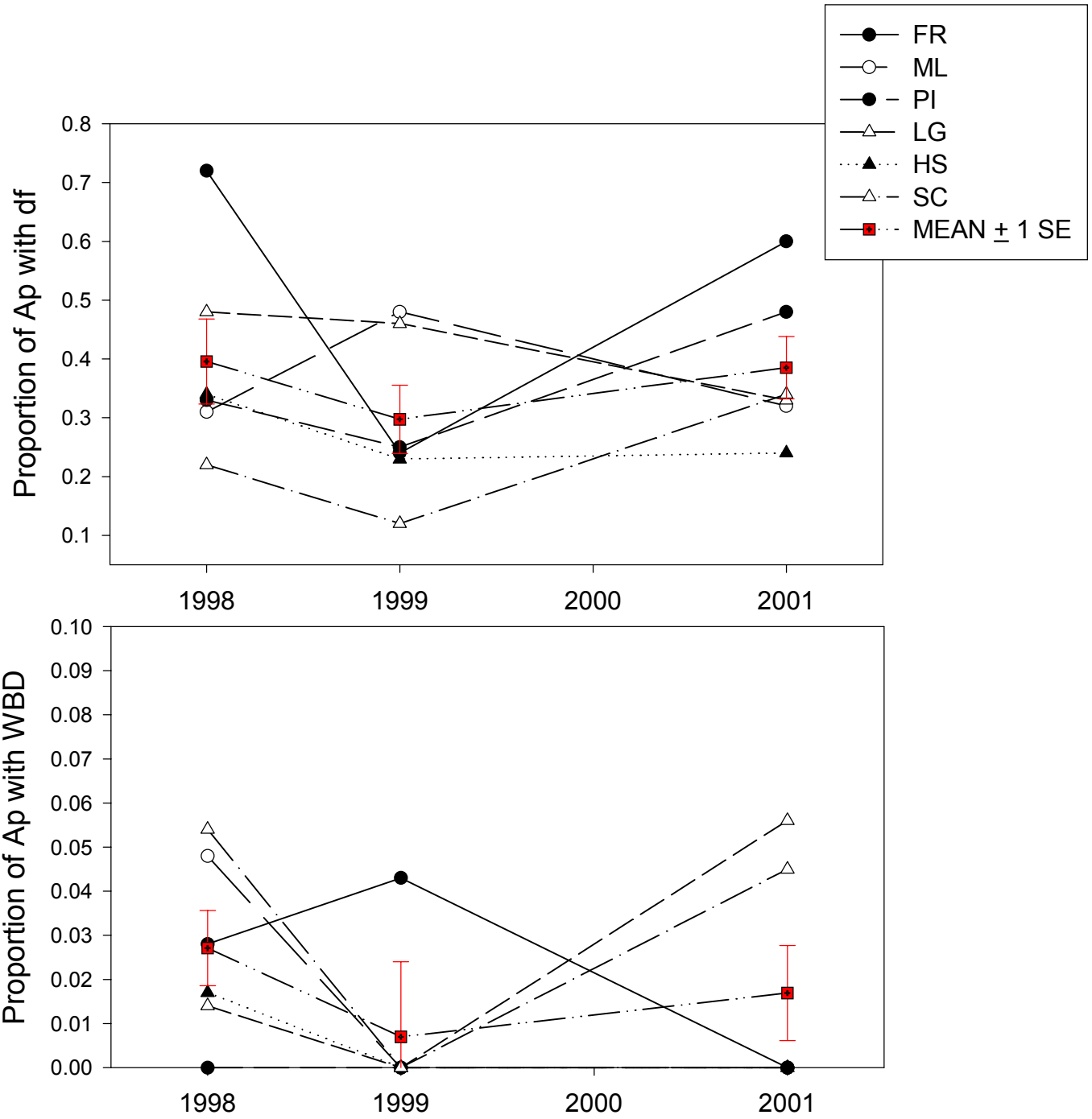


Fig. 5

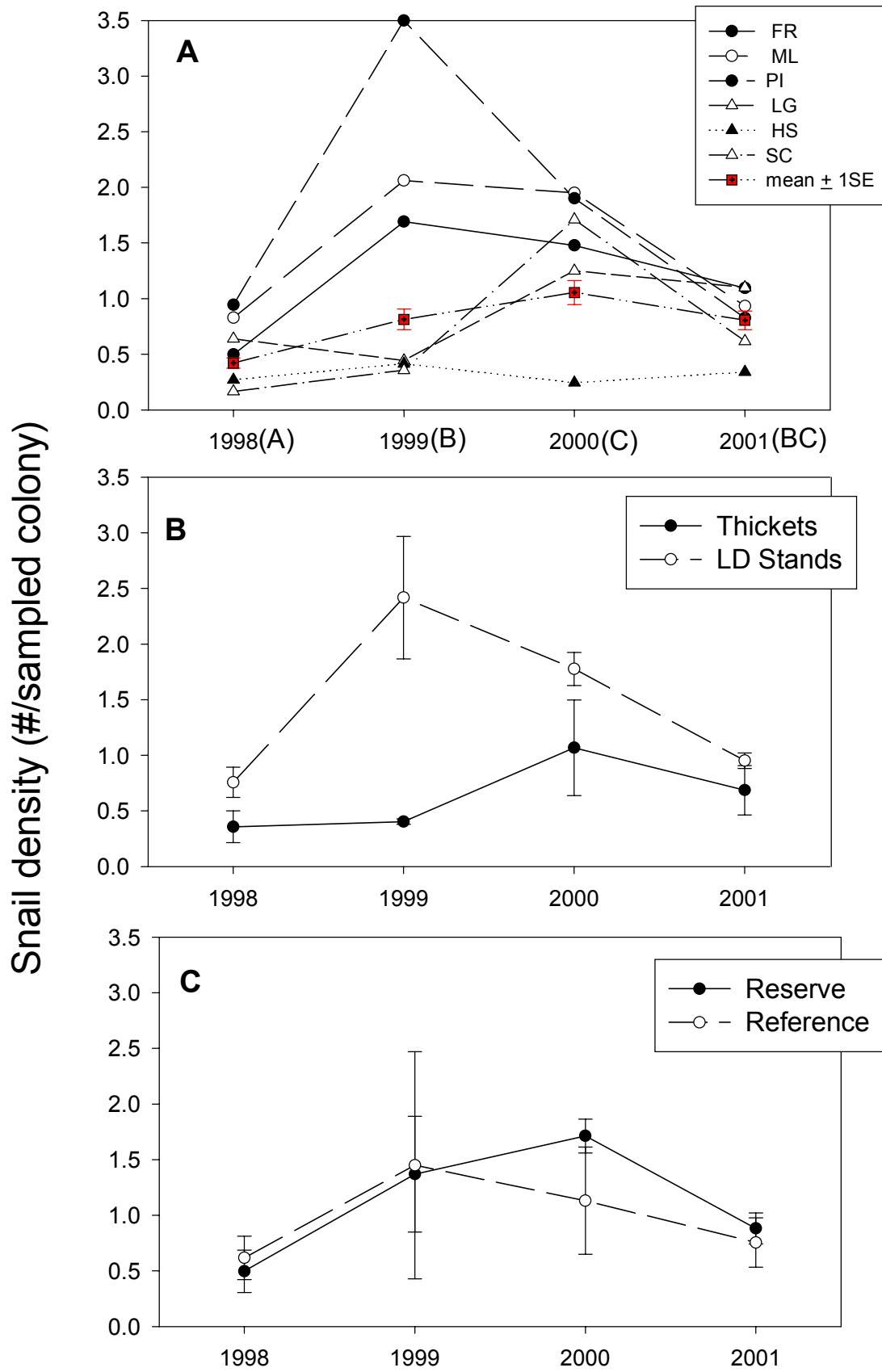


