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Evolutionary Ecology of the Corallivorous Gastropod, *Coralliophila abbreviata*: Implications for Imperiled Caribbean Corals

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UNIVERSITY OF MIAMI

EVOLUTIONARY ECOLOGY OF THE CORALLIVOROUS GASTROPOD,
CORALLIOPHILA ABBREVIATA: IMPLICATIONS FOR IMPERILED CARIBBEAN
CORALS

By
Lyza Johnston

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, FL
May 2012

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EVOLUTIONARY ECOLOGY OF THE CORALLIVOROUS GASTROPOD,
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CORALS

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Evolutionary Ecology of the Corallivorous

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Gastropod, *Coralliophila abbreviata*:

Implications for Imperiled Caribbean Corals.

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Dissertation supervised by Margaret Miller, Ph.D. and Diego Lirman, Ph.D.

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As the resiliency of coral reefs is eroded by a variety of natural and anthropogenic stressors, corallivory is becoming an increasingly important factor affecting the structure and function of these important ecosystems. Yet, little is known about the mechanistic drivers of coral-corallivore dynamics in many regions, including the Caribbean. In this dissertation, I used an integrated approach to investigate the evolutionary ecology of the coral-eating gastropod, *Coralliophila abbreviata*, on the reefs of Florida and the Caribbean. *Coralliophila abbreviata* snails live and feed on most of the major reef-building corals in the region and cause substantial and chronic mortality of the threatened acroporid corals, *Acropora palmata* and *A. cervicornis*. The overall objective of this research was to elucidate feedback mechanisms between coral community structure and snail population structure and dynamics. In the first age-based analysis of *C. abbreviata* populations, I identified remarkable coral-host-associated variation in life-history traits of snails on Florida reefs. Based on estimates of fitness correlates such as growth, longevity, and female reproductive output, *A. palmata* appears to be a superior host for *C. abbreviata* compared to two other common coral taxa investigated (*Diploria* spp. and *Montastraea* spp.). However, host-specific life-history trade-offs may exist for individual snails that act to balance snail population fitness across hosts. I then developed a set of five polymorphic microsatellite loci that were used in conjunction with mitochondrial

cytochrome b sequence data to assess the population genetic structure and demographic history of *C. abbreviata* from three coral host taxa (*A. palmata*, *Montastraea* spp., *Mycetophyllia* spp.) and six geographic locations spanning most of the species' range. I found no evidence of genetic differentiation among the snail populations sampled. Demographic analyses of population genetic data support a scenario of a large population expansion during the Pleistocene, a time of major carbonate reef development in the region. These results indicate that *C. abbreviata* are successful generalist coral predators with unrestricted gene flow throughout the greater Caribbean. On a reef scale, the density and identity of neighboring corals indirectly affected predation pressure on focal *A. cervicornis* colonies in a manipulative field experiment. Snails exhibited a strong feeding preference for *A. cervicornis* during the experiment but the presence of the alternative prey, *M. faveolata*, also contributed to predator abundance in the experimental plots. Thus, *M. faveolata* neighbors had a negative effect on *A. cervicornis* colonies through apparent competition. Overall, these results have implications for coral reef community structure and dynamics. Understanding these processes is necessary to develop effective conservation and management strategies for imperiled corals and predict how these communities will respond to further perturbations in the future.

To my family, whose unwavering support
and belief in me have given me the
strength and confidence to pursue my
dreams.

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TABLE OF CONTENTS

| | |
|--|------|
| LIST OF FIGURES | viii |
| LIST OF TABLES | xi |
| CHAPTER 1: INTRODUCTION | 1 |
| Overview | 1 |
| Theoretical Effects of Predation on Declining Prey Populations | 2 |
| Coral Reef Decline | 6 |
| The Role of Corallivores | 8 |
| CHAPTER 2: VARIATION IN THE LIFE-HISTORY TRAITS OF THE CORALLIVOROUS GASTROPOD, CORALLIOPHIL ABBREVIATA, ON THREE CORAL HOSTS | 15 |
| Overview | 15 |
| Materials and Methods | 17 |
| <i>Collection and Processing</i> | 17 |
| <i>Statistical Analyses</i> | 20 |
| Results | 21 |
| <i>Size and Age Structure</i> | 21 |
| <i>Growth and Mortality</i> | 25 |
| <i>Reproductive Characteristics</i> | 27 |
| Discussion | 33 |
| CHAPTER 3: ISOLATION AND CHARACTERIZATION OF POLYMORPHIC MICROSATELLITE LOCI FOR THE CORALLIVOROUS GASTROPOD, CORALLIOPHILA ABBREVIATA | 41 |
| Overview | 41 |
| Materials and Methods | 46 |
| Results and Discussion | 48 |
| CHAPTER 4: REGIONAL AND HOST-SPECIFIC POPULATION GENETIC STRUCTURE AND DEMOGRAPHIC HISTORY OF CORALLIOPHILA ABBREVIATA | 51 |
| Overview | 51 |
| Materials and Methods | 54 |
| <i>Sample Collection and Processing</i> | 54 |
| <i>Characterization of Genetic Variation</i> | 57 |
| <i>Population Structure Analyses</i> | 58 |
| <i>Demographic History Analyses</i> | 60 |

| | |
|---|-----|
| Results..... | 62 |
| <i>Genetic Variation</i> | 62 |
| <i>Population Genetic Structure</i> | 65 |
| <i>Demographic History</i> | 69 |
| Discussion..... | 71 |
| <i>Population Genetic Structure</i> | 72 |
| <i>Demographic History</i> | 75 |
| <i>Implications for Coral Reef Conservation</i> | 76 |
| <i>Conclusions</i> | 78 |
| CHAPTER 5: FORAGING BEHAVIOR OF CORALLIOPHILA ABRREVIATA IN AN EXPERIMENTAL PATCHY ENVIRONMENT: NEGATIVE INDIRECT EFFECTS OF NEIGHBORS ON AN IMPERILED SCLERACTINIAN CORAL..... | 79 |
| Overview..... | 79 |
| Materials and Methods..... | 84 |
| <i>Experimental Setup</i> | 84 |
| <i>Neighborhood Effects on Focal Colonies</i> | 88 |
| <i>Prey Preference and Neighborhood Selection</i> | 89 |
| <i>Movement and Space Use</i> | 91 |
| Results..... | 91 |
| <i>Neighborhood Effects on Focal Colonies</i> | 91 |
| <i>Prey Preference</i> | 95 |
| <i>Neighborhood Selection</i> | 97 |
| <i>Movement and Space Use</i> | 101 |
| Discussion..... | 104 |
| CHAPTER 6: SUMMARY AND SYNTHESIS..... | 109 |
| Summary..... | 109 |
| <i>Host Effects on Life-History and Fitness</i> | 110 |
| <i>Microsatellite Development</i> | 111 |
| <i>Population Genetic Structure and Demographic History</i> | 113 |
| <i>Foraging Behavior and Indirect Coral-Coral Interactions</i> | 114 |
| Synthesis: Implications for Imperiled Caribbean Corals..... | 116 |
| WORKS CITED..... | 119 |

LIST OF FIGURES

| | |
|---|----|
| Figure 1.1 The three major predator functional responses (number of prey consumed per predator per unit of time as a function of the prey density) and corresponding prey mortality due to predation described by Holling (1959). | 5 |
| Figure 1.2 The theoretical relationship between prey mortality rate due to predation (teal line) and the intrinsic rate of increase of the prey population in the absence of predators (orange line) for Type II (a) and Type III (b) functional responses. Green dots mark stable equilibria and red dots mark unstable equilibria. Redrawn from Sinclair et al (1998). | 6 |
| Figure 1.3 <i>Coralliophila abbreviata</i> snails (indicated with yellow arrows) feeding on colonies of <i>Acropora palmata</i> (a) and <i>Montastraea annularis</i> (b)..... | 10 |
| Figure 1.4 Basic life-cycle of <i>Coralliophila abbreviata</i> in a two prey system. Possible predator mediated indirect interactions between coral host taxa are indicated by dashed arrows (coral and snail illustrations by D.M. Holstein). | 14 |
| Figure 2.1 <i>Coralliophila abbreviata</i> operculum. Annual growth striae are indicated by yellow crosshairs. | 19 |
| Figure 2.2 <i>Coralliophila abbreviata</i> age (a) and size (b) frequency distributions by coral host. . | 23 |
| Figure 2.3 Mean shell length (a) and age (b) of males and females on <i>Acropora palmata</i> (A), <i>Diploria</i> spp. (D), and <i>Montastraea</i> spp. (M). Boxes and whiskers represent 95% confidence limits and minimum and maximum values, respectively. Shell length varied significantly among hosts (Two-way ANOVA; $df = 2$, $F = 159.46$, $P < 0.01$) and between sexes ($df = 1$, $F = 183.72$, $P < 0.01$). Age (# of striae) also varied significantly among hosts (Two-way ANOVA; $df = 2$, $F = 91.96$, $P < 0.01$) and between sexes ($df = 1$, $F = 134.94$, $P < 0.01$). | 24 |
| Figure 2.4 Gompertz growth curves fitted to size-at-age data for <i>Coralliophila abbreviata</i> on the three coral host taxa (ACR: <i>Acropora palmata</i> ; DIP: <i>Diploria</i> spp.; MONT: <i>Montastraea</i> spp.) 26 | |
| Figure 2.5 Relationship between female shell length and total egg capsule area for <i>Coralliophila abbreviata</i> ($n = 84$, $y = 0.0023x^{3.42}$, $R^2 = 0.90$, $P < 0.01$)..... | 29 |
| Figure 2.6 Relationship between egg capsule area and number of veligers for female <i>Coralliophila abbreviata</i> on <i>Acropora palmata</i> (ACR), <i>Diploria</i> spp.(DIP), and <i>Montastraea</i> spp. (MON; $n = 72$, $y = 26.39x + 257.28$, $R^2 = 0.84$, $P < 0.01$)..... | 29 |
| Figure 2.7 Logistic maturity model fitted to the proportion of females at each age (a) and size (b) found on <i>Acropora palmata</i> (ACR), <i>Diploria</i> spp.(DIP), and <i>Montastraea</i> spp.(MONT). The dotted lines correspond to the model predictions for age and size at which 50% of snails are female (γ) for each coral host. The orange symbols are statistical outliers that were not used to fit the model..... | 31 |
| Figure 4.1 Map of major sampling localities across the greater Caribbean. Coordinates for specific reef sites within each locality can be found in Table 1..... | 55 |
| Figure 4.2 Median joining network for <i>cyt b</i> haplotypes from a sample of 130 <i>Coralliophila abbreviata</i> from five geographic locations. Circles represent individual haplotypes. The size of the circle is proportional to the frequency of the haplotype in the sample and branch lengths are | |

| | |
|--|----|
| proportional to the number of mutational steps (range: 1-3). Small black circles represent missing/theoretical haplotypes..... | 64 |
| Figure 4.3 Results of STRUCTURE analysis of five microsatellite loci and 309 individuals of <i>Coralliophila abbreviata</i> . Shown are STRUCTURE plots for K = 2 (a), K = 4 (b), and K = 10 (c), where individuals are groups by sampling locality (1: Bahamas; 2: Curacao; 3: Florida; 4: Navassa; 5: Panama; 6: St. Vincent and the Grenadines)..... | 68 |
| Figure 4.4 Results of STRUCTURE analysis of five microsatellite loci from 309 individuals of <i>Coralliophila abbreviata</i> . Shown is the mean estimated Ln P(K) plotted against K..... | 69 |
| Figure 4.5 Mismatch distribution. The observed number of pairwise nucleotide differences (open circles) for <i>cyt b</i> sequences plotted with the expected number of pairwise nucleotide differences under a model of sudden demographic expansion (solid line) and the 95% confidence intervals for the model estimation (dashed lines)..... | 70 |
| Figure 4.6 Bayesian skyline plot for <i>Coralliophila abbreviata</i> created using <i>cyt b</i> sequence data. The solid black line represents the median female effective population size (N_{ef}) multiplied by the generation time (t), plotted on a log scale. The thin grey lines are the upper and lower 95% highest posterior distribution (HPD) for the population size estimator. The BSP shows a population expansion occurring approximately 250 k years ago..... | 71 |
| Figure 5.1 Schematic of the experimental neighborhood plot design. The four neighborhood treatments (bottom) were replicated five times each and arranged randomly on the reef (top). The four black circles represent the permanent stakes..... | 86 |
| Figure 5.2 Average number of snails (\pm SE) per plot for each neighborhood treatment over the first nine weeks of the experiment. Superscripts identify statistically similar treatments identified in post hoc tests..... | 92 |
| Figure 5.3 Mean proportional change (\pm SD) in total branch length for focal <i>Acropora cervicornis</i> colonies in each neighborhood treatment; CON: conspecific; ALT: alternative prey; NON: non-prey; SOL: solitary. Results were not statistically significant (one-way ANOVA: $F_{3,16} = 1.98$; $P = 0.16$)..... | 93 |
| Figure 5.4 Relationship between neighborhood quality and number of snails per colonized plot at week four (a) and mortality (proportion of replicates) of focal <i>A. cervicornis</i> colonies due to predation after nine weeks (b)..... | 94 |
| Figure 5.5 Observed and expected proportional use of <i>Acropora cervicornis</i> and <i>Montastraea faveolata</i> prey colonies by the <i>Coralliophila abbreviata</i> population at each sampling date. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use is calculated based on the proportional availability of prey at a given sampling period. Chi-squared goodness-of-fit P -values are denoted by * ($P < 0.01$) and † ($P < 0.05$). The test was not significant ($P > 0.05$) where no symbol is associated with the sampling date. Hash marks on the x-axis denote the beginning of monthly sampling..... | 96 |
| Figure 5.6 Observed (blue triangles) and expected (red dashed line) proportional use of each neighborhood treatment by <i>Coralliophila abbreviata</i> at each sampling date. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use values were calculated based on the proportional availability of neighborhood plots in the experimental | |

area. Chi-squared goodness-of-fit P -values are denoted by $*$ ($P < 0.01$) and \dagger ($P < 0.05$). The test was not significant ($P > 0.05$) where no symbol is associated with the sampling date. Hash marks on the x-axis denote the beginning of monthly sampling. 99

Figure 5.7 Observed (blue triangles) and expected (red dashed line) proportional use of each neighborhood treatment by *Coralliophila abbreviata* determined by combining all neighborhood use data. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use value was calculated based on the proportional availability of neighborhood plots in the experimental area. Chi-squared test analysis for neighborhood selection showed that patch selection was not independent of neighborhood treatment ($\chi^2 = 230.25$, $df = 3$, $n = 756$, $P < 0.0001$). 100

Figure 5.8 Percent of observations in each habitat type for 54 tagged snails that remained in the experimental area for at least three months. Habitat types include the four neighborhood treatments (SOL: solitary; NON: non-prey; ALT: alternative prey; CON: conspecific) and substrate (SUB). 100

Figure 5.9 Example of movement path (a) and home range estimates (b) of an individual *Coralliophila abbreviata* snail. The solid line on the right image is the perimeter of 100% MCP area estimate. The 50% (core), 75%, and 95% (range) fixed kernel estimates are indicated. The grey boxes represent neighborhood plots; the bottom plot was a conspecific plot and the top plot was an alternative prey plot. 102

Figure 5.10 Mortality of focal *Acropora cervicornis* colonies in each neighborhood treatment through time. 106

LIST OF TABLES

| | |
|---|----|
| Table 2.1 Sampling locations in Key Largo, Florida, and number of individuals collected from <i>Acropora palmata</i> (ACR), <i>Diploria</i> spp. (DIP), and <i>Montastraea</i> spp. (MONT), at each site. ... | 19 |
| Table 2.2 Estimated Gompertz growth function parameters and associated coefficient of determination (R^2) for model fit for <i>Coralliophila abbreviata</i> by coral host. Parameters: L_r is the length at recruitment, g is the rate at which snails reach the asymptotic shell length, L_∞ . All regressions were significant ($P < 0.01$)..... | 26 |
| Table 2.3 P -values for overall and pairwise likelihood ratio tests for the coincidence of Gompertz growth curves (Coinc.) as well as individual parameters. Coral host taxa: <i>Acropora palmata</i> (ACR), <i>Diploria</i> spp. (DIP), <i>Montastraea</i> spp. (MONT)..... | 27 |
| Table 2.4 Summary of female reproductive characteristics of snails from three coral host taxa, means \pm SD (n)..... | 28 |
| Table 2.5 Logistic maturity model parameters and associated R^2 for model fit for <i>Coralliophila abbreviata</i> by coral host. Model was fit to both size and age data. Parameters: k represents the rate at which individuals change sex and γ is the size or age at which 50% of individuals are predicted to have changed sex to female. All regressions were significant ($P < 0.01$)..... | 32 |
| Table 2.6 P -values for overall and pairwise likelihood ratio tests for the coincidence of logistic maturity curves (Coinc.) as well as individual parameters for models fit to size and age data. Coral host taxa: <i>Acropora palmata</i> (ACR), <i>Diploria</i> spp. (DIP), <i>Montastraea</i> spp. (MONT). | 32 |
| Table 3.1 Characteristics of the eight microsatellite loci developed for <i>Coralliophila abbreviata</i> . <i>Coralliophila abbreviata</i> were collected from the Florida Keys (FL; $n = 31$) and St. Vincent and the Grenadines (GR; $n = 29$). The number of alleles (N_a), expected (H_E) and observed (H_O) heterozygosities, and estimated null allele frequencies are shown for each population. Loci correspond to GenBank accession numbers HM156485-HM156492..... | 50 |
| Table 4.1 Sample sizes for mitochondrial Cytochrome b sequences (mtDNA) and five microsatellite markers (Msats). Sample sizes from each coral host taxon at each site are in parenthesis. GTC, Green Turtle Cay; SVG, St. Vincent and the Grenadines; A, <i>Acropora palmata</i> ; M, <i>Montastraea</i> spp.; MY, <i>Mycetophyllia</i> spp..... | 56 |
| Table 4.2 Genetic diversity indices, neutrality test statistics, and mismatch distribution parameters for mitochondrial cytochrome <i>b</i> sequences of <i>Coralliophila abbreviata</i> collected from Florida (FL), Navassa (NAV), St. Vincent and the Grenadines (SVG), Curacao (CUR), Panama (PAN), as well as all individuals combined (GLOBAL). Genetic diversity indices: N , sample size; N_h , number of haplotypes; N_p , number of polymorphic sites; h , haplotype diversity; π , nucleotide diversity. Neutrality statistics: D , Tajima's statistic (Tajima 1989); F_s , Fu's statistic (FU 1997). Mismatch distribution: τ (tau), time since beginning of expansion in mutational units; θ_0 and θ_1 , initial and final population size estimators, respectively; P (SSD), probability of sum of squared deviations; R_g , raggedness statistic (Harpending 1994); P (Rg), probability of Rg..... | 63 |
| Table 4.3 Characteristics of five polymorphic microsatellite loci for <i>Coralliophila abbreviata</i> . Shown, for each locus, are the forward (F) and reverse (R) primer sequences, repeat motif, size | |

range of alleles in base pairs (bp), global sample size (N), number of observed alleles (N_a), observed (H_O) and expected (H_E) heterozygosities, fixation index (F_{IS}), and uncorrected P-value for test of departure from Hardy Weinberg Equilibrium (P_{HW}). Loci correspond to GenBank accession numbers HM156485, HM156486, HM156490-HM156492..... 64

Table 4.4 Analysis of molecular variance (AMOVA) results for populations of *Coralliophila abbreviata* based on (a) mtDNA and (b) microsatellite datasets grouped by coral host taxa (*Acropora* spp, *Montastraea* spp., and *Mycetophylia* spp.) and major geographical sub-regions in the Caribbean (East and West)..... 66

Table 4.5 Pairwise F_{ST} values between samples from different coral hosts at each locality for microsatellite data (above the diagonal) and mtDNA (below the diagonal). There were no significant ($P < 0.05$) values after Bonferroni correction for multiple comparisons. 67

Table 5.1 Characteristics of neighborhood treatments including the associational effect(s) that they were designed to test, the identity of the neighboring corals surrounding a focal *A. cervicornis* colony. NQ is the neighborhood quality score (see text for explanation) which shows the postulated gradient in resource concentration amongst the treatments. 89

Table 5.2 Repeated measures ANOVA results for test of the effects of neighborhood treatment and time on the number of snails per plot..... 93

Table 5.3 Preference indices calculated for *Acropora cervicornis* (*A. cerv*), *Montastraea faveolata* (*M. fav*), and *Porites asteroides* (*P. ast*). Reported are the proportion availability of each prey in the entire experimental area, the total number of *C. abbreviata* observed in contact with an experimental coral at each sampling time (No. snails), the proportion of those found on each coral species and the calculated selection indices (α)..... 97

Table 5.4 Growth and movement data for male and female *Coralliophila abbreviata* recovered after a total of 129 days. SL refers to shell length. 103

CHAPTER 1: INTRODUCTION

Overview

Globally and across biomes, humans are rapidly changing the physical and biological structure of natural communities through habitat destruction, introduced species, overharvesting, pollution, and climate change (Clavel et al 2011). In these altered ecosystems, the identity, strength, and/or outcome of trophic interactions may shift, resulting in unforeseen trophic cascades and alternate stable states (Knowlton 2004; Connell et al 2011; DeCesare et al 2010). Although predation is a key ecological process long recognized for regulating populations, stabilizing communities, and maintaining biodiversity (Paine 1966; Connell 1970a; Chesson 2000), it is increasingly being linked to failed population recoveries and reintroductions, continued population declines, and species endangerment (Sinclair et al 1998; DeCesare et al 2010). It is thus becoming increasingly important that we understand the mechanistic drivers of predator-prey dynamics in natural communities. This information is necessary to develop effective conservation and management strategies and to predict how communities will respond to further environmental perturbations in the future (Connell et al. 2011).

The research presented herein is an examination of the evolutionary ecology of the coral-eating gastropod, *Coralliophila abbreviata*, on the coral reefs of Florida and the Caribbean. *Coralliophila abbreviata* snails live in close association with scleractinian coral hosts that provide both food and habitat. I investigated how the unique environments associated with different coral-host taxa shape the life-history, demography, and population genetics of *C. abbreviata*. In addition, I investigated the effects of coral-host spatial structure on the foraging behavior and impact of *C.*

abbreviata. The results of this body of work provide insights into the ecological and evolutionary mechanisms shaping predator-prey dynamics on coral reefs and provide framework for predicting the impact of predation on declining coral populations.

Theoretical Effects of Predation on Declining Prey Populations

According to predator-prey theory, the impact of predation on a declining prey population will depend on the inherent density dependent rate of change of the prey population as well as the numerical and functional responses of predator populations to the changing prey community (Solomon 1949; Sinclair et al 1998). The *numerical* response of a predator population is the change in population size due to migration (i.e. aggregational response) and reproduction (i.e. demographic response), as a function of prey density. The *functional* response represents the number of prey consumed per predator per unit of time as a function of prey density and is based on search efficiency and prey handling time (Holling 1959b; Holling 1959a).

Aggregational responses are driven by behavioral and life-history characteristics such as social and resource associated cues, feeding preferences, longevity, and starvation tolerance. Because aggregational numerical responses are dependent on individual behavior and resource use patterns, they generally act on smaller spatial and temporal scales than demographic numerical responses (Holt and Kotler 1987; Bayliss and Choquenot 2002). Aggregational responses can affect the stability and persistence of local prey population through several mechanisms. For instance, if an acute disturbance substantially decreases the abundance of a prey population but has a weaker or no affect on the predator population, the extant predators may concentrate on the remaining prey, causing further decline and possible inhibiting recovery (Knowlton et al 1990). In a

heterogeneous environment, an aggregative response by a predator to the total prey abundance in a patch can lead to short term apparent competition between alternative prey species within a patch as well as spatial refuges in low prey density patches (Holt and Kotler 1987).

Holling (1959 a, b), based on earlier work by Solomon (1949), first categorized and developed simple models for three types of functional responses. A Type I functional response occurs when predation rate increases linearly as prey density increases up to a maximum density, at which point it remains constant due to satiation (Fig 1.1). Type I responses are not very common in nature, but may be characteristic of passive consumers with negligible prey handling time such as filter feeders (Jeschke et al 2004).

Type II functional response occurs when the number of prey consumed per predator increases at a decelerating rate as prey density increases until it reaches a plateau or asymptote, determined by handling time and satiation (Fig 1.1). Mortality due to predation (proportion of the prey population consumed) in this case is depensatory (Fig 1.1) and thus has the potential to cause instability and prey population collapse if prey abundances fall below a threshold level for whatever reason (unstable equilibrium; Fig 1.2). The initial driver of prey population decline could be any acute or chronic stressor. Once the prey population falls below the threshold, however, predation alone is capable of driving the population to extinction, even if the original stressor is removed or no longer acting. This occurs because, below this threshold abundance, the proportion of prey consumed is greater than the intrinsic rate of increase of the prey population (Fig 1.2). This is the only response that can theoretically drive a prey population to extinction. A Type II response is common for specialist predators but may also be expressed by

generalist predators that can persist on alternative prey but continue to feed on a declining prey population due to a feeding preference and/or incidentally due to high spatial overlap of prey species (i.e. apparent competition). In general, a rapid numerical response by the predator to declining prey will tend to stabilize the relationship, whereas as a delayed response will destabilize it.

Finally, A Type III functional response occurs when predation rate increases in a logistic fashion with increasing prey density (Fig 1.1). This sigmoid-shaped functional response results in two stable equilibria at high and low prey abundances and an intermediate unstable equilibrium (Fig 1.2). The lower stable equilibrium occurs due to prey switching or a decrease in handling and/or search efficiency due to learning as prey density increases. A Type III functional response is common for generalist predators that feed primarily on the most abundant prey species. This type of response can stabilize community dynamics and promote species coexistence because prey populations have a refuge from predation at low densities (Chesson 2000). However, prey populations may be driven to and maintained at such small sizes that they are then more susceptible to Allee effects and stochastic disturbances that could subsequently drive the population to extinction (Holt and Lawton 1994).