Fig. 6

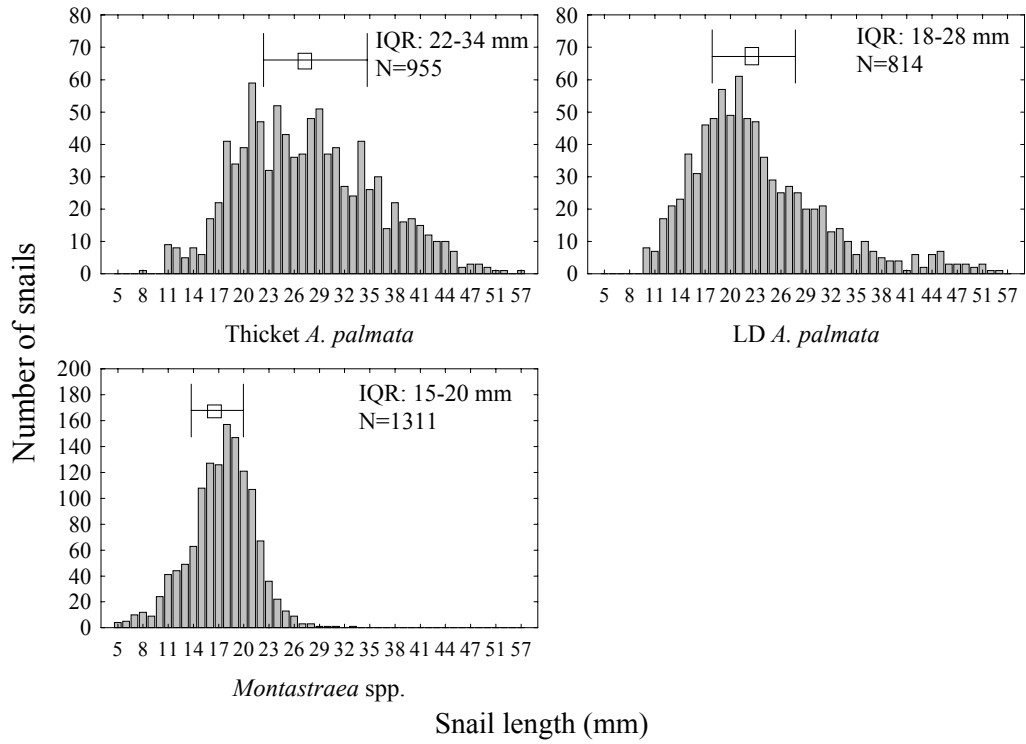