The *total* predator response to changing prey density is the product of the numerical and the functional responses. It is the interactions between the degree to which predator populations track prey populations numerically and the shape of the functional response that will ultimately determine the potential for predators to regulate prey populations and to drive them to extinction (Fig 1.2). Thus, the life-history and demographic characteristics of predator and prey populations as well as the availability,

relative abundances, quality, and spatial distribution of all potential resources are critical components of predator-prey dynamics. Understanding each of these components is necessary to predict the potential impact of predation on a decline prey population and to design effective conservation and management strategies (Sinclair et al 1998).

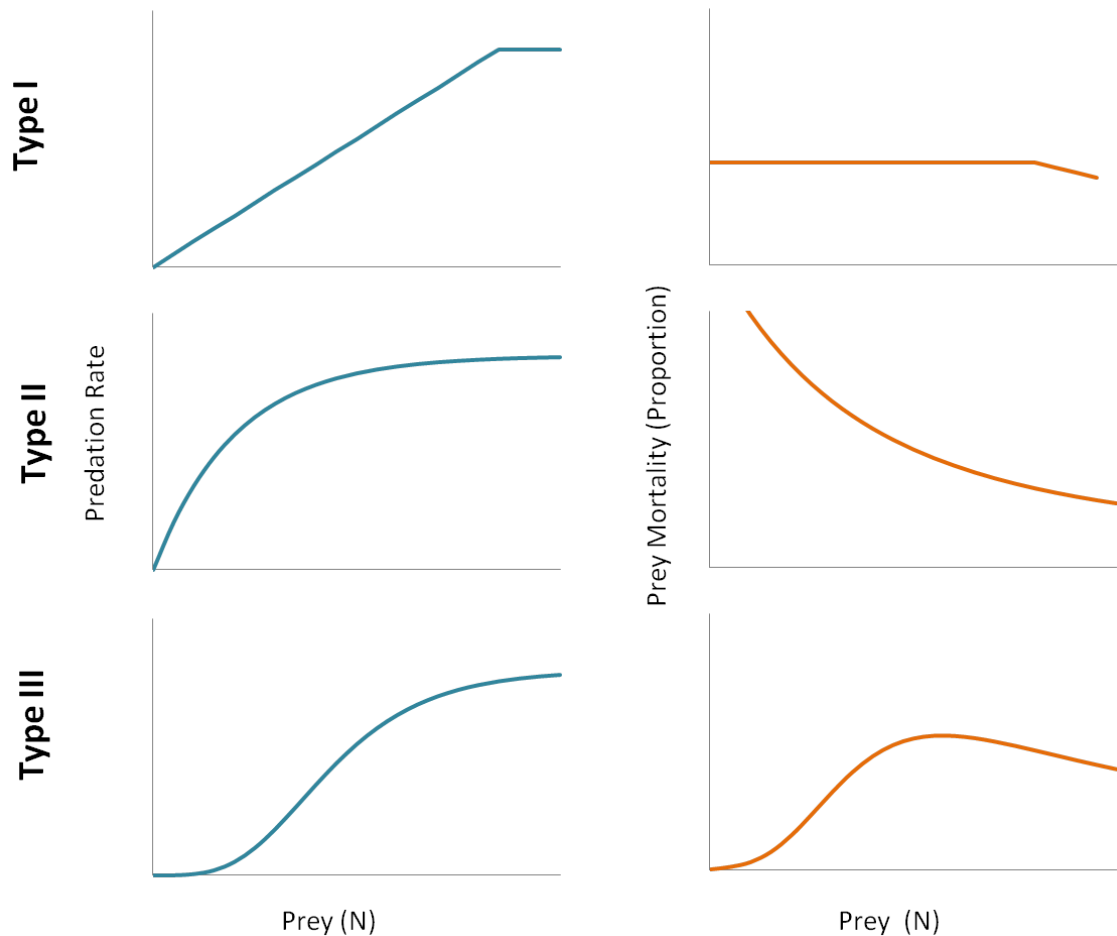


Figure 1.1 The three major predator functional responses (number of prey consumed per predator per unit of time as a function of the prey density) and corresponding prey mortality due to predation described by Holling (1959).

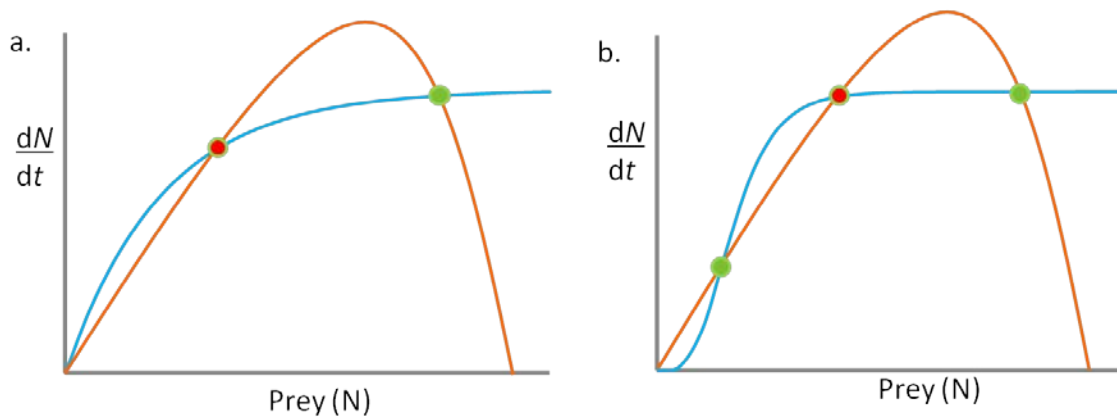


Figure 1.2 The theoretical relationship between prey mortality rate due to predation (teal line) and the intrinsic rate of increase of the prey population in the absence of predators (orange line) for Type II (a) and Type III (b) functional responses. Green dots mark stable equilibria and red dots mark unstable equilibria. Redrawn from Sinclair et al (1998).

Coral Reef Decline

Coral reefs, which are among the most biologically diverse and economically significant ecosystems on the planet, are declining worldwide (Hughes et al 2003). Over the last three decades, the Caribbean region has experienced some of the greatest losses in coral cover, exceeding 90% in some areas (Hughes 1994; Gardner et al 2003). This precipitous decline is thought to have been triggered largely by emergent diseases affecting dominant populations of both herbivores and foundational scleractinian corals and exacerbated by other acute and chronic stressors.

Specifically, from 1982-1984, a species-specific pathogen of unknown etiology spread rapidly throughout the Caribbean basin, killing up to 99% of the long-spine sea urchin, *Diadema antillarum* (Lessios et al 1984). Prior to the die-off, *D. antillarum* was the most functionally significant herbivore on Caribbean coral reefs due to high abundances and high algal consumption rates (Carpenter 1986).

Beginning in the late 1970s, and episodically thereafter, populations of the branching acroporid corals, *Acropora palmata* and *A. cervicornis*, have also been decimated by ‘white syndrome’ diseases (Gladfelter 1982; Aronson and Precht 2001; Williams and Miller in press). Historically, high growth rates, complex branching structure, and propensity for asexual reproduction through fragmentation, made the acroporid corals the dominant ecosystem engineers in shallow (< 20 m) high energy reef environments throughout the region. These corals characteristically formed extensive thickets in the ‘Acropora zone’ that supported a diverse array of life (Goreau 1959; Gladfelter et al 1978; Jackson 1992; Hughes 1994; Aronson and Precht 2001). Currently, populations of the acroporid corals have declined by up to 95% on many reefs across the Caribbean (Aronson and Precht 2001; Miller et al 2002). Consequently, *Acropora palmata* and *A. cervicornis* have become the first scleractinian corals to be listed as threatened species under the U.S. Endangered Species Act and as critically endangered by the IUNC Red List of Threatened Species.

Episodic hurricanes, bleaching and cold water events, as well as chronic stressors such as eutrophication, sedimentation, predation, and overfishing have also contributed to overall coral decline and eroded the resilience of coral reef ecosystems (Hughes et al 2003; Gardner et al 2003). Consequently, the balance among processes such as production, consumption, and competition within and among trophic groups has been altered, resulting in a phase shift from a coral dominated to an algal dominated state on most Caribbean coral reefs (Hughes 1994). The recovery of both *D. antillarum* and the acroporid corals has been slow and regionally isolated to absent over the last 30 years, raising great concern about the stability of this alternate macroalgal dominated state on

coral reefs (Knowlton 2004). Understanding the mechanisms responsible for the protracted recovery and often continual decline of Caribbean coral reefs, is crucial for reef conservation and management efforts. To date, almost all studies addressing these processes have focused on the interactions among herbivores, macroalgae, and corals (Mumby 2009; Burkepile and Hay 2009). Little to no attention has been paid to the potential impacts of coral predators on reducing coral populations and maintaining alternative stable states (Rotjan and Lewis 2008). As coral populations continue to decline and global climate change and ocean acidification threaten to further reduce the resilience of Caribbean coral reefs by suppressing coral growth and sexual reproduction (Renegar and Riegl 2005; Albright et al 2010), predation may represent a profound threat to the persistence and recovery of remnant coral populations and thus warrants further investigation.

The Role of Corallivores

Coral-eating predators (corallivores) are ubiquitous members of coral reef communities that belong to diverse phyla including Annelida, Echinodermata, Mollusca, and Chordata, among others. They range from generalist facultative consumers to host-specific obligate coral parasites (Glynn 1990; Rotjan and Lewis 2008). Corallivores are ecologically important members of a reef community as they affect coral population dynamics and community structure (Brawley and Adey 1982; Cox 1986; Knowlton et al 1990; Turner 1994; Rotjan and Lewis 2008) and provide a link from corals and their photosynthetic symbionts to higher trophic levels (Glynn 2004). Corallivores may also act as vectors for diseases affecting corals, suggesting a possible synergistic impact on prey populations above and beyond simple tissue consumption (Sussman et al 2003; Williams and Miller

2005; Sutherland et al 2011). The impact of corallivores on coral reef communities, however, varies greatly on both spatial and temporal scales, depending on the prevailing biotic and abiotic environmental conditions.

Although conspicuous damage to corals is often minimal when corallivore population abundances are low, population outbreaks of the crown-of-thorns seastar, *Acanthaster planci* (reviewed in: Moran 1986), and gastropods in the genus *Drupella* (reviewed in: Turner 1994) have resulted in extensive and acute coral mortality on reefs across the Indo-Pacific. These corallivores, however, feed primarily on fast growing, competitively dominant corals from the genera *Acropora*, *Montipora*, and *Pocillopora* (Colgan 1987; De'ath and Moran 1998). In the absence of additional disturbances, reefs that incur substantial coral losses due to *A. planci* recover relatively quickly (Colgan 1987; Graham et al 2011). This process might be an important part of a natural disturbance cycle that regulates coral populations and promotes species coexistence by opening up settlement sites and temporarily releasing slower growing massive corals from competition (Colgan 1987; Sebens 1994; Kayal et al 2011). However, the frequency and severity of outbreaks and other disturbances may be increasing due to anthropogenic influences such as eutrophication, over fishing, and global climate change, reducing reef resilience and resulting in an overall shift in coral species composition on many affected reefs (Fabricius et al 2010).

One of the prominent coral predators in the greater Caribbean region is the corallivorous gastropod, *Coralliophila abbreviata* (Fig. 1.3). These snails are obligate corallivores (Ward 1965) that live and feed on at least 16 species of scleractinian corals from five different families (Miller 1981). In light of catastrophic outbreaks of *A. planci*

in the Pacific, early investigators concluded that *C. abbreviata* was not a significant corallivore (Ott and Lewis 1972). Subsequent studies, however, have revealed that although damage to massive and plating corals appears minimal, *C. abbreviata* cause substantial and chronic mortality of the threatened acroporid corals, *Acropora palmata* and *A. cervicornis* (Brawley and Adey 1982; Hayes 1990b; Bruckner et al 1997; Miller 2001; Miller et al 2002; Baums et al 2003; Grober-Dunsmore et al 2006; Williams and Miller, in press). It has been estimated that *C. abbreviata* snails can consume from 1-9 cm^{-2} of live tissue per day per snail, a rate which could quickly outpace coral growth (Baums et al 2003b).

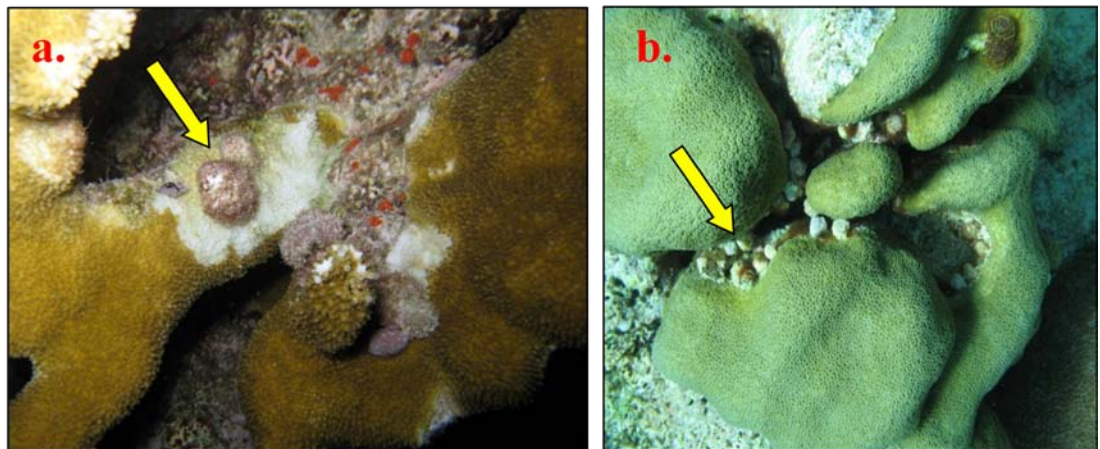


Figure 1.3 *Coralliophila abbreviata* snails (indicated with yellow arrows) feeding on *Acropora palmata* (a) and *Montastraea annularis* (b).

Several characteristics of *C. abbreviata* indicate that they have the potential to regulate populations of *Acropora* spp. corals, possibly maintaining them at an alternate low population size or even driving them to extinction (at least on a local scale). First, *C. abbreviata* has a wide diet breadth and high dispersal potential due to planktotrophic veliger larvae (Wells and Lalli 1977). Thus snail populations may be decoupled

numerically from local and regional population fluctuations of any one prey population as snail larvae may be supplied from distant locations and adult populations can be maintained on alternative coral prey. Furthermore, *C. abbreviata* do not appear to be greatly affected by the major disturbances that have drastically reduced acroporid populations, such as disease, hurricanes, and bleaching. Instead, when coral populations are impacted by these disturbances, the extant snails concentrate on the remaining corals, causing further population decline and impeding recovery (Knowlton et al 1990). Finally, *C. abbreviata* snails have a greater impact on acroporid corals (i.e. greater tissue consumption rate) than other prey species, making the acroporids vulnerable to further decline via mechanisms such as asymmetric apparent competition where prey populations overlap (discussed in detail in Chapter 5). Historically, the effects of predation on robust acroporid coral populations in the Caribbean might have been negligible or may have even contributed to species coexistence by reducing strong interspecific competition for space in some areas. However, in the wake of perturbations that have severely reduced the density and abundance of acroporid corals throughout the region, predation by *C. abbreviata* may have profound negative effects on the persistence and recovery of remnant populations. Understanding and managing this threat is thus crucial for reef conservation in the region.

Previous studies of *C. abbreviata* have characterized population size structure and abundances on different coral host taxa and found that snails are significantly larger on acroporid corals but often more abundant on other host taxa (Miller 1981; Hayes 1990b; Baums et al 2003a). Baums et al (2003b) estimated growth rates and metabolic functions of *C. abbreviata* on two coral host taxa (*Acropora palmata* and *Montastraea* spp.) and

found that although respiration rates did not vary, growth rates were significantly greater for snails feeding on *Acropora palmata*. Several investigators have estimated coral tissue consumption rates of *C. abbreviata* and there is growing evidence that *C. abbreviata* may act as a vector for diseases affecting the acroporid corals (Williams and Miller 2005; Sutherland et al 2011).

Although these studies characterize some fundamental components of predator-prey dynamics in this system, very little is known about the factors that influence the distribution, abundance, and host-use patterns of *C. abbreviata*. In order to understand and predict how *C. abbreviata* will affect declining coral populations over multiple spatial and temporal scales, it is necessary to know how each potential prey/host taxa affects snail life-history and fitness, the scale and patterns of population connectivity, both through larval dispersal and adult migration, and how coral community structure affects snail foraging behavior and resource use patterns (e.g. aggregational response). This dissertation focuses on these issues (Fig. 1.4). The results of this body of work provide a framework for understanding and predicting the impact of predation on species coexistence in a changing coral community.

In Chapter 2, I characterized and compared the life-history characteristics, including female reproductive output, of *C. abbreviata* populations from three coral host taxa (*Acropora palmata*, *Montastraea* spp., and *Diploria* spp.) in the Florida Keys. I applied population dynamic models to size and age data to estimate life-history parameters such as growth, mortality, and size and age at sex change for *C. abbreviata* and compared these estimates among the different coral hosts. The overall objective of this study was to compare the vital rates of *C. abbreviata* on different coral host taxa to

elucidate potential trade-offs in growth, reproduction, and survival among hosts, thereby gaining a better understanding of the factors affecting host use and distribution of snails across a reef.

In Chapter 3, I isolated, characterized, and tested a set of polymorphic microsatellite markers for *C. abbreviata*. Microsatellites markers are powerful molecular tools for studying the ecology and evolution of populations. The markers developed for *C. abbreviata* are now publicly available for future research.

In Chapter 4, I used the newly developed microsatellite markers in conjunction with mitochondrial DNA sequence data to assess the population genetics of *C. abbreviata* across the Caribbean. My overall objective was to characterize the genetic variation of *C. abbreviata* populations from different coral host taxa and geographical locations to assess a.) potential host-specific genetic differentiation, b.) the scale and patterns of gene flow across the Caribbean, and c.) the possible role of historical demographic fluctuations in shaping the observed patterns of genetic variation and population structure.

In Chapter 5, I conducted a manipulative field experiment to examine the effects of coral neighborhood composition on the dynamics and impact of *C. abbreviata*. I quantified the effects of coral neighbor composition on the magnitude and rate of snail colonization of neighborhood patches and the subsequent impact on focal *A. cervicornis* colonies in terms of growth and survival. Additionally, individually tagged snails were monitored in the experimental arena for five months to assess patterns of resource use as patches were depleted.

Finally, in Chapter 6, I summarize the major findings of each chapter, synthesize this information, and discuss the implications for the conservation and management of threatened scleractinian corals and coral reef ecosystems.

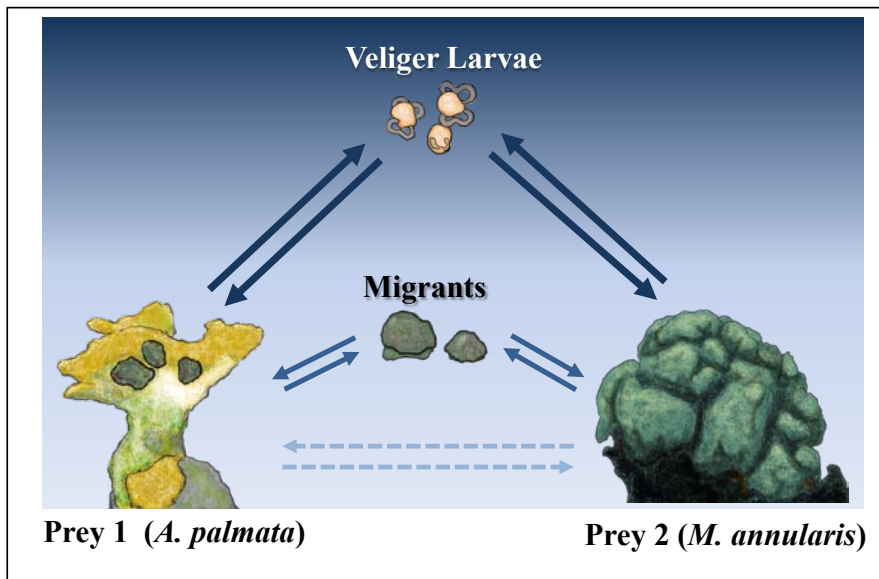


Figure 1.4 Basic life-cycle of *Coralliophila abbreviata* in a two prey system. Possible predator mediated indirect interactions between coral host taxa are indicated by dashed arrows (coral and snail illustrations by D.M. Holstein).

CHAPTER 2: VARIATION IN THE LIFE-HISTORY TRAITS OF THE CORALLIVOROUS GASTROPOD, *CORALLIOPHILA ABBREVIATA*, ON THREE CORAL HOSTS

Overview

Microconsumers often live in close association with larger host organisms that provide both food and habitat. Potential hosts may vary in nutritional quality, abundance, and other associated biotic (e.g. predation and competition) and abiotic conditions that result in host-specific selective forces acting on a given consumer. *Coralliophila abbreviata* are corallivorous gastropods that live and feed on at least 16 species of scleractinian coral from five different families (Miller 1981). These corals represent a wide range of morphological and life-history characteristics. For instance, the acroporid corals, *Acropora palmata* and *A. cervicornis* have branching morphologies and grow relatively fast (47-99 mm y⁻¹; Gladfelter et al 1978), whereas *Montastraea* spp. form massive, boulder-like colonies and grow slowly (6.6-8.9 mm y⁻¹; Gladfelter et al. 1978). Different coral host taxa, therefore, likely provide different food and habitat conditions for *C. abbreviata*. In this study, I investigated how these unique environments (i.e. hosts) affect the life-history of *C. abbreviata*.

Different selective pressures often represent host-associated life-history trade-offs in natural communities. For instance, one host may provide superior nutritional quality (growth) while another host provides enemy-free space (survival; Singer et al 2004). To minimize the fitness costs associated with trade-offs, generalist consumers often develop reaction norms for life-history traits, in which a given genotype can express a range of phenotypes in response to different environments (e.g. hosts: Stearns and Koella 1986; Nylin and Gotthard 1998). Phenotypic plasticity and a generalist strategy may be

advantageous in novel and heterogeneous environments when the ability to utilize multiple hosts results in increased net fitness (Richards et al 2006; Davidson et al 2011). However, phenotypic plasticity has associated fitness costs in terms of maintenance and imperfect phenotype-to-habitat matching among others (Tienderen 1991; DeWitt et al 1998; Agrawal 2001; Relyea 2002a) and, therefore, may be lost over time due to assimilation of fitter specialist genotypes (Nosil et al 2002; Pigliucci and Murren 2003; Aubret and Shine 2010).

Such host-associated adaptation is emerging as a prominent driver of ecological speciation in both terrestrial and marine ecosystems and may be largely responsible for the extreme diversity of phytophagous insects found in nature (Berlocher and Feder 2002; Sotka 2005b). Thus, the factors that affect host use, including the strength and identity of life-history trade-offs, have important ecological and evolutionary implications for community structure and function. Although these factors have been studied extensively in terrestrial systems (e.g. phytophagous insects: Bernays and Graham 1988; Camara 1997; Mira and Bernays 2002; Singer et al 2004) much less is known about the evolutionary ecology of host use in the marine environment (but see: Hay et al 1990; Duffy 1992; Ritson-Williams et al 2003; Sotka 2005b).

In the case of *C. abbreviata*, previous investigators have consistently reported host-specific differences in population structure and feeding behavior. Snails on acroporid corals are larger and consume more tissue than those on massive and plating corals (Hayes 1990b; Bruckner et al 1997; Baums et al 2003b). Baums et al. (2003b) attributed the host-specific size structure of *C. abbreviata* populations to differential growth rates. However, although snails appear to grow faster and reach larger sizes on the

acroporid corals, they are often more abundant on non-acroporid corals (Hayes 1990; Baums et al 2003a), suggesting that host use and distribution of *C. abbreviata* may be a result of trade-offs between growth and survival.

The overall objective of this study was to compare life-history characteristics of *C. abbreviata* on different coral host taxa to elucidate potential trade-offs in growth, reproduction, and survival among hosts, thereby gaining a better understanding of the factors affecting host use and distribution of snails across a reef. To this end, I conducted an age-based analysis of *C. abbreviata* populations from three coral host taxa (*Acropora palmata*, *Montastraea* spp., and *Diploria* spp.). I applied population dynamic models to size and age data to estimate life-history parameters such as growth, mortality, and size and age at sex change for *C. abbreviata* and compared these values among the different coral hosts. I also established a size-fecundity relationship for female *C. abbreviata* and compared reproductive output of females among populations.

Materials and Methods

Collection and Processing

Coralliophila abbreviata were collected using SCUBA in June through August, 2004 from four shallow (2-7 m) reef sites in the Key Largo sector of the Florida Keys National Marine Sanctuary (Table 2.1). At each site, coral host colonies were haphazardly selected and searched thoroughly for snails. Since female *C. abbreviata* often expel egg cases from the mantle cavity during collection in the field (Wells and Lalli 1977), all snails were removed from coral colonies and immediately placed in individual, labeled 50-ml collection tubes or bags where they remained until processing on shore.

On shore, the shell length (from the tip of the apex to the tip of the columella or siphonal notch) of each snail was measured with vernier calipers to the nearest 0.1 mm. The shell was then crushed with a hammer and removed and the soft tissue was examined for the presence of a penis (located above the right eye-stalk) and egg capsules (located in the mantle cavity of females). Individuals with a penis and no egg capsules were classified as male. Individuals with no penis (with or without egg capsules) were classified as female. Three individuals had both a penis and egg capsules and were classified as female. The flat chitinous egg capsules were removed from either the collection container or the mantle cavity of females with forceps and stored individually in 1.0 ml vials of ethanol until examination.

Egg capsule area was estimated as the product of the maximum length and width, measured to the nearest 0.1 mm. For each female, the areas of all egg capsules brooded were summed to give a total egg capsule area. A total of 72 egg capsules from 15 females ($n = 5$ for each host), with larvae in the fully developed veliger stage (as described by Wells and Lalli 1977), were broken open to determine the relationship between egg capsule area and number of veligers. For the *Acropora palmata* population, the five females were randomly selected from a pool of 20 with fully developed veligers. The maximum shell length of 300 veligers ($n = 20$ from each of the 15 females) was measured to the nearest 0.01 mm using digital imaging software (Scion Image for Windows; © 2000 Scion Corporation) after taking digital photographs through a dissecting microscope.

The operculum was removed from the foot of each snail with a scalpel and forceps. Age was estimated by counting the striae on the inner surface of the operculum

under a dissecting microscope (Fig. 2.1). These striae have been shown to represent annual growth marks in other gastropods (Cupul-Magaña and Torres-Moye 1996; Ilano et al 2004), including the congener *C. violacea* (Chen and Soong 2002). Some operculae ($n = 38$) were broken, lost, or otherwise unreadable and were not included in subsequent analysis.

Table 2.1 Sampling locations in Key Largo, Florida, and number of individuals collected from *Acropora palmata* (ACR), *Diploria* spp. (DIP), and *Montastraea* spp. (MONT), at each site.

| Reef site | Coordinates | Host | | |
|----------------|----------------------------|------|-----|------|
| | | ACR | DIP | MONT |
| Little Grecian | N 25° 07.111; W 80° 18.082 | 74 | 29 | 69 |
| Grecian Rocks | N 25° 06.463; W 80° 18.420 | 49 | - | - |
| Sand Island | N 25° 01.107; W 80° 22.044 | 60 | 40 | 32 |
| Pickles | N 24° 59.361; W 80° 24.812 | - | 39 | - |
| Total | | 183 | 108 | 101 |

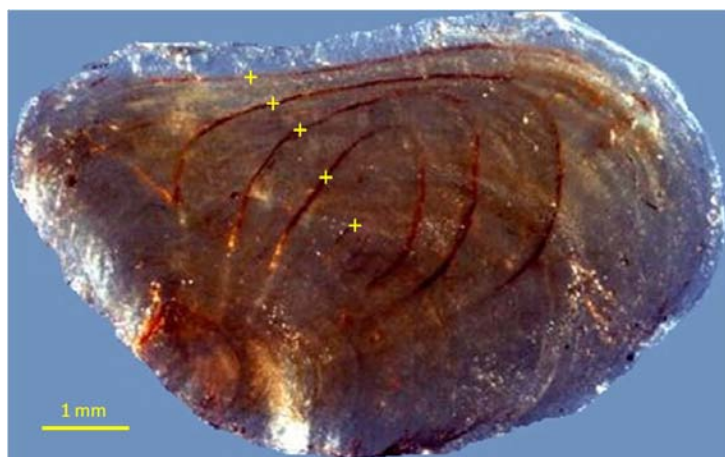


Figure 2.1 *Coralliophila abbreviata* operculum. Annual growth striae are indicated by yellow crosshairs.

Statistical Analyses

Data were transformed (natural log) where necessary to achieve homogeneity of variances. Two-way analysis of variance (ANOVA), followed by Tukey Unequal N HSD post-hoc tests were used to test the affect of host taxa and sex (independent factors) on shell length and on age. One-way ANOVA followed by Tukey Unequal N HSD post-hoc tests were used to test for differences in the female reproductive characteristics of snails among hosts. The relationships between egg capsule area and number of veligers and female shell length and total egg capsule area were assessed using regression analysis. After confirming homogeneity of slopes, ANCOVA was used to test for differences in the relationship between egg capsule area and number of veligers among hosts.

Length-at-age data were fitted to the Gompertz growth function:

$$L_t = L_\infty \exp[-G \exp(-gt)],$$

where L_t is the shell length at time t ; L_∞ is the asymptotic shell length; $G = \ln(L_\infty/L_r)$, where L_r is the shell length at recruitment; g describes the rate at which L_∞ is reached (a larger value indicates a shorter period of growth), and t is the time in years. The average maximum shell length of fully developed veligers was used as an initial estimate for L_r . Best-fit parameters were obtained using a least squares method to fit the Gompertz growth model to the data for each host. L_r was then constrained to the average L_r for all groups and the model was run again. Likelihood ratio tests (Kimura 1980) were used to compare curves. The hypothesis that all curves are coincident was tested first. If curves were found to be significantly different, subsequent pairwise tests were run to determine which individual parameters varied among hosts.

Timing of sex change was determined by fitting sex ratio-at-age data for snails from each host to the logistic maturity model:

$$m_t = 1 / (1 + \exp[-k(t-\gamma)]),$$

where m_t is the proportion of individuals that are female at age t , k is the rate of sex change, t is the age in years, and γ is the age at which 50% of snails are female ($t_{50\%}$).

The model was fit to the data using a least squares method and parameters were compared among groups with likelihood ratio tests as above.

Total instantaneous mortality rate (Z) was estimated for each population from the Gompertz growth parameters (g, L_∞, L_r) and the mean shell length (L_m) using the Beverton and Holt model (1956):

$$Z = g(L_\infty - L_m) / (L_m - L_r).$$

This model assumes that growth follows the growth function, that mortality can be represented by negative exponential decay, and that recruitment is continuous.

Results

Size and Age Structure

A total of 392 *Coralliophila abbreviata* were collected; 183 from *Acropora palmata*, 108 from *Diploria* spp., and 101 from *Montastraea* spp. (Table 2.1). Snails ranged from 5.8 mm- 50.1 mm in shell length (Fig.2.2a). Shell length varied significantly among hosts (Two-way ANOVA; $df = 2, F = 159.46, P < 0.01$) and between sexes ($df = 1, F = 183.72, P < 0.01$). The interaction effect (host*sex) was not significant ($df = 2, F = 91.96, P > 0.05$; Fig. 2.3a). Snails from *A. palmata* were significantly larger than snails inhabiting *Diploria* spp. and *Montastraea* spp. Females were significantly larger than males on all

host taxa and females from *A. palmata* were significantly larger than all other snails. Males from *A. palmata* were significantly larger than all other males, but were not significantly different from females on *Diploria* spp. and *Montastraea* spp.

Snail age across hosts ranged from 3-16 years (Fig. 2.2b). Age also varied significantly among hosts (Two-way ANOVA; $df = 2$, $F = 91.96$, $P < 0.01$) and between sexes ($df = 1$, $F = 134.94$, $P < 0.01$). The interaction effect (host*sex) was not significant ($df = 2$, $F = 0.21$, $P > 0.05$; Fig 2.3b). Snails from *A. palmata* were on average significantly older than snails on the other two hosts and females were older than males on all host taxa.

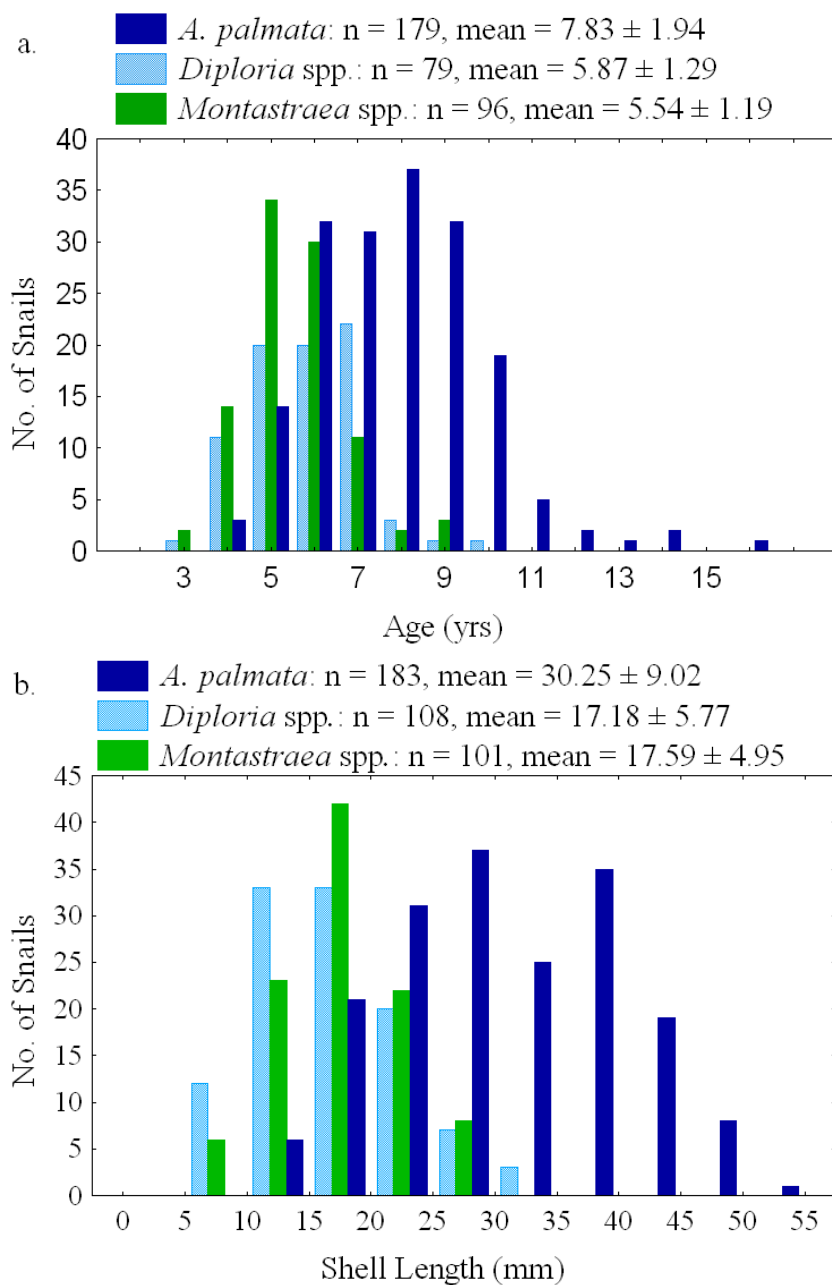


Figure 2.2 *Coralliophila abbreviata* age (a) and size (b) frequency distributions by coral host.

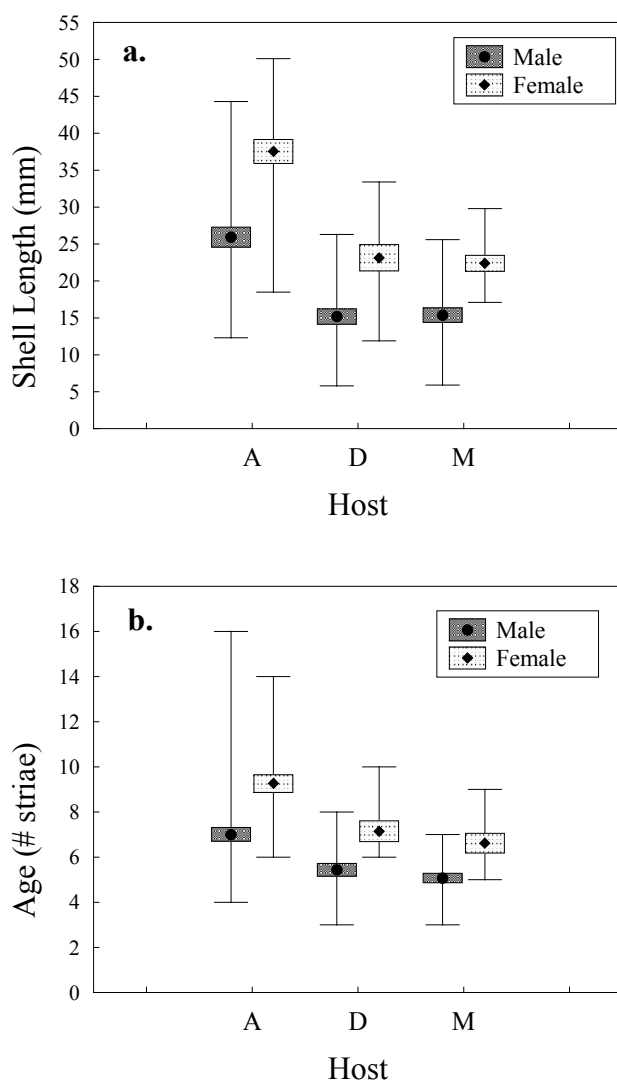


Figure 2.3 Mean shell length (a) and age (b) of males and females on *Acropora palmata* (A), *Diploria* spp. (D), and *Montastraea* spp. (M). Boxes and whiskers represent 95% confidence limits and minimum and maximum values, respectively. Shell length varied significantly among hosts (Two-way ANOVA; $df = 2$, $F = 159.46$, $P < 0.01$) and between sexes ($df = 1$, $F = 183.72$, $P < 0.01$). Age (# of striae) also varied significantly among hosts (Two-way ANOVA; $df = 2$, $F = 91.96$, $P < 0.01$) and between sexes ($df = 1$, $F = 134.94$, $P < 0.01$).

Growth and Mortality

Coral host had a significant effect on overall Gompertz growth curves ($X^2 = 63.72$, $df = 2$, $P < 0.001$) as well as individual growth parameters (L_∞ : $X^2 = 16.95$, $df = 1$, $P < 0.001$; g : $X^2 = 7.76$, $df = 1$, $P < 0.01$; Table 2.2; Table 2.3; Fig. 2.4). Pairwise tests revealed that although the overall growth curves for snails on *A. palmata* and *Diploria* spp. were not coincident ($X^2 = 30.68$, $df = 2$, $P < 0.001$), L_∞ and g did not vary significantly when tested separately (L_∞ : $X^2 = 0.62$, $df = 1$, $P = 0.43$; g : $X^2 = 0.34$, $df = 1$, $P = 0.56$). The growth curves for snails on *A. palmata* and *Montastraea* spp. were not coincident ($X^2 = 35.75$, $df = 2$, $P < 0.01$) and for these two hosts, L_∞ varied significantly ($X^2 = 14.09$, $df = 1$, $P < 0.001$) and g varied at the $\alpha = 0.05$ level of significance ($X^2 = 5.85$, $df = 1$, $P < 0.02$). For *Diploria* spp. and *Montastraea* spp., overall curves were not coincident ($X^2 = 13.31$, $df = 2$, $P < 0.01$) and both L_∞ and g varied significantly (L_∞ : $X^2 = 11.24$, $df = 1$, $P < 0.001$, g : $X^2 = 13.05$, $df = 1$, $P < 0.001$).

The total instantaneous mortality rate (y^{-1}) was estimated to be 0.17 for snails on *A. palmata*, 0.41 for snails on *Diploria* spp., and 0.25 for snails on *Montastraea* spp.

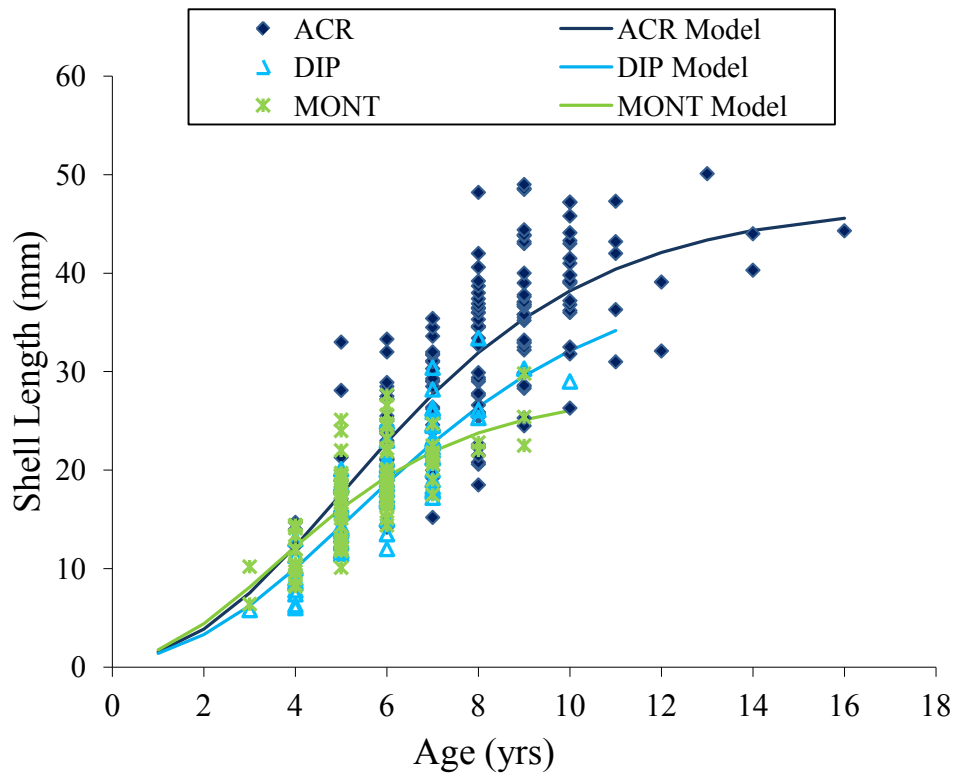


Figure 2.4 Gompertz growth curves fitted to size-at-age data for *Coralliophila abbreviata* on the three coral host taxa (ACR: *Acropora palmata*; DIP: *Diploria* spp.; MONT: *Montastraea* spp.)

Table 2.2 Estimated Gompertz growth function parameters and associated coefficient of determination (R^2) for model fit for *Coralliophila abbreviata* by coral host. Parameters: L_r is the length at recruitment, g is the rate at which snails reach the asymptotic shell length, L_∞ . All regressions were significant ($P < 0.01$)

| Host | Parameter | | | R^2 |
|-------------------------|-----------|------|------------|-------|
| | L_r | g | L_∞ | |
| <i>A. palmata</i> | 0.45 | 0.31 | 47.1 | 0.59 |
| <i>Diploria</i> spp. | 0.45 | 0.29 | 41.1 | 0.76 |
| <i>Montastraea</i> spp. | 0.45 | 0.40 | 28.1 | 0.57 |

Table 2.3 *P*-values for overall and pairwise likelihood ratio tests for the coincidence of Gompertz growth curves (Coinc.) as well as individual parameters. Coral host taxa: *Acropora palmata* (ACR), *Diploria* spp. (DIP), *Montastraea* spp. (MONT).

| Test | Coinc. | <i>g</i> | L_{∞} |
|------------|--------|----------|--------------|
| Overall | *** | *** | ** |
| ACR v DIP | *** | 0.43 | 0.56 |
| ACR v MONT | *** | 0.02 | *** |
| DIP v MONT | ** | *** | *** |

P* < 0.01; *P* < 0.001

Reproductive Characteristics

Female reproductive characteristics are reported in Table 2.4. The sex ratios (proportion female) were 0.37 for the *A. palmata* snail population, 0.25 for the *Diploria* spp. snail population, and 0.28 for the *Montastraea* spp. snail population. Eighty one percent (n = 55) of females on *A. palmata*, 56 % (n = 15) of females on *Diploria* spp., and 70 % (n = 14) of females on *Montastraea* spp. were brooding egg capsules. Although egg capsules from a single female contained larvae in a similar stage of development, the stage of larval development varied among females. The percent of brooding females that contained fully developed veligers was similar for each host; 36 % (n = 20) for *A. palmata*, 33 % (n = 5) for *Diploria* spp., and 36 % (n = 5) for *Montastraea* spp. Veligers ranged in shell length from 0.19 to 0.33 mm and were on average 0.28 ± 0.01 (SD) mm. Veliger size did not vary significantly among hosts (One-way ANOVA; df = 2, *F* = 2.109, *P* > 0.05).

Total egg capsule area increased as a power function with female shell length (n = 84, $R^2 = 0.90$, $y = 0.0023x^{3.42}$, *P* < 0.01, Fig. 2.5). Thus, on average, the larger females on

A. palmata brooded more, larger egg capsules, thereby having a greater total egg capsule area than the smaller females from the other two hosts (Tukey post hoc for each trait; $P < 0.01$). Total egg capsule area for females on *Diploria* spp. and *Montastraea* spp. varied slightly (Tukey post hoc; $P < 0.05$). There was a positive correlation between egg capsule area and number of veligers ($n = 72$, $R^2 = 0.84$, $y = 26.39x + 257.28$, $P < 0.01$, Fig.2.6). Total egg capsule area, therefore, can be used to estimate the per capita reproductive output (brood size) of female *C. abbreviata*.

Table 2.4 Summary of female reproductive characteristics of snails from three coral host taxa, means \pm SD (n).

| | <i>A. palmata</i> | <i>Diploria</i> spp. | <i>Montastraea</i> spp. | <i>F</i> |
|--|------------------------|-----------------------|-------------------------|----------|
| Sex ratio (proportion female) | 0.37 | 0.25 | 0.28 | |
| Length of females (mm) | | | | |
| Range | 18.5 - 50.1 | 11.9 - 33.4 | 18.0 - 29.8 | |
| Mean | 37.5 \pm 6.7 (68) | 23.2 \pm 4.5 (27) | 22.7 \pm 3.0 (20) | 120.2* |
| Proportion of females brooding capsules | 0.81 | 0.56 | 0.70 | |
| No. of capsules female ⁻¹ | | | | |
| Range | 0-10 | 0-6 | 0-5 | |
| Mean/brooding female | 7.2 \pm 1.3 (55) | 3.9 \pm 1.1 (15) | 3.2 \pm 0.8 (14) | 14.0* |
| Capsule area (mm ²) | | | | |
| Range | 21.8 - 192.0 | 18.0 - 65.1 | 11.3 - 59.8 | |
| Mean | 99.8 \pm 33.7 (395) | 36.7 \pm 14.7 (55) | 31.5 \pm 11.9 (51) | 93.9* |
| Total capsule area (mm ²) female ⁻¹ | | | | |
| Range | 133.1 - 1365.9 | 38.9 - 352.9 | 37.6 - 234.1 | |
| Mean | 710.1 \pm 300.8 (55) | 144.1 \pm 89.2 (15) | 96.1 \pm 51.1 (14) | 134.28* |

* one-way ANOVA; $P < 0.01$

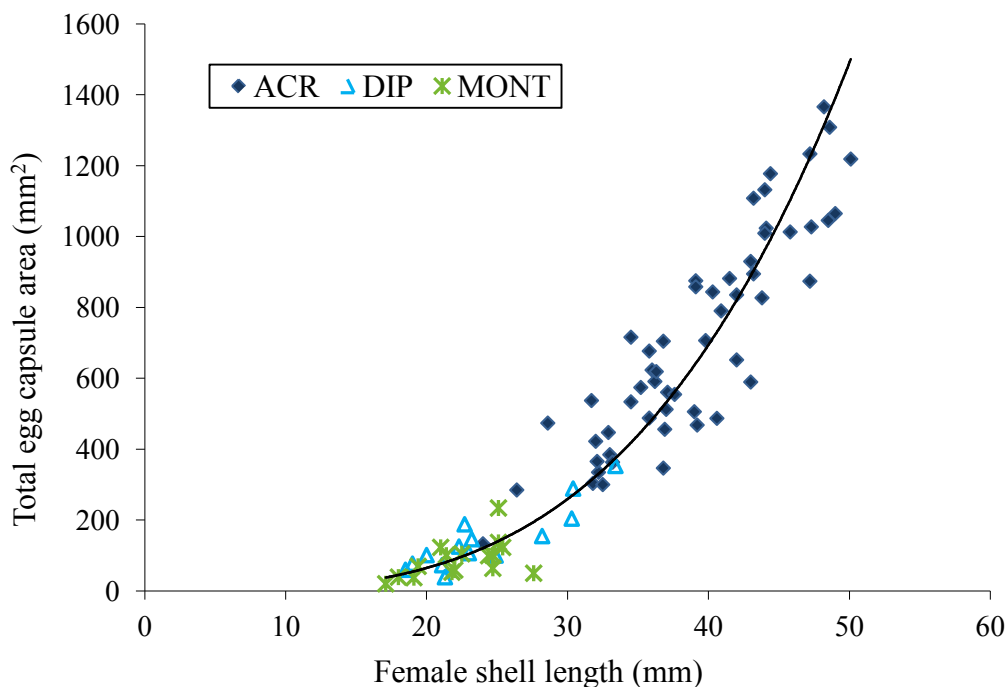


Figure 2.5 Relationship between female shell length and total egg capsule area for *Coralliophila abbreviata* ($n = 84$, $y = 0.0023x^{3.42}$, $R^2 = 0.90$, $P < 0.01$).

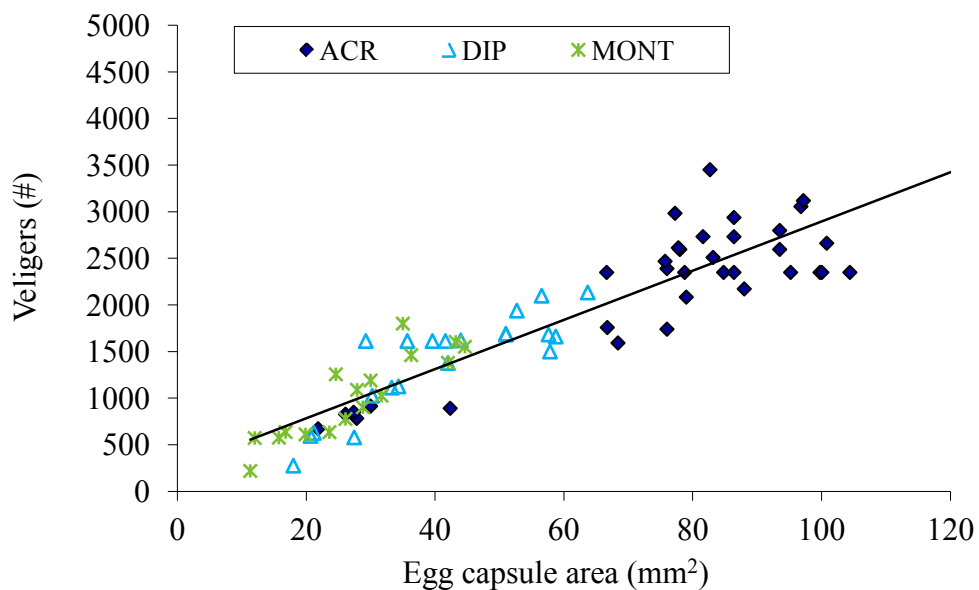


Figure 2.6 Relationship between egg capsule area and number of veligers for female *Coralliophila abbreviata* on *Acropora palmata* (ACR), *Diploria* spp. (DIP), and *Montastraea* spp. (MON; $n = 72$, $y = 26.39x + 257.28$, $R^2 = 0.84$, $P < 0.01$).