Fig. 7

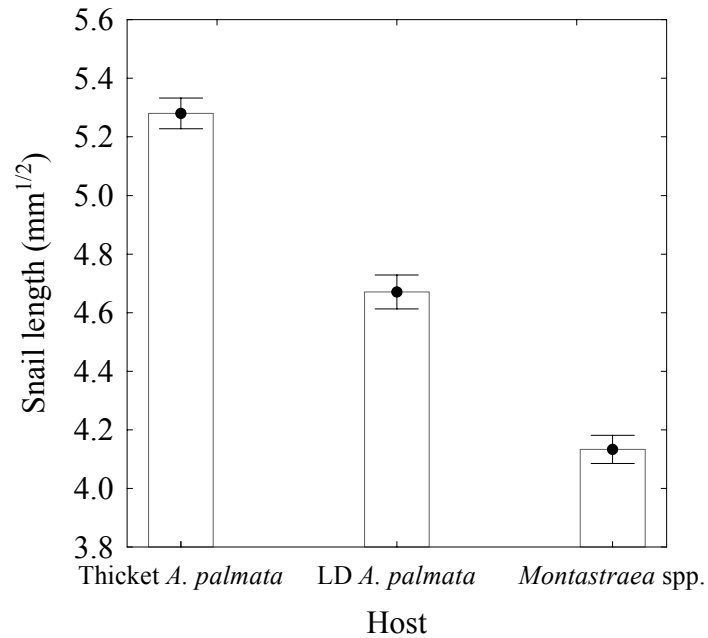