Size and Age at Sex Change

For the size-based analysis, after fitting the maturity model to the data for each coral host, three data points were identified as statistical outliers based on residuals and were removed from the analysis. The model was then fit again. Coral host had a significant effect on both the size and age of sex change ($P < 0.001$). Based on the maturity model, 50% of individuals (γ) will change sex by 8.54 yrs and 34.81 mm on *A. palmata*, 7.07 yrs and 22.67 mm on *Diploria* spp., and 6.24 yrs and 21.65 mm on *Montastraea* spp. (Table 2.5; Fig. 2.7). For the age-based analysis, the rate of change (k) was not significantly different in pairwise comparisons of snails from *A. palmata* vs. *Diploria* spp. ($P > 0.05$), but all other pairwise comparisons were significant ($P < 0.01$). For the size-based analysis, the maturity curves for snails from *Diploria* spp. and *Montastraea* spp. were not coincident at an alpha level of 0.05. However, the rate of change (k) between these two host taxa did not vary significantly ($P > 0.05$) and the difference in the size at which 50% were female (γ) was only marginally significant ($P = 0.04$). All other pairwise comparisons in the size-based analysis were highly significant ($P < 0.001$).

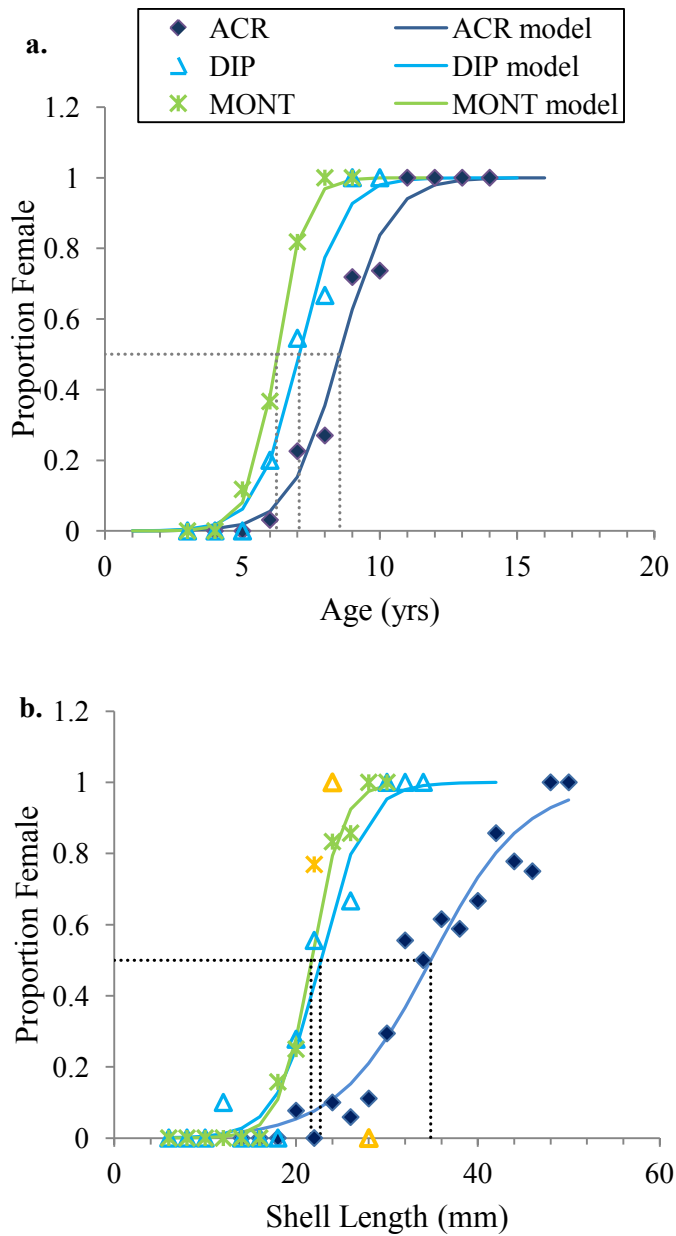


Figure 2.7 Logistic maturity model fitted to the proportion of females at each age (a) and size (b) found on *Acropora palmata* (ACR), *Diploria* spp.(DIP), and *Montastraea* spp.(MONT). The dotted lines correspond to the model predictions for age and size at which 50% of snails are female (γ) for each coral host. The orange symbols are statistical outliers that were not used to fit the model.

Table 2.5 Logistic maturity model parameters and associated R^2 for model fit for *Coralliophila abbreviata* by coral host. Model was fit to both size and age data. Parameters: k represents the rate at which individuals change sex and γ is the size or age at which 50% of individuals are predicted to have changed sex to female. All regressions were significant ($P < 0.01$)

| Metric | Parameter | Host | | |
|--------|-----------|-------------------|----------------------|-------------------------|
| | | <i>A. palmata</i> | <i>Diploria</i> spp. | <i>Montastraea</i> spp. |
| Size | k | 0.19 | 0.41 | 0.58 |
| | γ | 34.81 | 22.67 | 21.66 |
| | R^2 | 0.95 | 0.97 | 0.99 |
| Age | k | 1.12 | 1.32 | 1.96 |
| | γ | 8.53 | 7.07 | 6.24 |
| | R^2 | 0.98 | 0.98 | 0.99 |

Table 2.6 P -values for overall and pairwise likelihood ratio tests for the coincidence of logistic maturity curves (Coinc.) as well as individual parameters for models fit to size and age data. Coral host taxa: *Acropora palmata* (ACR), *Diploria* spp. (DIP), *Montastraea* spp. (MONT).

| Test | Size | | | Age | | |
|------------|--------|------|----------|--------|------|----------|
| | Coinc. | k | γ | Coinc. | k | γ |
| Overall | *** | *** | *** | *** | ** | *** |
| ACR v DIP | *** | *** | *** | *** | 0.30 | *** |
| ACR v MONT | *** | *** | *** | *** | *** | *** |
| DIP v MONT | 0.01 | 0.06 | 0.04 | *** | ** | *** |

** $P < 0.01$; *** $P < 0.001$

Discussion

Characterizing life-history traits allows us to develop testable hypotheses about the selective forces acting on organisms in different environments. Understanding how individuals and populations are affected by environmental variation in turn will help us understand the distribution of species as well as predict ecological and evolutionary responses to environmental changes in the future.

The host-specific size structure observed in this study, with acroporid corals harboring larger snails than massive corals, is consistent with reports from across the Caribbean (Hayes 1990; Bruckner et al. 1997; Baums et al. 2003a). Baums et al. (2003b) attributed this pattern to differential growth rates of snails on different hosts. They found that, during a reciprocal transplant experiment, snails feeding on *A. palmata* grew faster than those feeding on *Montastraea* spp. in the Florida Keys, regardless of the coral species from which they originated. In the present study, fitting size-at-age data to the Gompertz growth function also revealed variable growth parameters among hosts. The model indicates that snails on *A. palmata* grow faster for a longer period of time and, therefore, reach much larger sizes than those on *Montastraea* spp. corals, which is congruent with the results of Baums et al (2003b). Snails from *Diploria* spp. displayed intermediate growth parameters. Additionally, this study elucidated host-specific differences in the longevity and age structure of snail populations that contributed, along with growth, to the observed patterns in size. Snails on *A. palmata* had lower adult mortality, greater longevity, and were on average, significantly older than snails on the other two coral hosts.

These patterns of growth, reproduction, and longevity indicate that *A. palmata* has greater nutritional value for *C. abbreviata* than *Montastraea* spp. In a nutritional analysis, Baums et al (2003a) found that *Montastraea* spp. corals actually had more nitrogen and carbon per area of tissue than *A. palmata* in the Florida Keys. A food source with relatively higher concentrations of these constituents is generally considered to be more profitable. However, the nutritional quality of coral tissue may also be affected by the presence and concentrations of secondary metabolites, nematocysts, and structural defenses (Glynn and Krupp 1986). Thus, it is possible that slow growing massive corals are more chemically or physically defended than the fast growing acroporid corals. In the evolutionary ecology of plant/herbivore interactions for instance, there is a well established physiological trade-off for plants between growth and the production of chemical and structural defenses that reduce herbivore-induced damage and mortality (Herms and Mattson 1992). Unfortunately, investigations of chemical and structural defenses of reef invertebrates have largely been limited to sponges, gorgonians, and other soft corals (Pawlik 1993).

The relationship between shell length and brood size for *C. abbreviata* on *Montastraea* spp. observed in this study is comparable to the relationship found by Wells and Lalli (1977) for this species on the same host in Barbados. The inclusion of females from other host taxa revealed that the per capita brood size of snails increases as a power function with female shell length. The larger females found on *A. palmata*, therefore, had much higher per capita egg production than the relatively smaller females found on the other two hosts, suggesting that female *C. abbreviata* on *A. palmata* have the potential to contribute more offspring to the predator populations on coral reefs than snails feeding on

other coral prey. However, host specific life history trade-offs may exist that act to balance individual fitness across hosts. For instance, the benefits of the compounding effect of relatively early reproduction on individual fitness may counteract the negative effects of small size on per-brood fecundity and shorter life-span for females on *Diploria* spp. and *Montastraea* spp. In any case, the relative contribution of females from each host to overall population growth rate will also be dependent on the relative abundances of corals and the density of snails on each host.

Trade-offs between growth, reproduction, and mortality are ubiquitous in the theory of life history evolution (Stearns and Koella 1986; Stearns 1989). All else being equal, in high growth environments, theory predicts that organisms will grow faster, mature and reproduce earlier at larger sizes, and die younger than in poor growth environments. However, differences in extrinsic adult mortality, juvenile mortality, or both, may decouple this relationship (Stearns and Koella 1986; Kawecki and Stearns 1993; Beckerman et al 2010). When adult or overall mortality rate increases, fewer individuals survive to older ages, and older age classes, therefore, contribute less to overall fitness and the optimal age at maturation decreases (Gasser et al 2000). On the other hand, when mortality is greater for juveniles or small individuals, fitness is maximized by maturing later at larger sizes (Stearns and Koella 1986; Beckerman et al 2010). Resources are thus allocated to growth instead of reproduction through the vulnerable period.

Here, I found that *C. abbreviata* living and feeding on *A. palmata* changed sex later at much larger sizes than those on *Montastraea* and *Diploria* spp. corals, despite an apparent favorable growth environment. Host specific mortality regimes, therefore, likely

affect size and age at sex change for *C. abbreviata*. The higher instantaneous mortality rates (Z) for snails on *Montastraea* and *Diploria* spp. indicate higher adult mortality for snails on these corals compared to *A. palmata*, which may select for earlier sex change at smaller sizes for those snails. These patterns are also compatible with a theory of higher mortality rates for juveniles and small individuals on *A. palmata* compared to the other two hosts, which, conversely, would select for later sex change at larger sizes for snails on *A. palmata*. This hypothesis is also supported by the observed structure of snail populations across hosts. Although differences in colony morphology among coral taxa make a direct comparison of snail densities per area of coral tissue problematic, snail abundances are often greater on *Montastraea* spp. than on acroporid corals in the Caribbean (Jamaica: Miller 1981; Panama: Hayes 1990; Florida: Baums et al. 2003a). In this study, there were far fewer younger individuals found on *A. palmata* than on *Diploria* spp. and *Montastraea* spp.; only 17% of snails less than five years of age were from *A. palmata* even though 51% of all snails aged came from this host. These patterns of snail abundance and size/age structure would emerge if survival of young/small individuals was relatively low on *A. palmata* but there was an escape from predation at larger sizes. Other factors, such as differential recruitment and/or an ontogenetic shift in host, with snails moving from massive corals to branching corals as they get older or larger could also account for these patterns. However, since adult *C. abbreviata* appear to have low mobility, especially on massive and plating corals (Hayes 1990; Bruckner et al. 1997) and there is a large overlap in the size and age ranges of snails on the various hosts, these scenarios seem unlikely.

There are multiple factors that might contribute to host-specific predation risk for *C. abbreviata*. First, the three dimensional structure of different corals may attract different suites of predators. Topographic complexity has been positively correlated to the diversity of fishes and invertebrates on coral reefs (Lirman 1999; Idjadi and Edmunds 2006; Wilson et al 2007). *Acropora palmata* is a large branching coral with complex three dimensional structures and may, therefore, facilitate predation by a more diverse group of predators on *C. abbreviata*, compared to the boulder like colonies of *Montastraea* spp. and *Diploria* spp. There are many potential predators of *C. abbreviata* including the Caribbean spiny lobster (*Panulirus argus*; Baums, Szmant, pers. comm.), snapping shrimp (*Synalpheus fritzmuelleri*; Goldberg 1971), octopus (A. Bright, pers. comm.), as well as a multitude of other crabs and fishes. Furthermore, snails on massive and plating corals generally behave more like parasites, remaining relatively sedentary and cryptic along the tissue margin of the coral, whereas snails feeding on the acroporid corals move up from the base of the coral colony, rapidly consuming tissue and creating conspicuous white feeding scars (Hayes 1990; Baums et al. 2003a). Thus, snails are more visible on the acroporid corals than on massive and plating corals, putting them at higher risk of predation from visual predators. It is likely, though, that the organisms that are small enough (compared to larger, pelagic fishes) to access and find refuge in the arborous branches of the acroporid corals will be gape limited or limited in their shell crushing ability. Thus, larger snails that have thick, strong shells (pers. obs) will be less vulnerable to predation. These characteristics of *C. abbreviata* and their coral hosts support a theory of higher predation pressure on young/small snails inhabiting *Acropora* spp. corals.

Given the diversity of coral taxa that *C. abbreviata* feeds on, and the range of phenotypic variation expressed on the three coral hosts observed in the present study, it seems probable that *C. abbreviata* are phenotypically plastic, with reaction norms for life-history traits which allow individuals to adjust and maximize their fitness in the different environments associated with various coral hosts. High gene flow and a heterogeneous environment may be sufficient to maintain phenotypic plasticity over long periods of time, despite potential costs, if the average net fitness across environments is higher for the plastic genotype than for specialists (Sultan and Spencer 2002; Hollander 2008; Davidson et al 2011; Lind et al 2011).

A plastic response may be triggered by a variety of environmental cues such as light, temperature (Berrigand and Charnov 2004), nutrition (Blanckenhorn 1998; Tamburi and Martin 2009), as well as competitors and predators (Relyea 2002b). As discussed above, coral host taxa vary in a variety of ways including nutritional value and associated community which may drive the observed differences in size, growth, and timing of sex change across hosts for *C. abbreviata*.

The observed differences in morphology and life-history traits may also be due to adaptive genetic polymorphisms. When dispersal is high across a heterogeneous environment, such genetic polymorphisms may be maintained in a population through balancing selection when alternative genotypes exhibit greater fitness in different environments (Levene 1953; Hedrick et al 1976). In this case processes like strong disruptive selection or host fidelity by larvae and/or adults, resulting in assortive mating and reproductive isolation, could result in population differentiation even in the face of high dispersal. For example, Gittenberger and Gittenberger (2011) reported a large,

cryptic, adaptive radiation of 14 Coralliophilid species in the genus *Leptoconchus* that are associated with mushroom corals (Scleractinia, Fungiidae) in the Indo-West Pacific.

Many of these species are found in the same geographical area and can only be distinguished based on host association and molecular data. Thus, it is possible that *C. abbreviata* are somewhere along the spectrum of phenotypic plasticity and host-associated adaptation and genetic diversification into sibling species. Population genetic analyses are needed to fully elucidate the species status and population genetic structure of *C. abbreviata* (see Chapter 4).

Conclusions

This study identified remarkable host-specific variation in life history traits for *Coralliophila abbreviata*. *Coralliophila abbreviata* appear to display a high degree of plasticity in life-history characteristics such as timing of sex change, growth, reproduction, and longevity. In natural populations, life-history characteristics are often affected by environmental factors such as abundance and nutritional quality of available food, population density, and predation risk, as well as intrinsic physiological constraints and genetic variation (Stearns and Koella 1986; Kawecki and Stearns 1993). Thus, host-specific nutritional and mortality regimes are likely interacting in various ways to shape the growth trajectories and reactions norms for size and age at sex change for *C. abbreviata* across hosts. Based on these and previously published data viewed in the context of the theory of life-history evolution, I hypothesize that a host-associated trade-off exists for *C. abbreviata* between early survival and reproduction and later growth, longevity, and fecundity. This hypothesis needs to be addressed in future studies to fully

elucidate the factors affecting snail distribution, host use, and subsequent impact on the coral community.

CHAPTER 3: ISOLATION AND CHARACTERIZATION OF POLYMORPHIC MICROSATELLITE LOCI FOR THE CORALLIVOROUS GASTROPOD, CORALLIOPHILA ABBREVIATA

Overview

Both past and present demographic and evolutionary processes play a role in shaping the patterns of genetic variation found in contemporary populations. Thus, due to major advances in technology and theory over the last three decades, researchers in the fields of population genetics and phylogenetics have been able to shed light on demographic, ecological, and evolutionary processes that were previously unrecognized or unsubstantiated. For instance, genetic analyses have played a critical role in clarifying taxonomic uncertainties and identifying cryptic and sibling species (Knowlton 1993; Mathews 2006; Bickford et al 2007; Gittenberger and Gittenberger 2011), defining populations (Ayre and Hughes 2000; Taylor and Hellberg 2003; Baums et al 2005), and elucidating cryptic barriers to dispersal in natural populations (Baums et al 2005).

Microsatellites, in particular, have emerged as powerful molecular tools for studying the ecology and evolution of populations (Selkoe and Toonen 2006).

Microsatellites are short sections of DNA that contain tandem nucleotide repeats, generally of di-, tri-, or tetranucleotide motifs. These repetitive DNA units are abundant and ubiquitous across all eukaryotic genomes (Hamada et al 1982; Tautz and Renz 1984). They occur mainly in non-coding regions and are, therefore, assumed to evolve neutrally. They are also co-dominant and have a relatively high rate of mutation (on average: 5×10^{-4}) leading to high allelic diversity and heterozygosity in populations (Schlötterer 2000). Due to these characteristics, microsatellites can be used to assess genetic structure at a finer scale of resolution than most other molecular markers (Avice 1994). For instance,

they can be used to identify individuals (i.e. “DNA fingerprinting”) and to assess the relationships and patterns of genetic exchange within and among family groups, subpopulations, populations, and closely related species. Furthermore, because events such as population bottlenecks and expansions leave characteristic signatures in the patterns of genetic variation at neutral markers, microsatellites can be used to elucidate the demographic history of populations (Kimmel et al 1998; Luikart et al 1998; King et al 2000).

Microsatellites are thought to mutate mainly through a process called replication slippage, which occurs when, after replication has been initiated, the two strands dissociate and then realign out of register, creating a loop (Schlötterer and Tautz 1992). Depending on whether the loop is created in the nascent or template strand, the new sequence will be longer or shorter, respectively, than the template by a multiple of the repeat unit. Because polymorphisms are length based, genotyping can be accomplished using polymerase chain reaction (PCR) and gel electrophoresis techniques (Tautz 1989), which are relatively inexpensive and amenable to high throughput and automation.

On the other hand, there are a few potential challenges and caveats that need to be considered when developing and using microsatellites markers. First, although it is becoming less prohibitive, the development process can be costly and time consuming. Although the regions of DNA that flank microsatellites, from which primer sequences are developed, have a much lower mutation rate than the repetitive component, they are rarely conserved across broad taxonomic groups. Thus, new markers generally need to be developed for each species. Mutations in the flanking regions also occur at the intraspecific level, however, resulting in alleles that do not amplify with a given set of

primers, also called null alleles. Low frequencies of null alleles generally have a negligible impact on most population genetics analyses, and up to moderate levels (< 20%) can be statistically corrected for in downstream analyses (Dakin and Avise 2004; Chapuis and Estoup 2007). However, higher frequencies of null alleles will cause errors in many genetic estimates. High frequencies of null alleles and other amplification problems such as excessive stuttering (due to replication slippage during PCR amplification) and large allele drop out, as well as failure to amplify consistently are common and result in many potential microsatellite loci being rejected as usable markers for population genetic studies. However, within the last several years, methodological advances such as hybridization-capture techniques (Glenn and Schable 2005) and, even more recently, next generation sequencing technologies (Mardis 2008), have reduced the costs of microsatellite development substantially. Thus, even with some level of attrition, the costs of developing a large set of microsatellite loci for a given species are continually becoming less prohibitive.

Size homoplasy, in which alleles are identical in size but are derived from different lineages, has also been identified as a potential problem with microsatellite loci (Estoup et al. 1995; Viard et al 1998). Size homoplasy can conceal allelic diversity and potentially reduce estimates of population differentiation based on models of microsatellite evolution. The prevalence of homoplasy within and among populations is related to the mutational model, mutation rate, effective population size, and the time since divergence (Estoup et al 2002). Estoupe et al (2002) determined that size homoplasy at microsatellite loci is only potentially problematic in situations that involve high mutation rates and large effective population sizes coupled with allelic size

constraints. Additionally, they found that under most scenarios combining various mutation rates, mutation models, population sizes, and allelic constraints, homoplasy increased with time since population separation. Consequently, microsatellites are generally not suitable for higher level systematics. Most population genetic analyses, however, will not be significantly affected by homoplasy (Jarne and Lagoda 1996; Estoup et al 2002).

Finally, the mutational processes (rate, pattern, and possibly mechanism) of microsatellites appear to vary among alleles, loci, and species (Ellegren 2004). This heterogeneity, although currently poorly understood, might have important implications for some types of analyses, such as those based on allele size distributions among populations. However, the effects of heterogeneity in mutational processes on most population genetic analyses can be minimized by increasing the number of highly variable loci used (Ellegren 2004). Furthermore, because null alleles and homoplasy are also a function of mutational processes, these effects will also be largely compensated for by increasing the number of variability of loci in most analyses (Estoup 2002).

Coralliophila abbreviata is corallivorous gastropod that lives and feeds on most of the reef building corals throughout the greater Caribbean, including the imperiled *Acropora* spp. corals. As coral cover declines throughout the region, the impact of predation by *C. abbreviata* may represent a profound threat to remnant populations and impede recovery. The impact of predation, however, will depend largely on how snail populations interact with the coral community (Knowlton 2004). Previously, I showed that populations of *C. abbreviata* associated with the threatened acroporid corals, *Acropora palmata* and *A. cervicornis* display different behavioral, morphological,

demographic, and life-history characteristics than those that inhabit other coral host taxa. These results prompt hypotheses of possible host-associated genetic differentiation within *C. abbreviata*.

Thus, my objective here was to develop a set of polymorphic microsatellite markers that are suitable to assess the population genetic structure, connectivity, and patterns of gene flow among populations of *C. abbreviata* from different coral host taxa and geographical regions. Specifically, I wish to use these markers to assess a) potential host-specific genetic differentiation, b) the scale and patterns of gene flow across the Caribbean, and c) the possible role of historical demographic fluctuations in shaping the observed patterns of genetic variation and population structure. An understanding of these processes is necessary to understand contemporary community interactions, to predict the potential impact of *C. abbreviata* on the persistence and stability of threatened host corals in the future, and to develop effective control strategies.

Eight polymorphic microsatellite loci were isolated and characterized for *C. abbreviata*, and tested for cross-amplification in the congener, *C. caribaea* (Abbott 1958). The loci were screened using 60 *C. abbreviata* from two geographically disparate populations (Key Largo, FL USA and St. Vincent and the Grenadines). All loci were highly polymorphic with an average number of alleles per locus of 24 (range 13-34). Observed and expected heterozygosity values ranged from 0.375 - 0.969 and 0.877 - 0.981, respectively. Three loci deviated significantly from Hardy-Weinberg equilibrium in both populations, presumably due to null alleles. Loci were not well conserved in the congener *C. caribaea*, with only one locus amplifying consistently in this species. These are the first microsatellite markers developed for *C. abbreviata* and thus constitute a

valuable tool set that can be used to address a multitude of ecological and evolutionary questions for this species.

Materials and Methods

Genomic DNA was extracted from the foot tissue of snails using a QIAGEN DNeasy Tissue Kit. DNA samples from two individual *C. abbreviata* were used to construct a genomic DNA library enriched for microsatellite loci containing AACC, AACG, AAGG, AAC, AAG, AAT, ACT, and AC repeats, using a hybridization-capture technique modified from Glenn and Schable (2005). First, DNA samples were digested using the restriction enzymes *RsaI* and *Bst*UI. DNA fragments were then ligated to a double stranded linker (SuperSNX24 Forward: 5'-GTTTAAGGCCTAGCTAGCAGAATC-3' and SuperSNX24+4P Reverse: 5'-pGATTCTGCTAGCTAGGCCTTAAACAAAA-3') with DNA ligase at 16 °C. Two mixtures of the 3' biotinylated di-, tri-, and tetranucleotide repeat oligonucleotides were used as probes to enrich the DNA samples for microsatellite loci. The linker ligated DNA fragments were hybridized to the biotinylated microsatellite probes in a 2X Hyb Solution (12X SSC, 0.2% SDS) by denaturing the mixture at 95°C for 5 minutes, quickly ramping down to 70°C and then stepping down 0.2°C every 5 seconds for 99 cycles, maintaining at 50°C for 10 minutes, then ramping down 0.5°C every five seconds for 20 cycles, then quickly ramping down to 15°C. Enriched DNA fragments were then captured using Dynabeads (Invitrogen), amplified by PCR using the SuperSNX24 forward primer (5'-GTTTAAGGCCTAGCTAGCAGAATC-3'), and cloned using a TOPO TA Cloning System (2.1; Invitrogen), following the manufacturer's instructions. Positive colonies were amplified by PCR using universal M13 forward and reverse primers. PCR products

were visualized using gel electrophoresis and products in the 500-1000 bp size-range were then cleaned using a Montage PCR Cleanup Kit (Millipore) and sequenced using a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 3730 sequencer. Sequences were assembled and edited in SEQUENCHER v4.1 (Gene Codes Corp) and visually searched for microsatellite repeats. Thirteen primer pairs were designed for microsatellite flanking regions using Primer3 software (Rozen and Skaletsky1998; Code available at http://www-genome.wi.mit.edu/genome_software/other/primer3.html).

In initial amplifications of 24 individuals, 11 of the 13 loci amplified products of the expected size and eight were polymorphic. The eight polymorphic loci were then labeled with one of four fluorescent dyes (6-FAM, HEX, NED, VIC; Applied Biosystems) on the forward primer. PCR amplifications were then optimized and the loci were characterized further in a sample of 60 individual *C. abbreviata* collected from the Florida Keys National Marine Sanctuary in the western Atlantic ($n = 31$) and St. Vincent and the Grenadines in the Eastern Caribbean ($n = 29$). The eight polymorphic loci were also tested for cross amplification in 11 individuals of the congener, *C. caribaea*, collected from the Florida Keys ($n = 2$) and St. Thomas, USVI ($n = 9$).

PCR amplifications were carried out in a 10 μ L reaction volume containing 50-100 ng of genomic DNA, 1X PCR buffer (containing 1.5 mM MgCl₂; New England Biolabs), 0.2 mM of each dNTP, 0.15 μ M 5'-labeled forward primer, 0.15 μ M unlabelled reverse primer, and 1 U Taq DNA polymerase (New England Biolabs). The following touchdown thermal cycling program was used: 94 °C for five min, followed by three cycles of 94 °C for 15 s, 60 °C for 15 s, 72 °C for 45 s, 12 cycles of 94 °C for 15 s, 60 °C

- 54 °C (ramping down 0.5 °C per cycle) for 15 s, 72 °C for 45 s, 25 cycles of 94 °C for 15 s, 54 °C for 15 s, 72 °C for 45 s, and finally 72 °C for 10 min. The PCR products were separated on an ABI 3730 sequencer with an internal size standard to ensure accurate sizing (Gene Scan 500LIZ, Applied Biosystems) and alleles were then scored from electropherograms using GENEMAPPER v.4 software (Applied Biosystems).

For each microsatellite locus, the number of observed alleles, allele frequencies, and observed and expected heterozygosity were determined using the program GENEPOP v.4 (Raymond and Rousset 1995). GENEPOP was also used to calculate F_{IS} values and test for deviations from Hardy-Weinberg equilibrium (HWE) and linkage equilibrium for each locus. All microsatellite loci were checked for the presence of null alleles and errors due to stuttering and large allele dropout using the program MICRO-CHECKER (Van Oosterhout et al 2004).

Results and Discussion

Characteristics of the eight polymorphic microsatellite loci are reported in Table 3.1. Microsatellite sequences were deposited in GenBank under accession numbers HM156485-HM156492. No linkage disequilibrium between pairs of loci was detected ($P > 0.01$). After Bonferroni adjustment of α for multiple comparisons, three loci (Ca602, Ca606 and Ca607) deviated significantly from HWE due to heterozygote deficits in both populations ($P < 0.01$). Heterozygote deficiencies in microsatellite loci can result from several processes, including technical amplification and scoring errors such as large allele drop out and stuttering, as well as the presence of null alleles, population structuring, and inbreeding. The effects of population structure and inbreeding generally manifest across all loci and can, therefore, be tentatively ruled out here. Errors due to stuttering and large

allele dropout were not detected for any locus, whereas significant ($P < 0.01$) frequencies of null alleles were detected for all three of the loci that deviated from HWE. The estimated proportion of null alleles for these loci in the two populations ranged from 0.16-0.32. These are fairly high frequencies of null alleles, which may introduce biases and errors in some genetic estimates (Chapuis and Estoup 2007). These three markers, therefore, may not be suitable for population genetic studies.

Only one locus (Ca612) amplified specific products in the congener, *C. caribaea*. This locus was also polymorphic in *C. caribaea*, with 10 observed alleles (size range: 311bp - 386bp). Although the phylogenetic relationships among the Caribbean Coralliophilids are not well resolved, the lack of conservation of the majority of the microsatellite primer binding sites in *C. caribaea* indicates that these two species are not closely related. Nonetheless, the microsatellite markers developed here are the first reported for *C. abbreviata*. They are highly polymorphic and are largely suitable for population genetic studies for this species.

Table 3.1 Characteristics of the eight microsatellite loci developed for *Coralliophila abbreviata*. *Coralliophila abbreviata* were collected from the Florida Keys (FL; $n = 31$) and St. Vincent and the Grenadines (GR; $n = 29$). The number of alleles (N_a), expected (H_E) and observed (H_O) heterozygosities, and estimated null allele frequencies are shown for each population. Loci correspond to GenBank accession numbers HM156485-HM156492.

| Locus | Primer sequence (5'-3') | Repeat motif | Size range (bp) | Pop | N_a | H_E | H_O | Null Freq. |
|-------|---------------------------|----------------------|-----------------|-----|-------|-------|--------|--------------------|
| Ca600 | F: AAGGCAGAGGGGAAAACAGT | (CAT) ₁₇ | 181-235 | FL | 13 | 0.877 | 0.969 | 0.000 |
| | R: TTACCTGGGGACAACCTGGAG | | | GR | 16 | 0.900 | 0.821 | 0.040 |
| Ca601 | F: GAGCAGGGTGAAGAAAGACG | (AAG) ₂₃ | 210-401 | FL | 34 | 0.981 | 0.938 | 0.035 |
| | R: ACCCCTGCAAATTCTCCTTT | | | GR | 34 | 0.980 | 0.893 | 0.034 |
| Ca602 | F: CGTTTGACATAACTGAGCGTTT | (GT) ₁₅ | 192-256 | FL | 21 | 0.955 | 0.656* | 0.160 [†] |
| | R: GAGCTTGCCAATAAATTGTGG | | | GR | 21 | 0.951 | 0.500* | 0.221 [†] |
| Ca606 | F: GGGAAAGTAGTGTGGTGGACA | (CTGT) ₁₄ | 133-244 | FL | 25 | 0.971 | 0.656* | 0.173 [†] |
| | R: GCCACTTTTCATTCTAATCCA | | | GR | 20 | 0.939 | 0.607* | 0.212 [†] |
| Ca607 | F: CAAAAGATGTGGCGTCAAAA | (GT) ₂₂ | 196-258 | FL | 18 | 0.946 | 0.375* | 0.321 [†] |
| | R: GCTTCAGTGCGATACTCG | | | GR | 19 | 0.952 | 0.429* | 0.261 [†] |
| Ca608 | F: CTCCTTTCGTCTGGCTATGTG | (GT) ₂₆ | 179-253 | FL | 20 | 0.912 | 0.845 | 0.000 |
| | R: TAATGGGCAGTGGCAATTTT | | | GR | 20 | 0.933 | 0.964 | 0.011 |
| Ca609 | F: TTGGTGTGTGTAGGTTTTGTTC | (CT) ₂₂ | 178-264 | FL | 34 | 0.977 | 0.906 | 0.033 |
| | R: AAAAAGGGAGGGAAAGCAAA | | | GR | 29 | 0.972 | 0.929 | 0.000 |
| Ca612 | F: TGGGACAGATGCACAGGTAA | (GT) ₃₃ | 291-382 | FL | 25 | 0.962 | 0.969 | 0.000 |
| | R: TTCAGCAGCGAAAGGTATCA | | | GR | 27 | 0.965 | 0.893 | 0.029 |

* Significant ($P < 0.01$) deviation from expected values under Hardy-Weinberg equilibrium

[†] Significant ($P < 0.01$) frequency of null alleles

CHAPTER 4: REGIONAL AND HOST-SPECIFIC POPULATION GENETIC STRUCTURE AND DEMOGRAPHIC HISTORY OF CORALLIOPHILA ABBREVIATA

Overview

Although coral reefs are among the most biologically diverse ecosystems on the planet, the magnitude of this diversity and the mechanisms that drive and maintain it are still poorly understood (Reaka-Kudla 1997; Hughes et al 2002; Roberts et al 2002). In similarly diverse terrestrial ecosystems, it is estimated that 20% - 40% of all animal species are specialist phytophagous insects (May and Beverton 1990). Ecological niche partitioning has emerged, supported by a growing body of theoretical and empirical evidence, as a prominent mode of diversification for these insect herbivores and parasites (reviewed in: Berlocher and Feder 2002; Janz et al 2006). This process appears to be a dynamic continuum beginning when a subpopulation occupies a new host in response to some ecological trade-off such as reduced intraspecific competition or enemy free space that compensates for initial poor performance (Munday et al 2004). Subsequent adaptation to the new host may then induce reproductive isolation, often in the absence of geographic barriers to gene flow, through assortive mating and disruptive selection (Orr and Smith 1998; Dieckmann and Doebeli 1999; Nosil et al 2002). For speciation to occur, host-associated selection must be strong enough to overcome the potentially homogenizing effect of dispersal and gene flow from the original population (Kawecki 1997; Schluter 2009).

If coral reefs are the “rainforests of the sea,” then corallivores may be considered the coral reef counterparts to phytophagous insects. Corallivores are ubiquitous members of coral reef communities that belong to diverse phyla including Annelida,

Echinodermata, Mollusca, and Chordata and range from generalist facultative consumers to host-specific obligate coral parasites (Glynn 1990; Rotjan and Lewis 2008). However, whereas the role of plant-herbivore/parasite interactions in the evolution and ecology of terrestrial ecosystems is the subject of a vast literature, relatively little is known about the interactions among corals and their natural enemies (Rotjan & Lewis, 2008). If similar mechanisms of resource-associated ecological speciation are occurring on coral reefs, these coral-associated groups may harbor a large amount of cryptic biodiversity that has yet to be discovered (Knowlton 1993). Indeed, recent studies indicate that similar ecological speciation may be occurring in shallow marine ecosystems (Munday et al 2004; Sotka 2005a; Faucci et al 2007; Gittenberger and Gittenberger 2011; Krug 2011).

The Coralliophilidae are a diverse and widespread family of gastropods with approximately 200 – 250 species that feed exclusively on anthozoans. Members of this family are found from the intertidal to below 100 m and range from sessile endoparasites to mobile coral grazers (Oliverio et al 2009). The diversity, life-history, and ecology of the coralliophilids indicate that multiple adaptive radiations may have occurred in response to environmental variables such as depth and host. Supporting this theory, Gittenberger and Gittenberger (Gittenberger and Gittenberger 2011) reported a large, cryptic, adaptive radiation of 14 Coralliophilid species in the genus *Leptoconchus* that are associated with mushroom corals (Scleractinia, Fungiidae) in the Indo-West Pacific. Many of these species are found in the same geographical area and can only be distinguished based on host association and molecular data. On the other hand, Oliverio & Mariottini (2001) found no genetic differentiation between populations of *Coralliophila meyndorfii* that displayed host-specific size structure. Further studies are

clearly needed to elucidate the life-history characteristics and ecological conditions that facilitate genetic differentiation and speciation over phenotypic plasticity for coral associated organisms.

Coralliophila abbreviata are found on reefs throughout the Caribbean and tropical Western Atlantic. These snails live and feed on the tissue of at least 16 species of scleractinian coral from five different families that represent diverse growth forms and life-histories (Miller 1981). Different coral taxa, therefore, likely represent different food and habitat resources and different selective pressures for *C. abbreviata* (Baums et al 2003). Supporting this assertion, populations of *C. abbreviata* display host-specific behavioral, morphological, demographic, and life-history characteristics. Specifically, snail populations found on the branching acroporid corals, *Acropora palmata* and *A. cervicornis*, are larger (Hayes 1990b; Bruckner et al 1997; Baums et al 2003; Johnston and Miller 2007), due to increased growth (Baums et al 2003; Johnston and Miller 2007) and longevity (Johnston & Miller 2007), than on several massive and plating corals investigated. Because fecundity increases as a function of female size, females associated with acroporid corals produce more offspring per capita (Johnston and Miller 2007). Furthermore, feeding mode and tissue consumption rate of *C. abbreviata* also vary among coral host taxa. Snails on massive and plating corals generally behave more like parasites, remaining relatively sedentary along the tissue margin causing little appreciable damage. Snails feeding on the acroporid corals, however, move up from the base of the coral colony, rapidly consuming tissue and creating conspicuous white feeding scars (Hayes 1990; Baums et al. 2003b). Although the acroporid corals are presumed to be the preferred prey due to increased growth and reproduction, snail abundance and group sizes

are often greater on non-acroporid corals (Miller 1981; Baums et al. 2003a; Hayes 1990), indicating that different processes are regulating snail populations on the various coral hosts. Together, these factors make *C. abbreviata* an ideal candidate for investigating potential host-associated genetic differentiation and cryptic speciation on coral reefs.

Here, I assessed the Caribbean wide population genetic structure of *C. abbreviata* using newly developed microsatellite markers as well as mitochondrial DNA sequence data. My overall objective was to characterize the genetic variation of *C. abbreviata* populations from different coral host taxa and geographical locations to assess a) potential host-specific genetic differentiation, b) the scale and patterns of gene flow across the Caribbean, and c) the possible role of historical demographic fluctuations in shaping the observed patterns of genetic variation and population structure. An understanding of these processes is necessary to understand contemporary community interactions and to predict the potential impact of *C. abbreviata* on the persistence and stability of threatened host corals in the future.

Materials and Methods

Sample Collection and Processing

Individual *Coralliophila abbreviata* were collected using SCUBA from three coral host taxa at 18 reef sites and six localities spanning most of the species' range (Fig. 4.1; Table 4.1). After collection, shells were crushed with a hammer and snail tissue was placed in 70%-95% ethanol and stored at -80°C until processing. Genomic DNA was then extracted from the foot tissue of individual *C. abbreviata* using either a standard CTAB extraction protocol or a Qiagen DNeasy Tissue Kit, following the manufacturer's instructions. Published primers (UCYTB151F and UCYTB270R) and PCR conditions

were used to amplify a portion of the mitochondrial cytochrome b gene (*cyt b*; Merritt et al 1998). PCR products were purified using a Montage PCR Cleanup Kit (Millipore) and shipped to Elim Biopharmaceuticals (Hayward, CA, U.S.A.) for sequencing. Sequences were then assembled and edited in SeqMan and aligned using MegAlign (both DNASTAR, Inc).



Figure 4.1 Map of major sampling localities across the greater Caribbean. Coordinates for specific reef sites within each locality can be found in Table 1.

Table 4.1 Sample sizes for mitochondrial Cytochrome b sequences (mtDNA) and five microsatellite markers (Msats). Sample sizes from each coral host taxon at each site are in parenthesis. GTC, Green Turtle Cay; SVG, St. Vincent and the Grenadines; A, *Acropora palmata*; M, *Montastraea* spp.; MY, *Mycetophyllia* spp.

| Region | Locality | Reef name | Lat (°) | Long (°) | mtDNA | Msats |
|--------------|------------|------------------------------|---------|----------|-----------------|-----------------------|
| West | Florida | Little Grecian | 25.1184 | -80.3171 | 27 (A:12; M:15) | 56 (A:24;M:32) |
| | | Sand Island | 25.0179 | -80.3686 | - | 15 (A:13;M:2) |
| | | Florida Total | | | 27 (A:12; M:15) | 71 (A:37;M:34) |
| | Bahamas | Green Turtle Cav | 26.7667 | -77.3167 | - | 12 (A:12) |
| | Navassa | NW Point | 18.4138 | -75.0297 | 6 (M:6) | 9 (M:9) |
| | | W Pinnacles | 18.4047 | -75.0267 | 10 (A:4; M:6) | 14 (A:6; M:8) |
| | | DOT 118 | 18.3962 | -75.0189 | 12 (A:12) | 10 (A:10) |
| | | Navassa Total | | | 28 (A:16; M:12) | 33 (A:16; M:17) |
| | Panama | Hospital Pt. | 9.3380 | -82.2407 | 30 (MY:30) | 51 (MY:51) |
| | West Total | | | | | 85 (A:28; M:27;MY:30) |
| East | SVG | Blue Lagoon | 13.1285 | -61.1993 | 5 (A:5) | 15 (A:15) |
| | | Bequia | 13.0150 | -61.2491 | 16 (A:2; M:14) | 33 (A:7; M:26) |
| | | Conouan | 12.6943 | -61.3364 | 3 (A:3) | 11 (A:5; M:6) |
| | | Mustique | 12.8915 | -61.1863 | 3 (A:3) | 8 (A:8) |
| | | Tobago Cay | 12.6253 | -61.3499 | - | 12 (M:12) |
| | | Union Island | 12.5916 | -61.4160 | - | 1 (A:1) |
| | | SVG Total | | | 27 (A:13; M:14) | 80 (A:36; M:44) |
| | Bonaire | Taylors Made | 12.2238 | -68.4051 | - | 16 (A:7; M:9) |
| | Curacao | Awa Blanca | 12.0406 | -68.7834 | - | 2 (A:2) |
| | | Blue Bay | 12.1352 | -68.9898 | 4 (M:4) | 10 (A:2; M:8) |
| | | Playa Largu | 12.1470 | -69.5540 | 10 (M:10) | 21 (A:11; M:10) |
| | | Sea Aquarium Curacao/Bonaire | 12.0838 | -68.8958 | 4 (M:4) | 13 (A:3; M:10) |
| | | Total | | | 18 (M:18) | 46 (A:18; M:28) |
| East Total | | | | | 45 (A:13; M:32) | 142 (A:61; M:81) |
| TOTAL | | | | | 130 | 309 |

The five polymorphic microsatellite markers that were previously found suitable for population genetic analyses (Chapter 4) were used to create multi-locus genotypes for the entire data set. PCR amplifications were carried out in a 10 μ L reaction volume containing 50-100 ng of genomic DNA, 1X PCR buffer (containing 1.5 mM MgCl₂; New England Biolabs), 0.2 mM of each dNTP, 0.15 μ M 5'-labeled forward primer, 0.15 μ M unlabelled reverse primer, and 1 U Taq DNA polymerase (New England Biolabs). The following touchdown thermal cycling program was used: 94 °C for five min, followed by three cycles of 94 °C for 15 s, 60 °C for 15 s, 72 °C for 45 s, 12 cycles of 94 °C for 15 s, 60 °C - 54 °C (ramping down 0.5 °C per cycle) for 15 s, 72 °C for 45 s, 25 cycles of 94 °C for 15 s, 54 °C for 15 s, 72 °C for 45 s, and finally 72 °C for 10 min. The PCR products were separated on an ABI 3730 sequencer with an internal size standard to ensure accurate sizing (Gene Scan 500LIZ, Applied Biosystems) and alleles were then scored from electropherograms using GENEMAPPER v.4 software (AppliedBiosystems).

Characterization of Genetic Variation

Genetic diversity estimates for *cyt b* sequences, including the number of haplotypes, haplotype diversity (h), and nucleotide diversity (π) were calculated for all sampled populations using the program ARLEQUIN v. 3.5 (Excoffier et al 2005). The genealogical relationships among *cyt b* haplotypes were assessed by constructing a phylogenetic network using the median joining algorithm implemented in NETWORK v. 4.6 (Bandelt et al 1999) with default values.

For each microsatellite locus, the number of observed alleles, allele frequencies, and observed and expected heterozygosity were determined using the program GENEPOP v.4 (Raymond and Rousset 1995). GENEPOP was also used to calculate F_{IS} values and test for deviations from Hardy-Weinberg equilibrium (HWE) and linkage equilibrium for each locus. All microsatellite loci were checked for the presence of null alleles and errors due to stuttering and large allele dropout using the program MICRO-CHECKER (Van Oosterhout et al 2004).

Population Structure Analyses

To examine population differentiation, analysis of molecular variance (AMOVA), pairwise F_{ST} statistics, and exact tests of population differentiation were calculated for both mtDNA and microsatellite data using ARLEQUIN v. 3.5. Due to small sample sizes from several reef sites (Table 4.1), individuals were grouped by localities (Fig. 4.1), which thus represent the smallest geographical scale of comparison here. The small microsatellite sample from the Bahamas was only included in the STRUCTURE analysis, which does not take into account sample origin (see below). Previously, Baums et al. (Baums et al 2005) found regionally isolated populations of the host coral, *Acropora palmata* from the Eastern Caribbean, delineated by the Mona Passage (between Hispaniola and Puerto Rico) and including the Lesser Antilles, and the Western Caribbean including the Florida peninsula. This genetic break has been found in other coral reef organisms (Taylor and Hellberg 2003) and is consistently recovered in biophysical models of the region (Cowen et al 2006; Galindo et al 2006; Kool et al 2010). Thus, I conducted hierarchical nested analyses to assess population structure among all localities, among localities within these major geographical regions, and between regions.

To test the hypothesis of host associated genetic differentiation, individuals were grouped by coral host taxa. The significance of all AMOVA tests was assessed with 20,000 nonparametric permutations. Exact tests of population differentiation included 10,000 dememorisation steps followed by an additional 100,000 Markov chain steps.

To assess the relationship between genetic distance and geographical distance, Mantle tests were performed for both mtDNA and microsatellite data sets using ARLEQUIN v.3.5. The geographical distance matrix was constructed using the shortest distances between locations via major ocean surface currents. The significance of correlations was tested with 10,000 permutations.

For the microsatellite data, the Bayesian Markov Chain Monte Carlo (MCMC) clustering algorithms implemented in the program STRUCTURE v. 2.3 (Pritchard et al 2000) were used to infer population structure. This program approximates, *ad hoc*, the number of discrete populations (K) represented in a sample. It assigns individuals to populations and can identify migrants when prior population information is used. Here, the admixture, location prior (LOCPRIOR; Hubisz et al 2009), and correlated allele frequencies (Falush et al 2003) models within the program were used. These models were chosen because, due to the high dispersal capability of the planktotrophic veliger larvae of *C. abbreviata*, individuals from different populations are likely to have a common or an admixed ancestry and high gene flow. The selected models improve the clustering performance of STRUCTURE over other models in such situations where the signal of actual genetic structure may be weak, but do not tend to infer structure where there is none (Falush et al. 2003; Hubisz et al. 2009). Simulations were run for values of K from 1-10, with ten replicates per K value. All simulations were run with a burn-in

length of 10^5 steps followed by 10^6 steps for data collection. The log posterior probability of the data, $[\ln P(K)]$, was averaged across replicates for each K value and plotted against K to estimate the most likely number of populations using Structure Harvester v0.6.6 (Earl 2011).

Demographic History Analyses

Historical demographic trends were investigated using several distinct methods. First, the mismatch distribution, based on the number of observed nucleotide differences between pairs of mitochondrial *cyt b* sequences was compared to the distributions expected under models of pure demographic expansion (Rogers and Harpending 1992) and sudden spatial expansion (Excoffier 2004) using ARLEQUIN. Model parameters (θ_0 , and θ_1 , and τ) were estimated by a generalized non-linear least-square approach with confidence intervals obtained through parametric bootstrapping (10^5 replicates; Schneider and Excoffier 1999). For haploid, maternally inherited mitochondrial DNA, $\theta = 2N_e\mu$, where N_e is the female effective population size and μ is the mutation rate. The time scale parameter (τ) is in mutational units; $\tau = 2ut$, where t measures time in generations and u is the sequence mutation rate. The sums of squared deviations (SSD) of bootstrapped replicates were used to calculate the significance of the fit between the observed and expected mismatch distributions (Schneider & Excoffier 1999). To convert the time since expansion (τ) from mutational units to years, I used mutation rates of 0.6 % and 1.0 % per site per MY based on fossil calibrated estimates of mtDNA sequence divergence rates between geminate species of mollusks in the Caribbean and Eastern Pacific (Marko 2002), and a female generation time of 6 years, based on estimates of the age at which individuals change sex from male to female (Johnston & Miller 2007).

Second, Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) statistics were calculated for *cyt b* sequences to test for deviations from selective neutrality and to refine inferences of demographic history, using ARLEQUIN. These statistics are expected to be zero for populations of constant size and in mutation drift equilibrium. Significant deviations from neutrality may be caused by selection or historic demographic fluctuations such as population bottleneck and expansion (Fu 1997, Aris-Brosou and Excoffier 1996). Fu's F_S has been shown to be a particularly sensitive statistic for detecting sudden demographic expansion (Fu 1997; Ramos-Onsins and Rozas 2002). Statistical significance was assessed by comparing the observed statistic values to expected values based on 10^5 neutral coalescent simulations.

Next, I used the coalescent-based approach implemented in the program BEAST v1.6.1 to construct a Bayesian skyline plot (BSP; Drummond et al 2005; Drummond and Rambaut 2007). Bayesian skyline analysis provides an estimate of the population size through time by sampling the posterior distributions of model parameters. The HKY + G model of nucleotide substitution (determined using AIC implemented in jModelTest v.0.1.1; Posada 2008) was used with four gamma categories, estimated base frequencies, two codon partitions [(1+2), 3], and unlinked substitution rate parameters. A strict molecular clock was enforced with a rate of 1×10^{-8} substitutions per site per year. Operators were auto optimized. I ran three independent runs of 200 million MCMC steps sampled every 1000 steps after a 10% burn-in. The log and tree files for the three independent runs were combined using LOGCOMBINER v.1.6.1, discarding the burn-in and re-sampling every 1000 steps. Convergence and effective sample sizes (ESS) were evaluated in TRACER v1.5. After confirming that parameters showed good convergence

and all ESS values were greater than 200, the BSP was constructed using the combined files in TRACER v1.5.

Finally, using the microsatellite data set, I calculated the imbalance index (β), a statistic developed by Kimmel et al. (1998) and determined to be a powerful microsatellite-based approach for detecting past population fluctuations (King et al 2000). The imbalance index is based on the ratio of the allele-size variance and homozygosity (probability of size identity of alleles). Here, the index was calculated as the difference in the natural logarithm of the estimators of theta based on allele size variance (θ_V) and homozygosity (θ_H), calculated from the equations presented in Kimmel et al. (1998), averaged over all loci. This is the most sensitive estimator of $\ln \beta$ for detecting population expansion (King et al. 2000). Values of $\ln \beta$ greater than one are characteristic of populations that have undergone a recent demographic expansion preceded by a reduction in size, whereas a value of less than one indicates that the population was stable prior to a population expansion (Kimmel et al. 1998; King et al. 2000).