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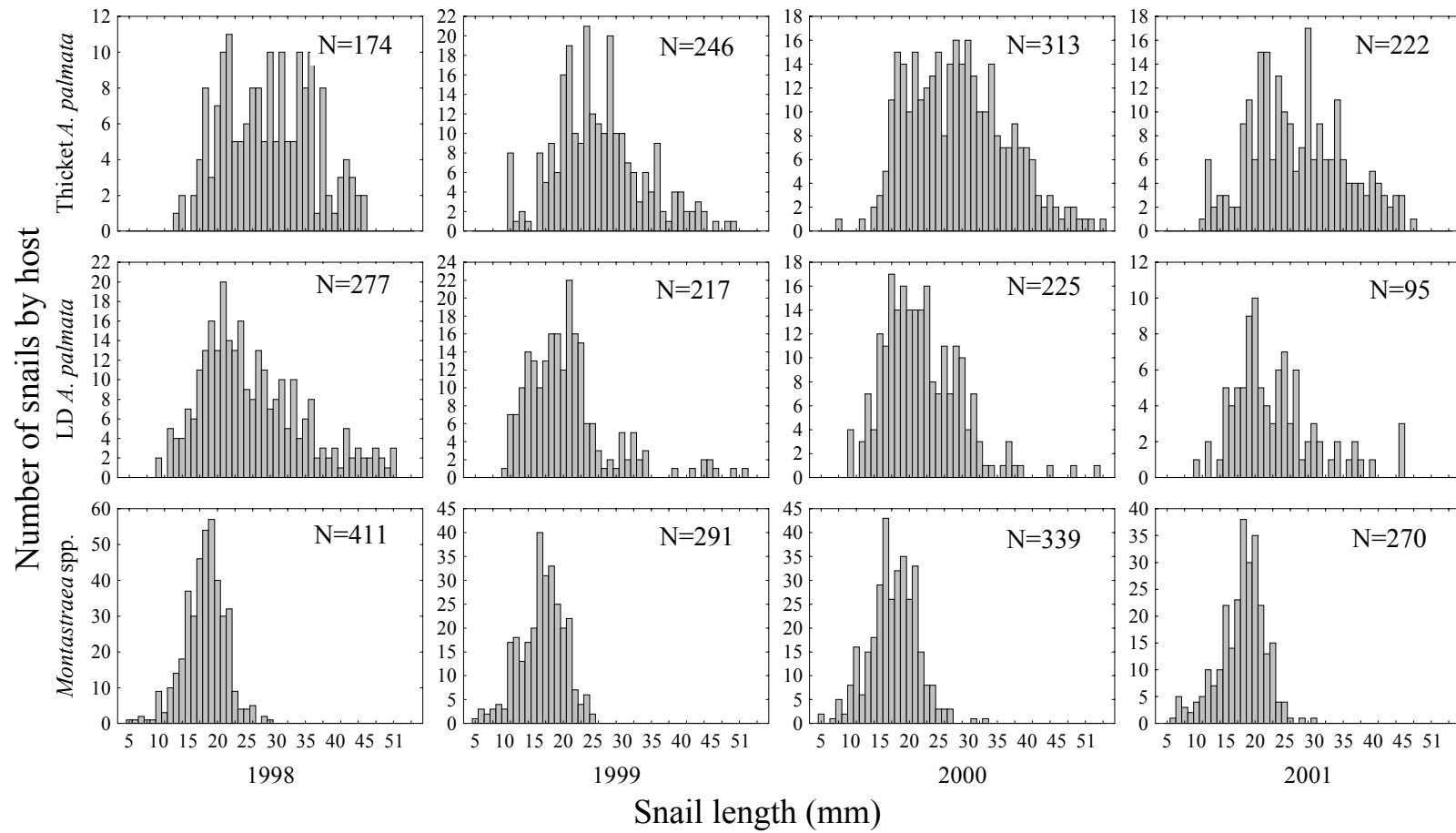