Results

Genetic Variation

A 366 bp fragment of the mtDNA *cyt b* gene was sequenced and analyzed for 130 *Coralliophila abbreviata* individuals. The sequence alignment contained 55 polymorphic sites, resulting in 57 unique haplotypes. Haplotype diversity (h) was moderate to high across localities, ranging from 0.613 to 0.902 (global $h = 0.773$) and nucleotide diversity (π) was low across populations, ranging from 0.003 to 0.005 (global $\pi = 0.004$; Table

4.2). One ancestral haplotype was shared among all populations and was the most common haplotype found in each population. Eighty-four percent of the divergent haplotypes were singletons and separated from the ancestral haplotype by only 1-3 mutational steps, resulting in a star-like haplotype network (Fig. 4.2).

Characteristics of each of the five polymorphic microsatellite loci, including the number of observed alleles, observed and expected heterozygosity, F_{IS} value, and the probability of deviation from HWE, are reported in Table 4.3. No significant ($P < 0.05$) linkage disequilibrium between pairs of loci was detected and no loci deviated significantly from HWE.

Table 4.2 Genetic diversity indices, neutrality test statistics, and mismatch distribution parameters for mitochondrial cytochrome *b* sequences of *Coralliophila abbreviata* collected from Florida (FL), Navassa (NAV), St. Vincent and the Grenadines (SVG), Curacao (CUR), Panama (PAN), as well as all individuals combined (GLOBAL). Genetic diversity indices: N , sample size; N_h , number of haplotypes; N_p , number of polymorphic sites; h , haplotype diversity; π , nucleotide diversity. Neutrality statistics: D , Tajima's statistic (Tajima 1989); F_S , Fu's statistic (FU 1997). Mismatch distribution: τ (tau), time since beginning of expansion in mutational units; θ_0 and θ_1 , initial and final population size estimators, respectively; P (SSD), probability of sum of squared deviations; Rg, raggedness statistic (Harpending 1994); P (Rg), probability of Rg.

| | | Sampling locality | | | | | |
|-----------------------|------------|-------------------|----------|---------|----------|----------|----------|
| | | FL | NAV | SVG | CUR | PAN | GLOBAL |
| Genetic diversity | N | 27 | 28 | 27 | 18 | 30 | 130 |
| | N_h | 11 | 19 | 13 | 13 | 17 | 57 |
| | N_p | 15 | 18 | 19 | 14 | 20 | 55 |
| | h | 0.612 | 0.881 | 0.701 | 0.902 | 0.791 | 0.773 |
| | π | 0.003 | 0.005 | 0.004 | 0.005 | 0.004 | 0.004 |
| Neutrality tests | D | -2.46** | -2.13* | -2.43** | -2.14* | -2.44* | -2.64** |
| | F_S | -8.37** | -20.70** | -9.50** | -11.80** | -17.12** | -28.01** |
| Mismatch distribution | τ | 1.64 | 1.91 | 1.85 | 1.82 | 1.58 | 1.62 |
| | θ_0 | 0.040 | 0.004 | 0.417 | 0.000 | 0.000 | 0.018 |
| | θ_1 | 2.066 | 9999 | 2.848 | 9999 | 9999 | 15.025 |
| | P (SSD) | 0.970 | 0.503 | 0.975 | 0.330 | 0.960 | 0.997 |
| | Rg | 0.034 | 0.068 | 0.018 | 0.109 | 0.043 | 0.034 |
| | P (Rg) | 0.979 | 0.315 | 0.995 | 0.187 | 0.677 | 0.795 |

* $P < 0.01$; ** $P < 0.001$

Table 4.3 Characteristics of five polymorphic microsatellite loci for *Coralliophila abbreviata*. Shown, for each locus, are the forward (F) and reverse (R) primer sequences, repeat motif, size range of alleles in base pairs (bp), global sample size (N), number of observed alleles (N_a), observed (H_O) and expected (H_E) heterozygosities, fixation index (F_{IS}), and uncorrected P-value for test of departure from Hardy Weinberg Equilibrium (P_{HW}). Loci correspond to GenBank accession numbers HM156485, HM156486, HM156490-HM156492.

| Locus | Primer sequence (5'-3') | Repeat motif | Size range (bp) | N | N_a | H_O | H_E | F_{IS} | P_{HW} |
|-------|--|---------------------|-----------------|-----|-------|-------|-------|----------|----------|
| Ca600 | F: AAGGCAGAGGGGAAAACAGT R: TTACCTGGGGACAACCTGGAG | (CAT) ₁₇ | 181-235 | 300 | 20 | 0.867 | 0.868 | 0.005 | 0.476 |
| Ca601 | F: GAGCAGGGTGAAGAAAGACG R: ACCCCTGCAAATTCTCCTTT | (AAG) ₂₃ | 210-401 | 289 | 67 | 0.927 | 0.978 | 0.046 | 0.039 |
| Ca608 | F: CTCCTTTCGTCTGGCTATGTG R: TAATGGGCAGTGGCAATTTT | (GT) ₂₆ | 179-253 | 299 | 35 | 0.926 | 0.936 | 0.016 | 0.267 |
| Ca609 | F: TTGGTGTTTGTAGGTTTTTGTTC R: AAAAAGGGAGGGAAAAGCAAA | (CT) ₂₂ | 178-264 | 293 | 50 | 0.952 | 0.974 | 0.021 | 0.030 |
| Ca612 | F: TGGGACAGATGCACAGGTAA R: TTCAGCAGCGAAAGGTATCA | (GT) ₃₃ | 291-382 | 298 | 48 | 0.940 | 0.960 | 0.022 | 0.027 |

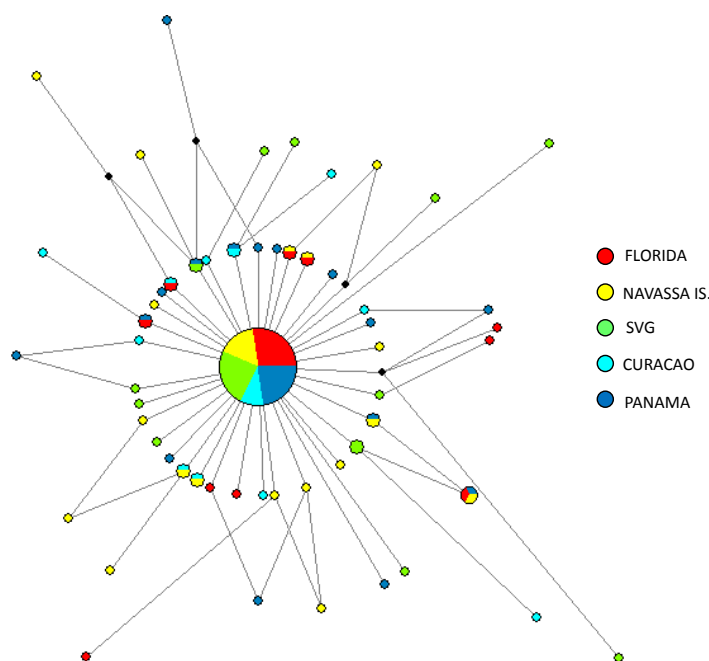


Figure 4.2 Median joining network for *cyt b* haplotypes from a sample of 130 *Coralliophila abbreviata* from five geographic locations. Circles represent individual haplotypes. The size of the circle is proportional to the frequency of the haplotype in the sample and branch lengths are proportional to the number of mutational steps (range: 1-3). Small black circles represent missing/theoretical haplotypes.

Population Genetic Structure

Genetic differentiation was not detected among *C. abbreviata* populations from different coral host taxa or at any geographical scale tested, regardless of marker type used. Cytochrome b haplotypes did not cluster by coral host taxa or geographic region (Fig 4.2). For all AMOVA analyses, at least 99% of the genetic variation was attributed to the within population source of variation (Table 4.4). There were no significant ($P < 0.05$) exact tests of population differentiation and no significant ($P < 0.05$) pairwise F_{ST} comparisons using mtDNA or microsatellite data after Bonferroni correction (Table 4.5). Furthermore, I found no significant correlation between genetic and geographical distances (mtDNA: $r = -0.299$, $P = 0.753$; msats: $r = -0.251$, $P = 0.828$). Finally, for the STRUCTURE analysis of the microsatellite data set, all individuals had approximately the same probability of originating from each hypothetical population, regardless of the K value (Fig. 4.3). The $[\ln P(K)]$ was greatest for $K = 1$ with no overall trend across K values from 1-10, indicating that all individuals were sampled from a single population (Fig 4.4).

Table 4.4 Analysis of molecular variance (AMOVA) results for populations of *Coralliophila abbreviata* based on (a) mtDNA and (b) microsatellite datasets grouped by coral host taxa (*Acropora* spp, *Montastraea* spp., and *Mycetophylia* spp.) and major geographical sub-regions in the Caribbean (East and West).

| a) mtDNA | | | | | | |
|-------------------|---------------------------------|------|-------|-------------|------------------|----------|
| Structure | Source of variation | d.f. | SS | % Variation | Φ statistic | <i>P</i> |
| Host | Among groups | 2 | 1.68 | -0.13 | -0.001 | 0.50 |
| | Among populations within groups | 5 | 4.23 | 0.76 | 0.008 | 0.14 |
| | Within populations | 122 | 93.10 | 99.37 | 0.001 | 0.09 |
| East, West | Among groups | 1 | 0.88 | 0.27 | 0.002 | 0.30 |
| | Among populations within groups | 3 | 2.26 | -0.07 | -0.001 | 0.53 |
| | Within populations | 125 | 95.86 | 99.79 | 0.003 | 0.37 |

| b) Microsatellites | | | | | | |
|--------------------|---------------------------------|------|---------|-------------|------------------|----------|
| Structure | Source of variation | d.f. | SS | % Variation | Φ statistic | <i>P</i> |
| Host | Among groups | 2 | 4.75 | 0.10 | 0.001 | 0.08 |
| | Among populations within groups | 6 | 12.14 | -0.18 | -0.002 | 0.98 |
| | Within populations | 593 | 1350.80 | 100.08 | -0.001 | 0.93 |
| East, West | Among groups | 1 | 2.13 | 0.05 | 0.001 | 0.5 |
| | Among populations within groups | 3 | 5.54 | -0.16 | -0.002 | 0.99 |
| | Within populations | 597 | 1360.03 | 100.12 | -0.001 | 0.99 |

Table 4.5 Pairwise F_{ST} values between samples from different coral hosts at each locality for microsatellite data (below the diagonal) and mtDNA (above the diagonal). There were no significant ($P < 0.05$) values after Bonferroni correction for multiple comparisons.

| | FL ACR | FL MON | NAV ACR | NAV MON | SVG ACR | SVG MON | CUR ACR | CUR MON | PAN MYC |
|---------|-----------|-----------|------------|------------|------------|------------|------------|------------|------------|
| FL ACR | | -0.006 | -0.015 | 0.023 | 0.020 | -0.015 | -- | -0.023 | -0.025 |
| FL MON | 0.001 | | 0.011 | 0.016 | 0.004 | 0.000 | -- | 0.002 | -0.005 |
| NAV ACR | 0.002 | 0.004 | | 0.035 | 0.037 | 0.015 | -- | 0.015 | 0.008 |
| NAV MON | -0.002 | -0.004 | 0.006 | | 0.040 | 0.007 | -- | 0.011 | 0.026 |
| SVG ACR | -0.001 | -0.001 | -0.002 | -0.001 | | 0.016 | -- | 0.021 | 0.017 |
| SVG MON | -0.001 | -0.001 | 0.000 | -0.004 | 0.001 | | -- | -0.017 | -0.010 |
| CUR ACR | -0.003 | -0.002 | -0.001 | -0.004 | -0.005 | -0.003 | | -- | -- |
| CUR MON | 0.001 | -0.002 | 0.005 | 0.003 | -0.002 | -0.003 | -0.004 | | -0.003 |
| PAN MYC | -0.001 | -0.002 | 0.006 | -0.003 | -0.001 | -0.001 | -0.001 | -0.004 | |

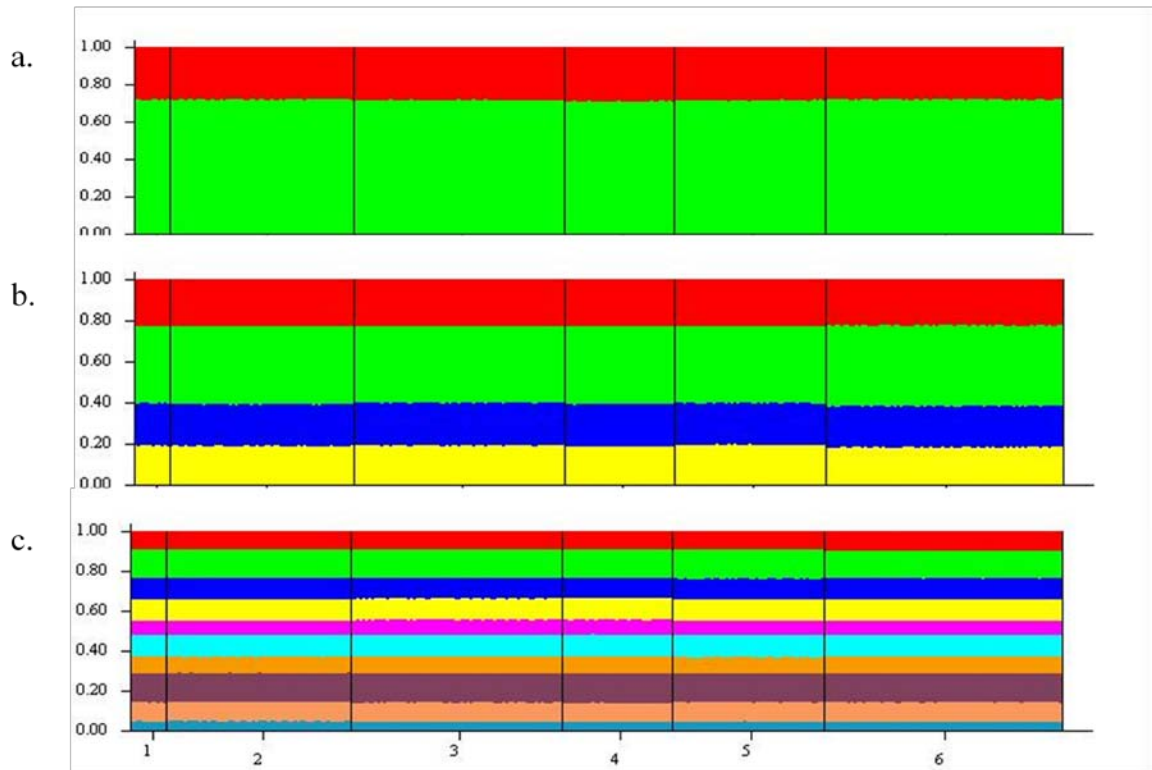


Figure 4.3 Results of STRUCTURE analysis of five microsatellite loci and 309 individuals of *Coralliophila abbreviata*. Shown are STRUCTURE plots for $K = 2$ (a), $K = 4$ (b), and $K = 10$ (c), where individuals are groups by sampling locality (1: Bahamas; 2: Curacao; 3: Florida; 4: Navassa; 5: Panama; 6: St. Vincent and the Grenadines).

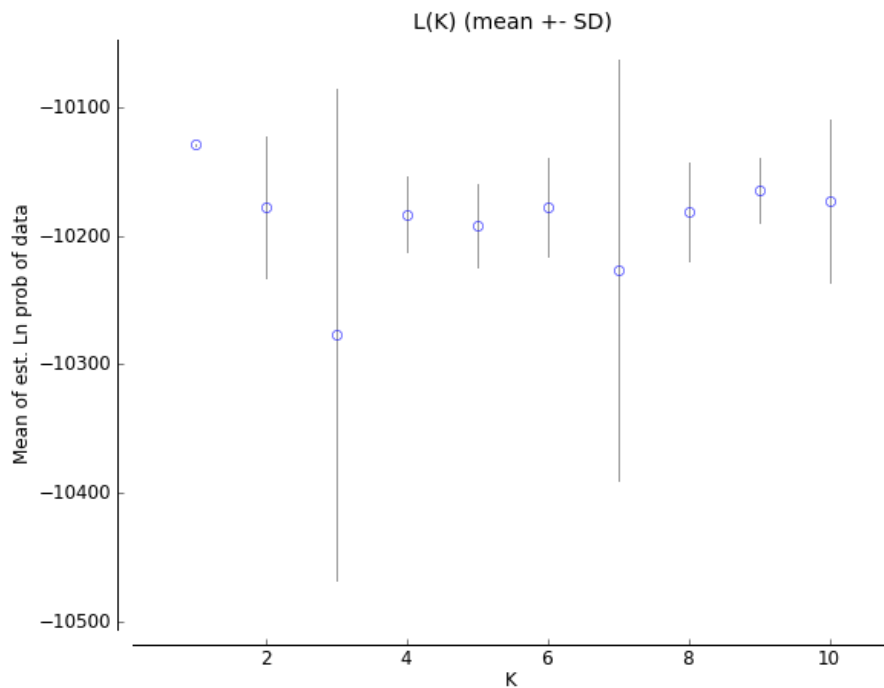


Figure 4.4 Results of STRUCTURE analysis of five microsatellite loci from 309 individuals of *Coralliophila abbreviata*. Shown is the mean estimated Ln P(K) plotted against K.

Demographic History

The overall mismatch distribution was unimodal and significantly coincident with the distribution expected under the sudden demographic expansion model. (Table 4.2; Fig 4.5). Based on the optimized value of τ (1.62), a generation time of 6 years, and mutation rates of 0.6 % and 1.0% site⁻¹ MY⁻¹, the expansion began during the Pleistocene, approximately 219,000 – 365,000 years ago. Tajima's D and Fu's F_S statistics were consistently negative and significantly different than expected under mutation-drift equilibrium (Table 4.2). The large negative values indicate an excess of rare alleles and a reduced number of common alleles, which is consistent with patterns expected as a result

of a large population expansion or a selective sweep (Tajima 1989, Aris-Brosou & Excoffier 1996, Fu 1997).

The Bayesian skyline analysis implemented in BEAST indicated that the current median female effective population size is 7.2×10^6 (Fig 4.6). The mean time since the most common recent ancestor (tMRCA) in the *cyt b* gene genealogy was 0.248 Ma (lower 95% HPD: 0.159 Ma; upper 95% HPD: 0.370 Ma), at which point a large population expansion began (Fig 4.6).

The imbalance index calculated from the microsatellite dataset also supports a scenario of recent demographic expansion; the natural logarithm of the variance and homozygosity estimators of theta were calculated ($\theta_V = 6.64$ and $\theta_H = 5.49$), and an imbalance index of $\ln \beta = 1.15$, was obtained. Values of $\ln \beta$ greater than one are characteristic of populations that have undergone a recent demographic expansion preceded by a reduction in size (Kimmel et al. 1998, King et al. 2000).

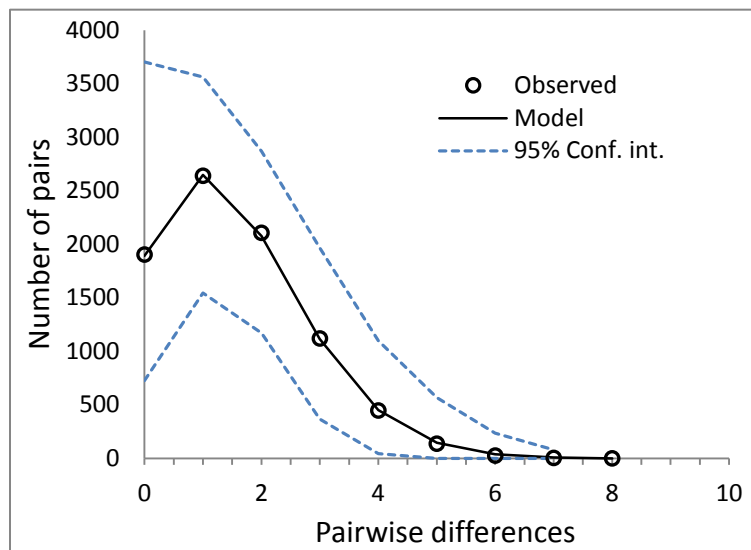


Figure 4.5 Mismatch distribution. The observed number of pairwise nucleotide differences (open circles) for *cyt b* sequences plotted with the expected number of pairwise nucleotide differences under a model of sudden demographic expansion (solid line) and the 95% confidence intervals for the model estimation (dashed lines).

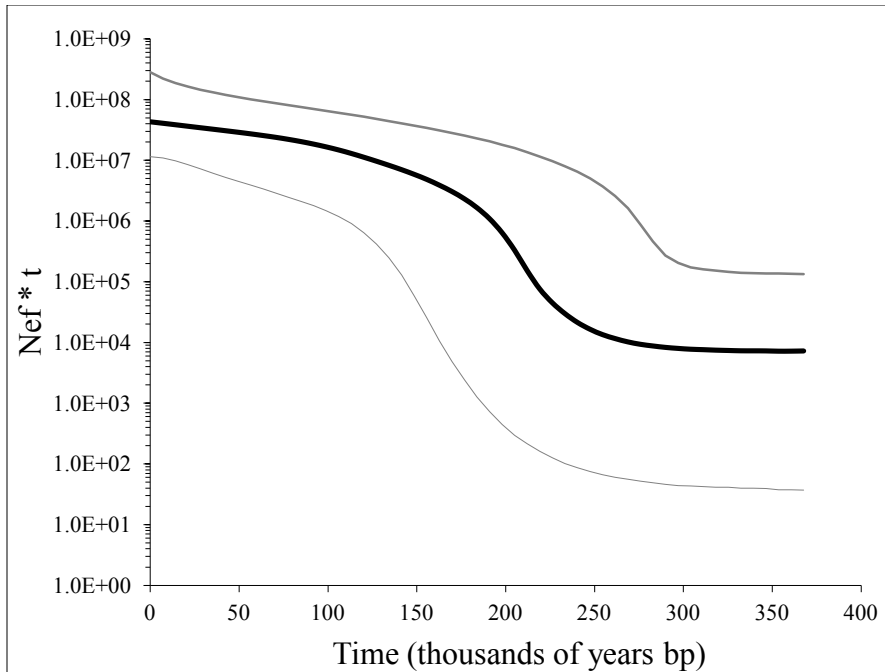


Figure 4.6 Bayesian skyline plot for *Coralliophila abbreviata* created using *cyt b* sequence data. The solid black line represents the median female effective population size (N_{ef}) multiplied by the generation time (t), plotted on a log scale. The thin grey lines are the upper and lower 95% highest posterior distribution (HPD) for the population size estimator. The BSP shows a population expansion occurring approximately 250 k years ago.

Discussion

Molecular and ecological studies over the last couple of decades have begun to unravel the relative effects of extrinsic factors such as current regimes, historic large scale climatic oscillations and other vicariance events, and intrinsic and ecological factors such as reproductive mode, resource use, and behavior on present day marine biogeography (Benzie 1999a; Mcmillen-Jackson and Bert 2003; Barber and Bellwood 2005; Baums et al 2005; Krug 2011, Hart and Marko 2010; Eytan and Hellberg 2010; Polato et al 2010). Here, I contribute to this effort by presenting data on the broad scale population genetic

structure of an ecologically important coral associated gastropod in the greater Caribbean in the context of geography, ecology and resource use patterns, and demographic history.

Population Genetic Structure

Genetic differentiation of *C. abbreviata* populations was not detected at any geographical scale assessed in this study, including between populations separated by more than 3500 km, or among populations collected from different coral host taxa. These results indicate that gene flow and population connectivity are high across the species' range. High gene flow is consistent with expectations based on snail life-history characteristics including high fecundity (Johnston & Miller 2007) and planktotrophic veliger larvae with a putative pelagic larval duration (PLD) of more than 30 days (Johnston, unpub. data). Although PLD has been decoupled from dispersal distance and gene flow in several Caribbean reef fishes (Taylor and Hellberg 2003; Bowen et al 2006) long distance dispersal and genetic homogeneity are prevalent in other species of fish (Bowen et al 2006; Purcell et al 2006; Haney et al 2007; Shulzitski et al 2009) and invertebrates (Mitton et al 1989; Silberman et al 1994) with high dispersal potential.

In addition to continued gene flow, genetic homogeneity among populations may be maintained over long periods of time after an expansion and subsequent demographic isolation when effective population sizes are large and there is consequently a smaller influence of genetic drift and longer times to drift-mutation equilibrium (Avice 1994). There is evidence that *C. abbreviata* underwent a large population expansion during the Pleistocene and may not be in an equilibrium state (discussed below). Estimates of contemporary gene flow based on the mitochondrial sequence data should, therefore, be interpreted cautiously as genetic homogeneity may reflect historic rather than modern day

demographic processes. Despite this caveat, it is probable that *C. abbreviata* populations across the Caribbean are demographically connected over ecologically relevant time scales. We base this assertion on the timing of the expansion, population genetic homogeneity in both the mtDNA and microsatellite dataset, and the life-history of the species (i.e. high dispersal potential, as discussed above).

Although high dispersal and gene flow appears to preclude local adaptation and diversification in many marine invertebrates (Krug 2011; Sotka 2005), there are a growing number of cases reported of host or habitat associated differentiation at various spatial scales for marine organisms with moderate to high dispersal potential (Stevens 1990; Mokady and Brickner 2001; Taylor and Hellberg 2003; Munday et al 2004; Faucci et al 2007; Tsang et al 2009). Diversification in these cases appears to occur through strong disruptive selection acting on ecotypes and/or strong micro-habitat (e.g. host) fidelity by larvae and/or adults resulting assortive mating and reproductive isolation. Here, we found no genetic differentiation among populations of *C. abbreviata* collected from three coral host taxa (*A. palmata*, *Montastraea* spp., and *Mycetophyllia* spp.). These results indicate that the host-specific selective forces acting on *C. abbreviata* may not be strong enough to overcome the homogenizing effects of high gene flow to form distinct host races or sibling species.

These results, however, do not preclude the presence of adaptive genetic polymorphisms at genes under selection. When dispersal is high across a heterogeneous environment, such genetic polymorphisms may be maintained in a population through balancing selection when alternative genotypes exhibit greater fitness in different environments (Levene 1953; Hedrick et al 1976). For instance, Schmidt and Rand (2001)

found that different alleles at the mannose-6-phosphate isomerase locus were selected for in different populations of the northern acorn barnacle (*Semibalanus balanoides*) in habitats characterized by different physical stress levels. Allele frequencies at one allozyme locus and a mtDNA marker, however, were homogeneous across populations.

Although, Baums et al (2003b) conducted a reciprocal transplant experiment in which *C. abbreviata* snails were originally collected from both *A. palmata* and *Montastraea* spp. coral colonies. Regardless of the original coral host, snails feeding on *A. palmata* grew faster than those feeding on *Montastraea* spp. corals. Thus, snail growth, at least, appears to be a plastic trait that varies under different environmental conditions (i.e. coral hosts). Phenotypic plasticity, in which a single genotype can express multiple phenotypes under different environmental conditions, may be adaptive in novel and heterogeneous environments and might even evolve rapidly during the colonization of novel environments (Bossdorf et al 2005; Richards et al 2006; Davidson et al 2011). Phenotypic plasticity also has associated fitness costs in terms of maintenance and imperfect phenotype to habitat matching among others (Tienderen 1991; DeWitt et al 1998; Relyea 2002a) and may be lost over time due to assimilation of fitter specialist genotypes (Pigliucci and Murren 2003). High gene flow across a heterogeneous environment, however, may be sufficient to maintain phenotypic plasticity over long periods of time if the average net fitness across environments is higher for the plastic genotype than for a specialist (Sultan and Spencer 2002; Hollander 2008). Given the diversity of coral hosts of *C. abbreviata*, high dispersal potential, and the range of phenotypic variation expressed across hosts (Johnston and Miller 2007), it seems probable that *C. abbreviata* have evolved adaptive phenotypic plasticity. Reaction norms

for plastic life-history traits in this case would allow individuals to adjust and maximize their fitness in the different environments associated with various coral hosts. Further research, however, is needed to fully assess the potential influence of selection acting on distinct genotypes on different coral hosts.

Demographic History

Since genetic substructure was not detected, I was able to combine all samples to assess the population demographic history of *C. abbreviata* in the Caribbean. The multi-locus analyses reported here consistently support a scenario of Pleistocene demographic expansion preceded by a reduction in size for *C. abbreviata*. The shallow *cyt b* gene genealogy with a single dominant haplotype and many new mutations (singleton haplotypes), resulting in moderate/high haplotype diversity ($h = 0.773$) and low nucleotide diversity ($\pi = 0.4\%$) suggests a single colonization/founder event or a selective sweep followed by a rapid demographic expansion. Based on the mismatch distribution, the expansion began during the Pleistocene, approximately 219,000 – 365,000 years ago. This time frame is in agreement with the mean tMRCA and onset of expansion (~250,000 years ago) determined through Bayesian skyline analysis (Fig 4.6).

The Plio-Pleistocene was a time of faunal turnover and subsequent changes in the diversity and structure of Caribbean corals reefs. After a late Pliocene/early Pleistocene extinction of scleractinian corals (4 - 1.5 Ma; Budd et al 1996), there was an ecological shift from small, free-living species to the dominance of a relatively few large reef building species (Budd and Johnson 2001; Budd and Klaus 2001). The *Acropora* spp. and *Montastraea* spp. corals in particular achieved ecological dominance during the

Pleistocene and remained dominant through recent geological time (Johnson et al 1995; Budd and Johnson 2001; Budd and Klaus 2001, Johnson et al 2008).

Demographic contractions and expansions in response to sea level fluctuations that isolated basins and altered current patterns during Pleistocene glacial cycles are thought to have occurred in tropical marine taxa across the Indo-Pacific (McMillan and Palumbi 1995; Benzie 1999b; Rohfritsch and Borsa 2005; Ravago-Gotanco and Juinio-Meñez 2010) and to a lesser extent in the Caribbean and tropical western Atlantic (Bowen et al 2006). Our data, however, indicate that *C. abbreviata* populations persisted in high numbers through the last glacial maxima (~20,000 years ago). I thus hypothesize that *C. abbreviata* colonized the greater Caribbean region during the mid-late Pleistocene and subsequently expanded with the expansion of reef habitat and potential prey. Indeed, Johnson et al (2007) reported that the widespread increase in carbonate reef development that followed the phase shift in coral community structure led to an increase in the diversity of reef associated mollusks during the Pleistocene to recent. Additionally, Plio-Pleistocene invasions from the Indo-Pacific and eastern Atlantic to the Caribbean and western Atlantic have been demonstrated for several species of fish (Rocha et al 2005; Bowen et al 2006; Rocha et al 2007) and at least 33 species of mollusks (Vermeij and Rosenberg 1993). The colonization success and diversification of mollusks during this time is thought to be due to the large scale expansion of reef habitat (Vermeij and Rosenberg 1993; Johnson et al 2007).

Implications for Coral Reef Conservation

The *Acropora* spp. corals have declined drastically throughout the Caribbean over the last three decades due to a variety of natural and anthropogenic stressors, resulting in their

listing as threatened species under the U.S. Endangered Species Act in 2006 (Anonymous 2006; Federal Register 71:26852-26861). Active, host-specific snail removal has thus been proposed as a necessary action for coral recovery and restoration. However, corallivores are ecologically important members of a reef community not only because they can directly affect the population dynamics and community structure of foundational coral species, but also because they provide a link from corals and their photosynthetic symbiotic algae to higher trophic levels (Glynn 2004). Thus, indiscriminant removal of a natural corallivore to protect coral, may have unforeseen cascading consequences on coral reef community structure and function as a whole. The results of this study indicate that *C. abbreviata* constitute a large, highly interconnected meta-population throughout the greater Caribbean region. The major consequence of this in regards to coral community interactions is that snail populations are decoupled ecologically from local and regional population fluctuations of their (presumed) preferred prey, the threatened acroporid corals, *A. palmata* and *A. cervicornis*. Local snail populations may be supplied from distant locations and maintained on alternative coral prey.

The implications of this for coral conservation are multi-faceted. First, targeted removal of snails from local populations of acroporid corals should not substantially affect other community trophic interactions. Second, it has been demonstrated both theoretically and empirically that the presence of alternative hosts may facilitate parasite/predator mediated local population extinctions of rare or threatened species, especially if such populations represent preferred prey (reviewed in: (Holt and Lawton 1994). This occurs because the predator population is maintained on alternative prey even when the preferred prey becomes rare. For the rare species to then recover, the intrinsic

rate of increase needs to exceed the attack rate times the average enemy abundance ($r > aP$; Holt & Lawton 1994). Targeted snail removal, therefore, may be imperative to ensure the persistence and/or recovery of particularly vulnerable *Acropora* colonies such as small fragmented or remnant colonies, nursery transplanted colonies and new recruits. However, removal efforts will be constantly mitigated by input from other local and regional sources. Control strategies, therefore, need to be designed accordingly.

Conclusions

Coralliophila abbreviata are ecologically significant coral predators that closely associate with coral host colonies. Because of the variation in phenotypes of *Coralliophila* feeding on different coral host species, I hypothesized that host-associated adaptation has led to genetic differentiation of these snail populations. Such host adaptation is often observed in phytophagous insects (reviewed in: Berlocher and Feder 2002; Janz et al 2006). However, no genetic differentiation was found among snail populations feeding on different coral hosts or from locations separated by up to 3500 km. Instead, *C. abbreviata* constitute a large metapopulation that has expanded dramatically since the Pleistocene, a time of large faunal turn over and reef habitat increases in the Caribbean. The evolution and maintenance of phenotypic plasticity for *C. abbreviata* may thus be a result of the combined effects of colonization history, high dispersal potential and local and meta-population scale environmental heterogeneity. The lack of host specialization and the high connectivity among locations translate into continuous predation pressure on severely declining stands of the preferred but threatened *Acropora* spp. corals.

CHAPTER 5: FORAGING BEHAVIOR OF CORALLIOPHILA ABRREVIATA IN AN EXPERIMENTAL PATCHY ENVIRONMENT: NEGATIVE INDIRECT EFFECTS OF NEIGHBORS ON AN IMPERILED SCLERACTINIAN CORAL

Overview

Direct tissue consumption by the corallivorous gastropod, *Coralliophila abbreviata*, is a substantial source of chronic mortality of the threatened Caribbean acroporid corals, *Acropora palmata* and *A. cervicornis* (Brawley and Adey 1982; Hayes 1990b; Knowlton et al 1990; Grober-Dunsmore et al 2006; Williams and Miller 2012). Remnant colonies, fragments, and new recruits may be particularly vulnerable to predation as tissue consumption rates can quickly outpace growth for small colonies (Baums et al 2003). There is also evidence that *C. abbreviata* may act as a vector for diseases affecting these corals, suggesting a potential synergistic impact beyond direct tissue consumption (Williams and Miller 2005; Sutherland et al 2011). Thus, the foraging behavior and patterns of host use of *C. abbreviata* have important consequences for the health, persistence, and recovery of foundational *Acropora* spp. populations and overall reef health.

Individual foraging behavior and habitat use of a consumer may be influenced by factors such as the abundance, quality, and spatial distribution of resources, social cues, and physiological requirements that may vary in space and time (Krebs and Davies 1978; Bernstein et al 1988a). Patterns of resource use will in turn determine the likelihood of direct and indirect interactions among organisms. In the case of rare and imperiled species, such interactions may affect the persistence and recovery of local populations (Holt 1977; Holt and Lawton 1994; DeCesare et al 2010).

The role of consumer mediated indirect interactions in shaping the structure and function of natural communities has been the subject of extensive ecological investigation (reviewed in: Holt and Lawton 1994; Barbosa et al 2009; Wootton 2002). Although it has been demonstrated theoretically and empirically that indirect interactions are important drivers of community structure, little is known about the identity, strength, and dynamics of these interactions in many complex communities (Wootton 2002). As humans rapidly change the physical and biological structure of natural communities (Clavel et al 2011), trophic interactions often shift, resulting in unforeseen trophic cascades and alternate stable states (Knowlton 2004; Connell et al 2011). It is thus becoming increasingly important that we understand how indirect interactions among organisms contribute to community regulation. This information is needed to effectively conserve and manage ecosystem structure and function as well as predict how communities will respond to further environmental perturbations in the future (Connell et al 2011).

Associational resistance and associational susceptibility are terms that describe the indirect interactions that occur when the composition and structure of near neighbors indirectly affect predation (inclusive of parasitism and herbivory) on another organism or population by affecting the abundance, search efficiency, or attack rate of one or more predators (Holt and Lawton 1994; Agrawal et al 2006; Barbosa et al 2009). Associational resistance generally maintains local diversity by providing refuges from predation for the focal population, whereas associational susceptibility has variable effects on community structure and stability depending on the identity and strength of the particular interactions (Holt and Lawton 1994; Chesson 2000; Barbosa et al 2009).

Predator mediated density dependent mortality is a common mechanism of population regulation in natural communities (Hixon et al 2002). In the absence of other major disturbances, predator mediated density or frequency dependent mortality generally contributes to population stability and species coexistence because both inter- and intraspecific competition is reduced when densities are high (stabilizing effect) and per capita predation pressure is reduced when densities are low (equalizing effect; Chesson 2000).

Apparent competition, however, is a form of associational susceptibility that is increasingly being linked to population declines and species endangerment and extinction (DeCesare et al 2010). Apparent competition occurs when two species that may or may not be directly competing for resources, interact indirectly via a shared natural enemy (Holt 1977). This is a reciprocally negative interaction between prey species (-,-) that may be symmetrical or asymmetrical. Asymmetrical apparent competition occurs when populations of the shared predator respond numerically to combined prey density or benefit from some resource (e.g., enemy-free/reduced space) provided by one species, but the other 'focal' species is more susceptible to predation due to low abundances, lack of defenses, and/or a prey preference (Chaneton and Bonsall 2000). Thus, the focal prey species experiences a disproportionately negative impact of predation due to the presence of the alternative prey. If the asymmetry is great enough or the focal population declines appreciably from other factors, apparent competition could impair recovery or even lead to local extinction (Holt and Lawton 1994; DeCesare et al 2010).

In a heterogeneous environment, there are often refuges in space for prey. Optimal foraging theory predicts that consumers should concentrate foraging activities in

patches with high densities of resources (Bernstein et al 1988b). An aggregative response by a predator to total resources in a patch can lead to apparent competition between alternative prey species within a patch, possibly excluding vulnerable members (Holt and Kotler 1987; Holt and Lawton 1994). However, the same behavior will result in a spatial refuge from predation for prey in low densities or otherwise in low quality patches (Holt and Kotler 1987).

Currently, very little is known about the movement patterns and prey/habitat selection of *C. abbreviata*. Hayes (1990) reported that snails populations feeding on *A. cervicornis* were more active, moving on and off colonies, whereas populations on *Montastraea* spp. corals were relatively sedentary. Knowlton et al. (1990) reported that snail populations concentrated on remnant populations of *A. cervicornis* in Jamaica after a hurricane substantially reduced colony size and density of corals. Predation by *C. abbreviata* in this case essentially halted the recovery of *A. cervicornis* population. The acroporid corals are presumed to be the preferred prey of *C. abbreviata* due to greater fitness correlates such as growth and longevity (Baums et al 2003; Johnston and Miller 2007). However, efforts to detect actual feeding preference of individual snails have been inconclusive (Hayes 1990a) and snails are often more abundant on *Montastraea* spp. corals (Miller 1981; Hayes 1990b; Baums et al 2003).

Coralliophila abbreviata are generalist coral predators that constitute a single, large population throughout the Caribbean, characterized by high gene flow and host-associated phenotypic plasticity (Johnston and Miller 2007; Johnston et al, in review; Chapters 2 and 4 of this dissertation). Although damage to massive and plating corals appears minimal, *C. abbreviata* cause substantial and chronic mortality of *A. cervicornis*

and *A. palmata* (Brawley and Adey 1982; Hayes 1990b; Knowlton et al 1990; Miller et al 2002; Baums et al 2003; Grober-Dunsmore et al 2006). Because these snails have a wide diet breadth but greater impact on and possible preference for *Acropora* spp., asymmetric apparent competition could have a profound influence on the structure and persistence of declining acroporid coral populations (Knowlton 2004). A better understanding of the foraging behavior and subsequent patterns of distribution and host use is thus crucial for predicting the potential impact of predation by *C. abbreviata* on threatened coral species and degraded reefs.

Here I investigate the effects of coral neighborhood composition and structure on the foraging behavior and impact of *C. abbreviata* on focal *A. cervicornis* colonies. I conducted a manipulative field experiment in which the density and composition of neighboring corals surrounding focal *A. cervicornis* colonies were manipulated, as well as the density of *C. abbreviata* at the study site. The neighborhood treatments consisted of a central *A. cervicornis* colony surrounded by one of the following configurations: (1) no neighbors (neighborhood control), (2) four conspecific neighbors, (3) four alternative prey (*M. faveolata*) neighbors, or (4) four non-prey (*P. asteroides*) neighbors. *Acropora cervicornis* was presumed to be the preferred prey over *M. faveolata* based on snail life history characteristics described in Johnston and Miller (2007; Chapter 2). Snail prevalence on *P. asteroides* is extremely low (Jamaica, Miller 1981; Florida Keys, pers. obs.) or absent (Navassa Island, Williams and Miller 2003) in the Caribbean. *Porites asteroides* was thus considered a non-prey species. Thus, the neighborhood plots were designed to represent a range of prey/habitat quality for *C. abbreviata* and potential associational effects on focal *A. cervicornis* colonies (Fig. 5.1).

My objectives were to test the hypotheses that 1) snails respond numerically to overall neighborhood quality (based on the identity and density of corals present) and thus 2) *A. cervicornis* experience predator mediated density dependent mortality, 3) the alternative prey species, *M. faveolata*, has an apparent competitive effect on *A. cervicornis*, and 4) the non-prey species, *P. asteroides* provides associational resistance to predation for *A. cervicornis*. I also analyzed the movement, habitat use, and foraging behavior of individual tagged snails through time as neighborhood patches were depleted and tested for differences in movement patterns between male and female snails.

Materials and Methods

Experimental Setup

The experiment was conducted from July to December, 2009, at Conch Reef in the Florida Keys National Marine Sanctuary (N24 56.78; W80 27.52). The experimental area was a 15 m x 30 m (long axis oriented east to west) shallow reef flat (~5 m depth) with low scleractinian coral cover (< 1%; pers. obs.) and low structural complexity. *Acropora cervicornis* and *M. faveolata* colonies were obtained from local coral nurseries (*A. cervicornis*: Coral Restoration Foundation, Inc., Tavernier, FL; *M. faveolata*: Florida Keys National Marine Sanctuary coral nursery, Key West, FL). *Acropora cervicornis* colonies were the product of the asexual propagation of three distinct genotypes over several years and *M. faveolata* colonies were originally salvaged from the substrate prior to marine construction projects. *Porites asteroides* colonies were collected at the study site using a hammer and chisel. *Montastraea faveolata* and *P. asteroides* colonies ranged from 10 cm – 15 cm maximum diameter. The size of *A. cervicornis* colonies was

assessed by measuring the length of all branches to the nearest 1 mm and then summing these measurements to obtain a total branch length for each colony (similar to Knowlton 1990). The mean total branch length of experimental *A. cervicornis* colonies at the beginning of the experiment was 264.75 mm (\pm 117.98 SD).

Experimental neighborhoods were constructed in 1 m² randomly distributed plots within the study area. The neighborhood treatments consisted of a central *A. cervicornis* colony surrounded by one of the following configurations (Fig. 5.1):

1. No neighbors (neighborhood control; SOL)
2. Four non-prey (*P. asteroides*) neighbors (NON)
3. Four alternative prey (*M. faveolata*) neighbors (ALT)
4. Four conspecific neighbors (CON)

Each neighborhood treatment was replicated five times for a total of 20 neighborhood plots. The exact location of the center colony for each plot was determined using a random number generator to generate coordinates within the study area. The margins of each plot were separated from other plots by at least 1 m. If other scleractinian corals larger than 4 cm diameter were found within the randomly designated area, the plot was moved to the closest 1 m² area with no corals present. All coral fragments were transported to the experimental area and haphazardly assigned to plots of the appropriate treatment, arranged in neighborhood configurations, and affixed to the reef substrate using marine epoxy (AllFix). Individual colonies within a plot/neighborhood were separated by approximately 30 cm with no direct contact with other corals. Plots were established on the reef three months prior to the initiation of the study.

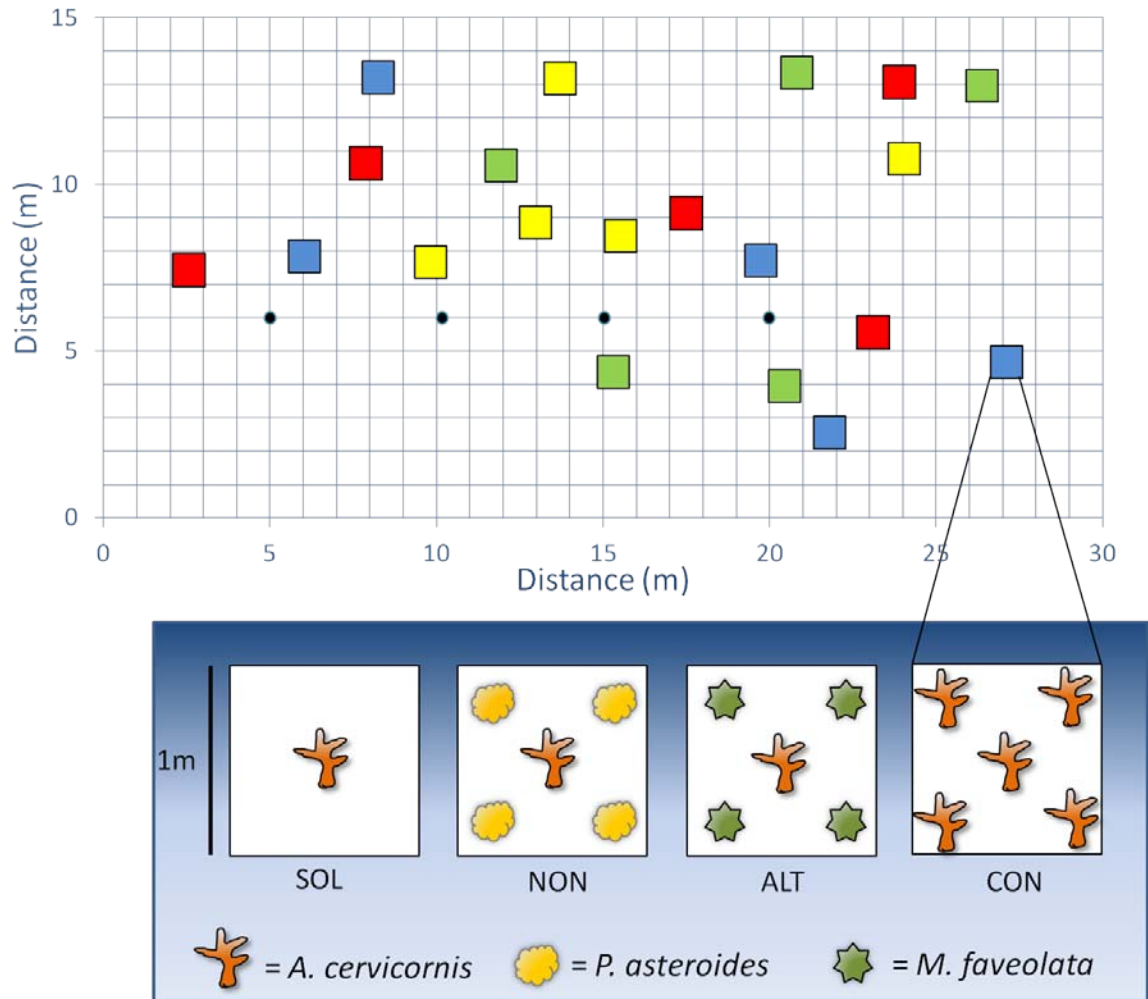


Figure 5.1 Schematic of the experimental neighborhood plot design. The four neighborhood treatments (bottom) were replicated five times each and arranged randomly on the reef (top). The four black circles represent the permanent stakes.

One hundred fifteen snails were then collected from multiple coral colonies at a nearby reef, brought to shore overnight, measured, and tagged with individually numbered shell tags. The snails were collected from a common host/prey species not used in the experiment (*Diploria* spp.) to avoid potentially confounding effects of injestive conditioning. Because we were interested in the effects of prey neighborhood composition on snail colonization, snails were distributed uniformly within the

experimental area. To uniformly distribute the snails, a transect was laid out every three meters along the entire length of the study area and individual snails were placed at one meter intervals. If the one meter mark fell within an experimental plot, the snail was placed directly outside of the plot.

Plots were monitored weekly for approximately 11 weeks and then two additional censuses occurred at monthly intervals. At each visit, the number and identity of snails found within each plot and on each experimental coral colony were recorded. Once per month, *A. cervicornis* colonies were measured as the sum of the lengths of all branches. Initial total branch length for the central *A. cervicornis* colonies did not vary significantly among neighborhood treatments (ANOVA: $F_{3,16} = 0.68$; $P = 0.58$). Linear growth was calculated as the proportional change in total branch length over the course of the experiment.

Four permanent rebar stakes were hammered into the reef substrate along a straight line transect oriented east to west through the experimental area. Locations of tagged snails and corals were mapped by taking distance measurements (to the nearest cm) from the two closest stakes and then using triangulation to calculate the exact location on a grid. We attempted to locate and map a specific subset of 20 snails at every census that were haphazardly selected at the beginning of the study. Once per month, the entire study area was searched thoroughly and the locations of all snails found were mapped. Additionally, the location of all snails found within neighborhood plots was recorded at every census. At the end of the experiment, the entire study area was searched thoroughly and all located snails were mapped and collected. On shore, all recovered tagged snails were measured and sexed.

Neighborhood Effects on Focal Colonies

To test for neighborhood treatment effects on the initial rate and magnitude of snail colonization, I used repeated measures ANOVA on snail abundance data with time as the within-subject main effect. Growth and survival over the first nine week period were used as performance measures for the central *A. cervicornis* colonies in each treatment.

Growth of the central *A. cervicornis* colonies was compared among treatments with a one-way ANOVA.

The three coral species were ranked from 0-2, *a priori*, based on their quality as prey for *C. abbreviata* which was determined using previously published, host-specific snail life-history characteristics and observations. Snails associated with *Acropora* spp. corals in the Caribbean grow to larger sizes, live longer, experience lower adult mortality, and produce more offspring per capita than those on *Montastraea* spp. corals (Baums et al 2003a; Baums et al 2003b; Johnston and Miller 2007). *Acropora cervicornis* was thus assigned the highest quality rank (2), followed by *M. faveolata* (1), and *P. asteroides* (0). Although Miller (1981) reported that *C. abbreviata* were found on *Porites asteroides* colonies in Jamaica, only two of the 83 coral-corallivore associations observed involved this species and no *C. abbreviata* were observed on abundant *P. asteroides* in systematic surveys of all coral species at Navassa Island (Williams and Miller 2003). Furthermore, in the FKNMS, *P. asteroides* are abundant yet rarely colonized by *C. abbreviata* (personal obs.). Thus, *P. asteroides* was considered a non-prey species. The ranks of all corals present in a neighborhood were then summed to provide an index of neighborhood quality (NQ). Thus, conspecific plots had a NQ of 10, alternative prey plots had a NQ of

6, and non-prey and solitary plots has a NQ of 2 (Table 5.1). I used a general linear regression procedure to evaluate the relationships between NQ and initial colonization (the number of snails per colonized plot at week four) and the mortality of central *A. cervicornis* colonies over the course of the experiment.