Fig. 9

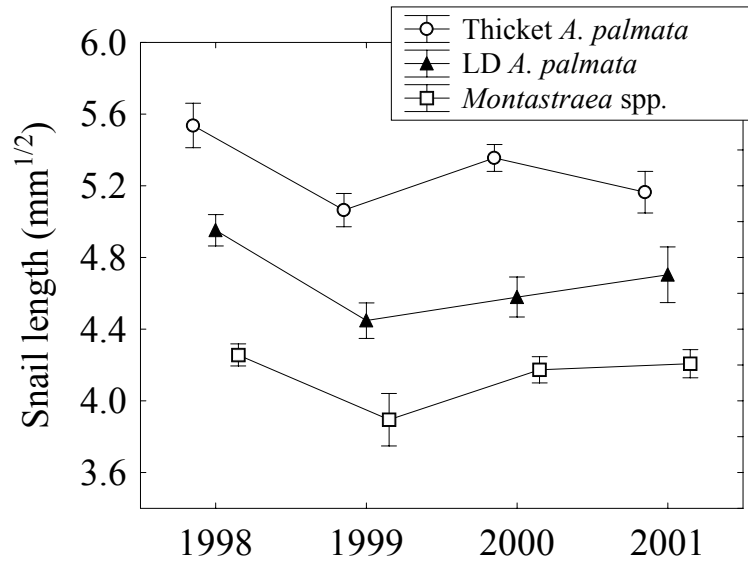


Fig. 10

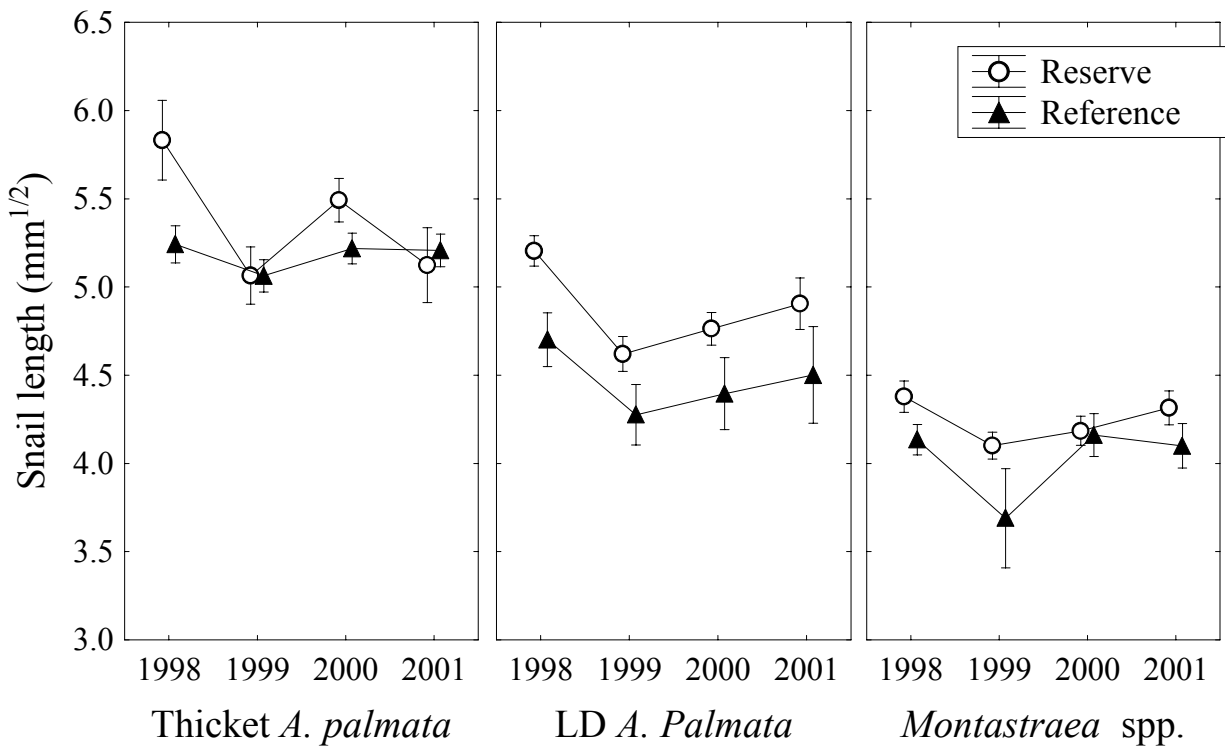


Fig. 11

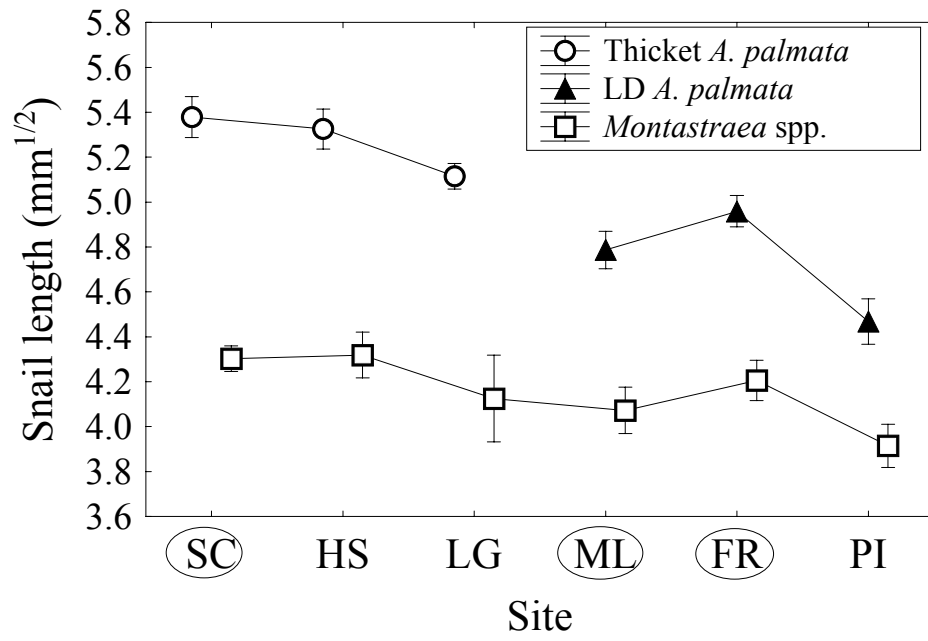


Fig. 12



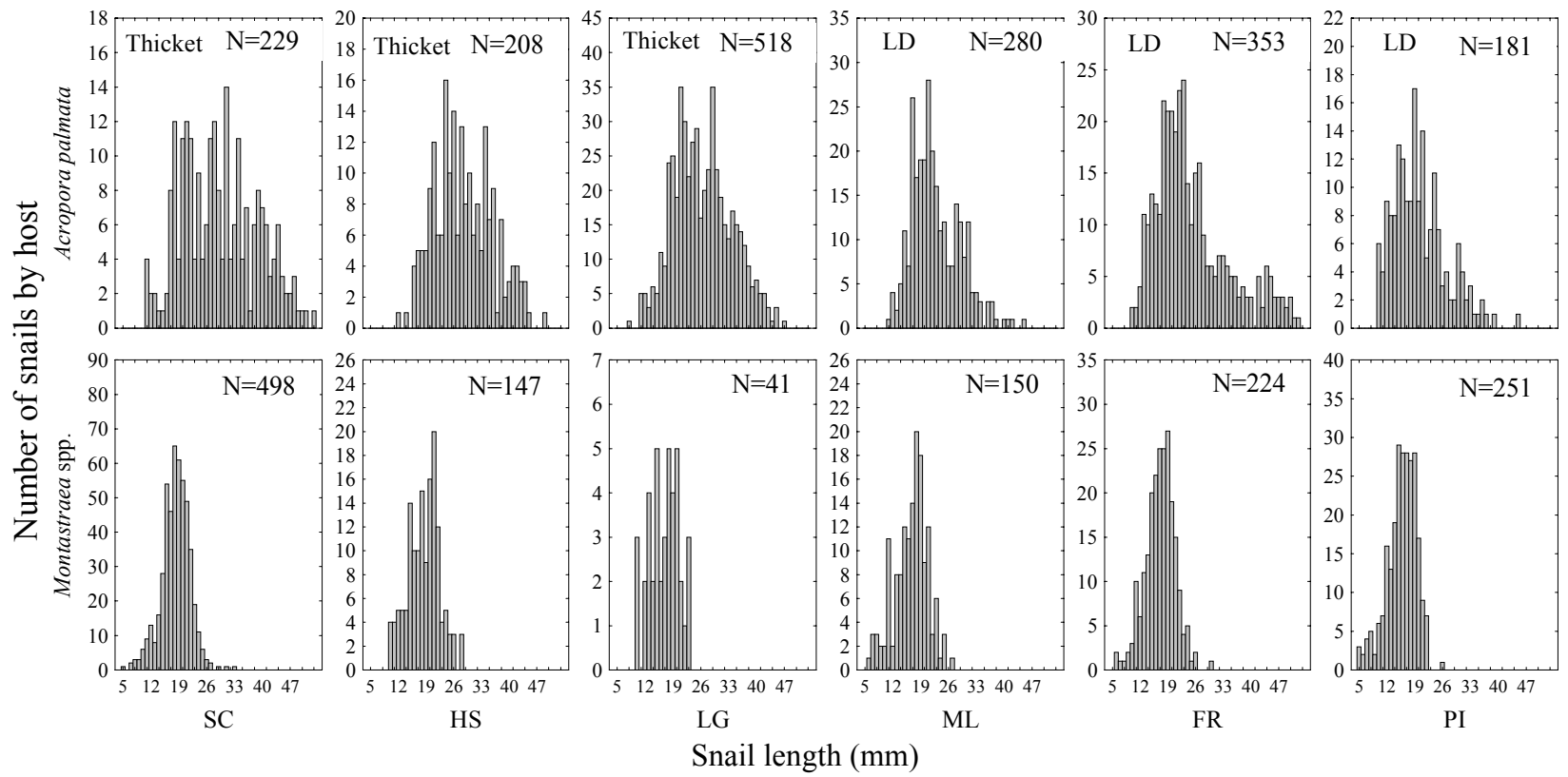


Fig. 13