Table 5.1 Characteristics of neighborhood treatments including the associational effect(s) that they were designed to test, the identity of the neighboring corals surrounding a focal *A. cervicornis* colony. NQ is the neighborhood quality score (see text for explanation) which shows the postulated gradient in resource concentration amongst the treatments.

| Treatment | Associational Effects Tested | Neighbors (x4) | NQ |
|------------------------|------------------------------|-----------------------|----|
| Conspecific (CON) | AS:DD | <i>A. cervicornis</i> | 10 |
| Alternative prey (ALT) | AS:AC | <i>M. faveolata</i> | 6 |
| Non-prey (NON) | AR | <i>P. asteroides</i> | 2 |
| Solitary (SOL) | Control | None | 2 |

AS: associational susceptibility; DD: density dependence; AC: apparent competition; AR: associational resistance

Prey Preference and Neighborhood Selection

I tested for neighborhood and prey selection using the Neu method (Neu et al 1974) which involves a chi-squared goodness-of-fit test combined with the establishment of confidence intervals around proportional use data to determine if selection for a habitat type or prey species is significantly disproportionate to its availability in the environment. The confidence intervals are determined using Bonferonni corrected Z-statistics (Neu et al 1974). I calculated selection indices using proportional use and availability data pooled from each census date and overall to assess how habitat and prey selection changed through time as neighborhood plots became depleted. I held the availability of

neighborhood types constant throughout the experiment, but adjusted the proportional availability of prey species as colonies were consumed. Although the Neu method is based on pooled resource use and availability data and is therefore relatively insensitive to individual variation, it has been shown to be among the most consistent methods for accurately identifying habitat selection patterns in animal populations (McClellan et al 1998).

I also quantified host/prey preference of *C. abbreviata* expressed in the experiment by calculating the selection index for each coral species (α_i ; Manley et al 1972) at each sampling time using the following equation:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^q r_j/n_j}$$

where r_i and n_i represent the proportional use and availability, respectively, of the i th prey species. The selection index is a measure of the proportion of total snails found on each coral species, corrected for prey abundance in the environment. The values range from 0 (no use) to 1 (sole use). The selection indices were calculated using the overall coral densities and proportional use values from the entire study area.

Finally, for each snail that remained in the study area for at least three months, I recorded the habitat type in which it was found at each sampling date. Habitat types for this analysis included the four neighborhood treatments and the reef substrate. If a snail was not observed in a neighborhood plot at a given sampling date, but was subsequently found in the study area, it was presumed that it was on the substrate during the period it was not observed, as all neighborhood plots were searched thoroughly for snails at each sampling date.

Movement and Space Use

Home range estimates and movement patterns were analyzed for all tagged snails that were recovered at the end of the experiment and compared between sexes. Home range was estimated using two commonly used estimators: the 100% minimum convex polygon (MCP) estimator and the fixed kernel estimator with the smoothing factor calculated using least-squares cross-validation to determine the width of the base of a kernel (Seaman and Powell 1996). The 100% MCP estimator connects the extreme points observed to form the smallest convex polygon. The fixed kernel estimator plots all locations on a grid and uses the frequency with which different regions of the grid were used to calculate an area of use. I calculated the 95% and 50% kernel estimates to represent the overall range area and the core area of use, respectively. All home range estimates were calculated using the program BiotasTM v. 2.0a 3.8 (Ecological Software Solutions LLC). Total linear distance traveled was calculated as the sum of the straight lines connecting sequential point locations. Home range estimates were compared between sexes using t-tests.

Results

Neighborhood Effects on Focal Colonies

The repeated measures ANOVA revealed significant ($P < 0.05$) effects of neighborhood treatment and time on *C. abbreviata* colonization. There was also a significant neighborhood*time interaction ($P = 0.03$), indicating that the rate of colonization varied among neighborhood treatments (Table 5.2; Fig.5.2). A Fisher LSD post hoc test indicated that snail colonization was significantly ($P < 0.05$) greater for the conspecific

treatment compared to the non-prey treatment and the solitary treatment. The alternative prey treatment experienced an intermediate level of colonization that was statistically similar to the solitary treatment and the non-prey treatment ($P > 0.05$) as well as the conspecific treatment ($P = 0.05$). Three plots (one conspecific plot, one alternative prey plot, and one solitary plot) were not colonized by snails during the initial nine week period and were therefore not included in the repeated measures ANOVA analysis to eliminate heteroscedasticity.

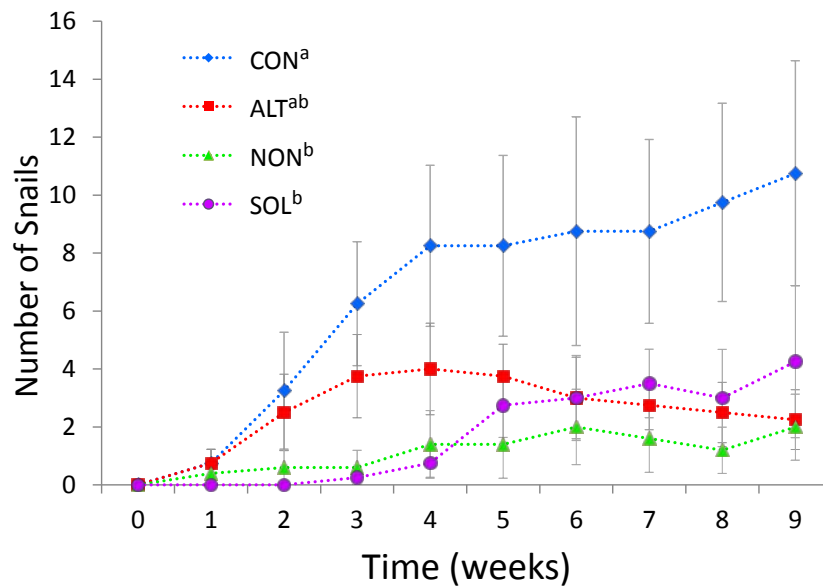


Figure 5.2 Average number of snails (\pm SE) per plot for each neighborhood treatment over the first nine weeks of the experiment. Superscripts identify statistically similar treatments identified in post hoc tests.

Table 5.2 Repeated measures ANOVA results for test of the effects of neighborhood treatment and time on the number of snails per plot.

| Source of variation | d.f. | MS | <i>F</i> | <i>P</i> |
|---------------------|------|-------|----------|----------|
| Neighborhood | 3 | 269.6 | 3.8 | 0.04 |
| Error | 13 | 70.5 | | |
| Time | 8 | 34.4 | 6.8 | < 0.001 |
| Neighborhood *Time | 24 | 8.96 | 1.76 | 0.03 |
| Error | 104 | 5.07 | | |

Although all focal colonies grew (hence positive proportional change values), the average proportional change in total branch length was approximately double for the solitary and non-host treatments (0.67 ± 0.16 SE and 0.70 ± 0.13 SE, respectively) compared to the alternative prey and conspecific treatments (0.34 ± 0.12 SE for and 0.39 ± 0.11 SE, respectively) over the nine week period (Fig. 5.3). These results were not statistically significant, however, likely due to small sample sizes (one-way ANOVA: $F_{3,16} = 1.98$; $P = 0.16$).

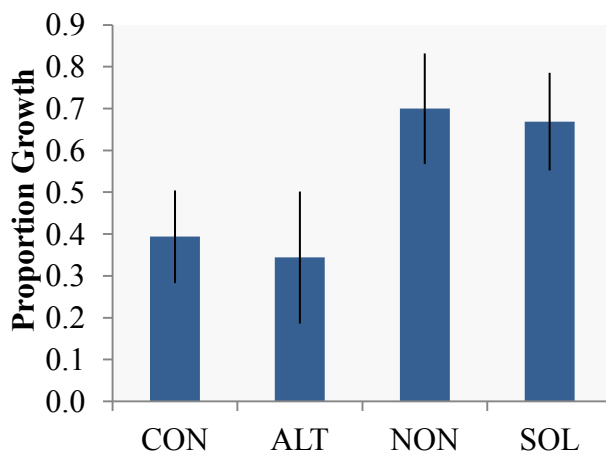


Figure 5.3 Mean proportional change (\pm SD) in total branch length for focal *Acropora cervicornis* colonies in each neighborhood treatment; CON: conspecific; ALT: alternative prey; NON: non-prey; SOL: solitary. Results were not statistically significant (one-way ANOVA: $F_{3,16} = 1.98$; $P = 0.16$)

There was no total colony mortality observed for central *A. cervicornis* in the solitary and non-prey treatments after nine weeks, whereas 40% and 60% of colonies were completely consumed in the alternative prey and conspecific treatments, respectively. All mortality of *A. cervicornis* was directly attributed to predation by *C. abbreviata*. No whole colony mortality and no partial tissue loss due to predation were observed for *M. faveolata* or *P. asteroides* colonies during the experiment. Finally, there was a strong positive relationship between NQ and initial colonization (the number of snails per colonized plot after four weeks; $R^2 = 0.79$, $P < 0.001$; Fig. 5.4a) and the overall mortality of the central *A. cervicornis* colonies ($R^2 = 0.97$, $P = 0.01$; Fig. 5.4b).

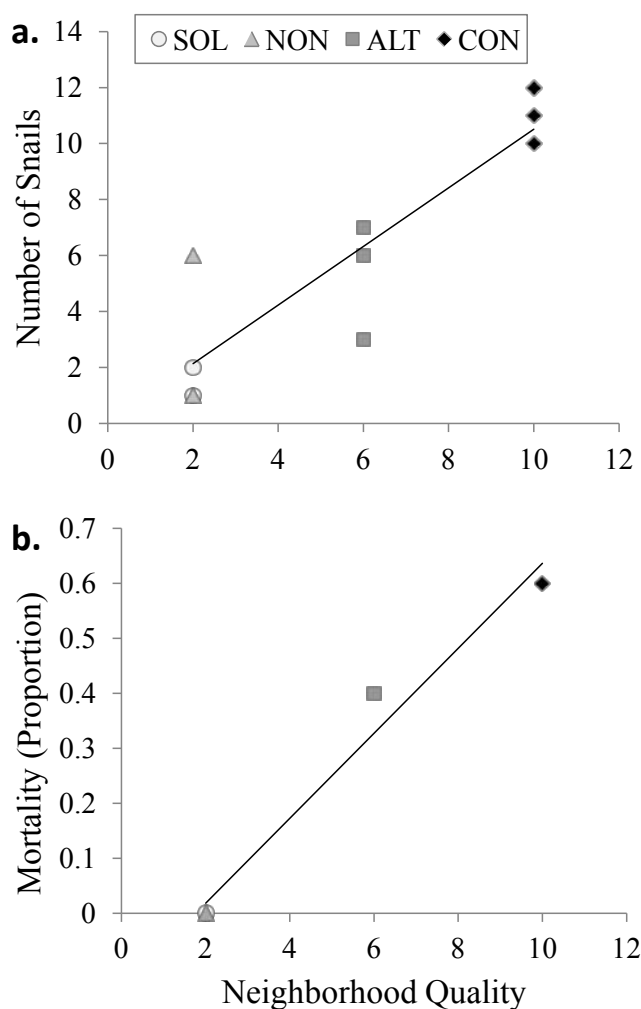


Figure 5.4 Relationship between neighborhood quality and number of snails per colonized plot at week four (a) and mortality (proportion of replicates) of focal *A. cervicornis* colonies due to predation after nine weeks (b).

Prey Preference

Chi-squared goodness-of-fit tests revealed that *Coralliophila abbreviata* displayed significant positive selection for *A. cervicornis* and significant negative selection for *M. faveolata* throughout most of the experiment, even as *A. cervicornis* colonies declined and became proportionately less abundant in the environment (Fig 5.5; Table 5.3). In other words, snails were selecting for *A. cervicornis* colonies significantly more frequently than would be expected if selection were random, given their abundance in the environment, and *M. faveolata* less than would be expected. Although a few snails were observed feeding on *P. asteroides* at the last two monthly censuses (Table 5.3), to be conservative in prey selection estimates, these corals were not included as potential prey in the chi-squared analysis for the first 11 weeks. The standardized selection indices averaged over all sample periods, were as follows (\pm SD): *A. cervicornis* mean $\alpha = 0.72 \pm 0.14$; *M. faveolata* mean $\alpha = 0.28 \pm 0.15$; *P. asteroides* mean $\alpha = 0.02 \pm 0.05$.

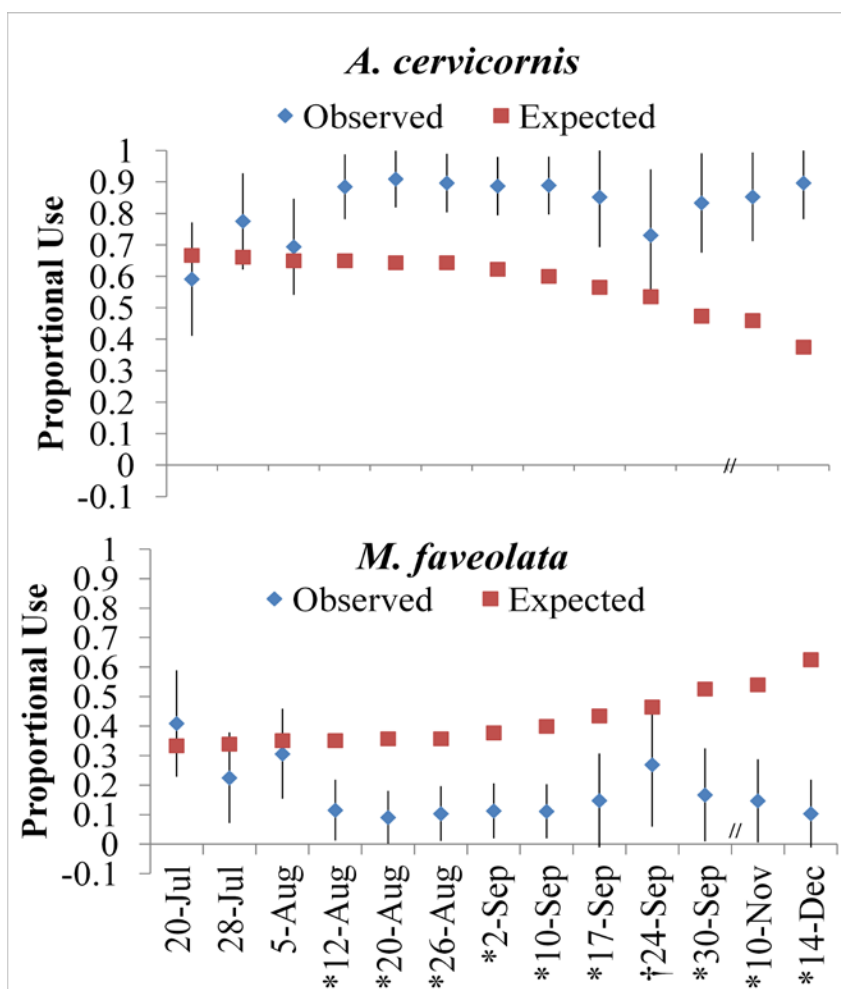


Figure 5.5 Observed and expected proportional use of *Acropora cervicornis* and *Montastraea faveolata* prey colonies by the *Coralliophila abbreviata* population at each sampling date. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use is calculated based on the proportional availability of prey at a given sampling period. Chi-squared goodness-of-fit P -values are denoted by * ($P < 0.01$) and † ($P < 0.05$). The test was not significant ($P > 0.05$) where no symbol is associated with the sampling date. Hash marks on the x-axis denote the beginning of monthly sampling.

Table 5.3 Preference indices calculated for *Acropora cervicornis* (*A. cerv*), *Montastraea faveolata* (*M. fav*), and *Porites asteroides* (*P. ast*). Reported are the proportion availability of each prey in the entire experimental area, the total number of *C. abbreviata* observed in contact with an experimental coral at each sampling time (No. snails), the proportion of those found on each coral species and the calculated selection indices (α).

| Date | No. snails | Prey availability (proportion) | | | Prey use (proportion) | | | Selection Index (α) | | |
|--------|------------|--------------------------------|--------|--------|-----------------------|--------|--------|------------------------------|--------|--------|
| | | A. cerv | M. fav | P. ast | A. cerv | M. fav | P. ast | A. cerv | M. fav | P. ast |
| 20-Jul | 22 | 0.50 | 0.25 | 0.25 | 0.59 | 0.41 | 0.00 | 0.42 | 0.58 | 0.00 |
| 28-Jul | 40 | 0.49 | 0.25 | 0.25 | 0.78 | 0.23 | 0.00 | 0.64 | 0.36 | 0.00 |
| 5-Aug | 49 | 0.48 | 0.26 | 0.26 | 0.69 | 0.31 | 0.00 | 0.55 | 0.45 | 0.00 |
| 12-Aug | 52 | 0.48 | 0.26 | 0.26 | 0.88 | 0.12 | 0.00 | 0.81 | 0.19 | 0.00 |
| 20-Aug | 55 | 0.47 | 0.26 | 0.26 | 0.91 | 0.09 | 0.00 | 0.85 | 0.15 | 0.00 |
| 26-Aug | 58 | 0.47 | 0.26 | 0.26 | 0.90 | 0.10 | 0.00 | 0.83 | 0.17 | 0.00 |
| 2-Sep | 62 | 0.45 | 0.27 | 0.27 | 0.89 | 0.11 | 0.00 | 0.83 | 0.17 | 0.00 |
| 10-Sep | 63 | 0.43 | 0.29 | 0.29 | 0.89 | 0.11 | 0.00 | 0.84 | 0.16 | 0.00 |
| 17-Sep | 27 | 0.39 | 0.30 | 0.30 | 0.85 | 0.15 | 0.00 | 0.82 | 0.18 | 0.00 |
| 24-Sep | 24 | 0.37 | 0.32 | 0.32 | 0.73 | 0.27 | 0.00 | 0.70 | 0.30 | 0.00 |
| 30-Sep | 30 | 0.31 | 0.34 | 0.34 | 0.83 | 0.17 | 0.00 | 0.85 | 0.15 | 0.00 |
| 10-Nov | 34 | 0.30 | 0.35 | 0.35 | 0.85 | 0.15 | 0.03 | 0.85 | 0.12 | 0.02 |
| 14-Dec | 38 | 0.23 | 0.38 | 0.38 | 0.90 | 0.10 | 0.31 | 0.78 | 0.05 | 0.16 |
| Mean | 42.62 | 0.41 | 0.29 | 0.29 | 0.82 | 0.18 | 0.03 | 0.75 | 0.24 | 0.01 |
| SD | 14.68 | 0.09 | 0.04 | 0.04 | 0.10 | 0.10 | 0.09 | 0.14 | 0.15 | 0.05 |

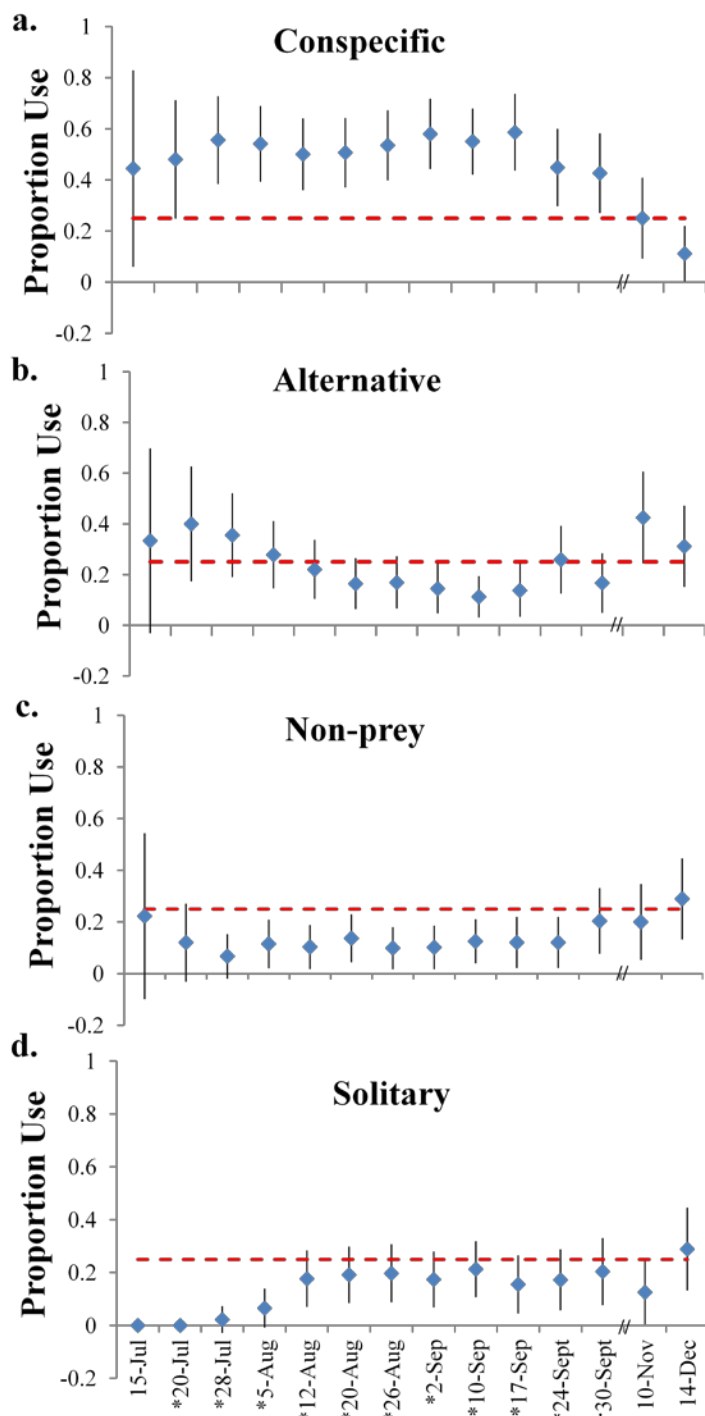
Neighborhood Selection

Neighborhood plot use varied over time. Confidence intervals showed that selection for conspecific plots was significantly positive for most sampling periods, except the first week and the last two monthly samples. In the second to last sample, the conspecific plots were occupied in proportion to their abundance whereas in the last sample they were occupied significantly less than expected (Fig. 5.6a). Selection for alternative prey plots fluctuated around expected use values under a random distribution. Selection was initially positive (although not significant), drifted downwards in the middle of the

experiment and then increased again over the last third of the experiment (Fig. 5.6b). There was consistent negative selection for non-prey neighborhoods throughout the experiment until the last three sample periods at which point they were neither selected for nor avoided (Fig 5.6c). There was strong negative selection for solitary plots over the first month of the study and then snails began to occupy solitary plots in proportion to their availability in the environment (Fig 5.6d). Combining all neighborhood use data, chi-squared test analysis for neighborhood selection showed that the snail population selected neighborhood patches non-randomly ($\chi^2 = 230.25$, $df = 3$, $n = 756$, $P < 0.0001$). Bonferroni corrected 95% confidence intervals showed overall strong positive selection for conspecific plots, neutral selection for alternative prey plots, and negative selection for non-prey and solitary plots (Fig. 5.7).

There were 54 tagged snails that remained in the study area for at least 3 months. These snails were used to assess habitat usage by individual snails. Habitat use was highly variable (Fig 5.8). On average, individual snails utilized 2.04 ± 0.80 (SD) of the four neighborhood treatment types over the course of the study. Snails were observed, on average, $34\% \pm 14\%$ (SD) of time on the substrate, $35\% \pm 28\%$ (SD) in conspecific plots, $10\% \pm 18\%$ (SD) in alternative prey plots, $7\% \pm 16\%$ (SD) in non-prey plots, and $12\% \pm 18\%$ (SD) in solitary plots.

Figure 5.6 Observed (blue triangles) and expected (red dashed line) proportional use of each neighborhood treatment by *Coralliophila abbreviata* at each sampling date. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use values were calculated based on the proportional availability of neighborhood plots in the experimental area. Chi-squared goodness-of-fit P -values are denoted by * ($P < 0.01$) and † ($P < 0.05$). The



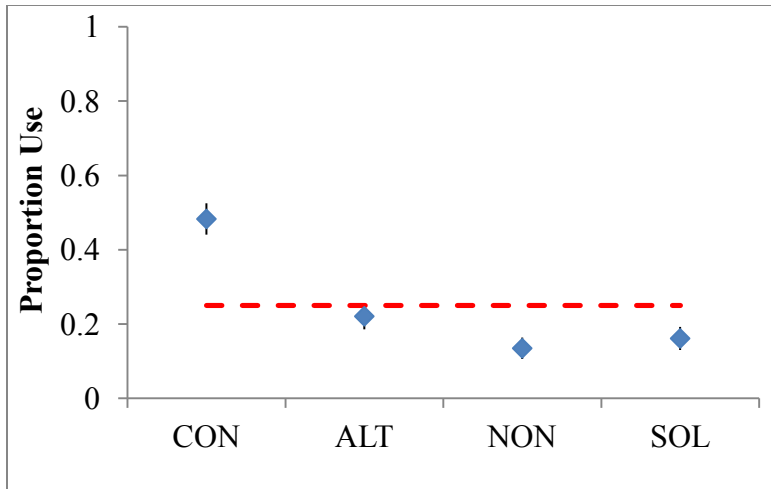


Figure 5.7 Observed (blue triangles) and expected (red dashed line) proportional use of each neighborhood treatment by *Coralliophila abbreviata* determined by combining all neighborhood use data. Bars represent Bonferonni corrected 95% confidence intervals for observed use values. Expected use value was calculated based on the proportional availability of neighborhood plots in the experimental area. Chi-squared test analysis for neighborhood selection showed that patch selection was not independent of neighborhood treatment ($\chi^2 = 230.25$, $df = 3$, $n = 756$, $P < 0.0001$).

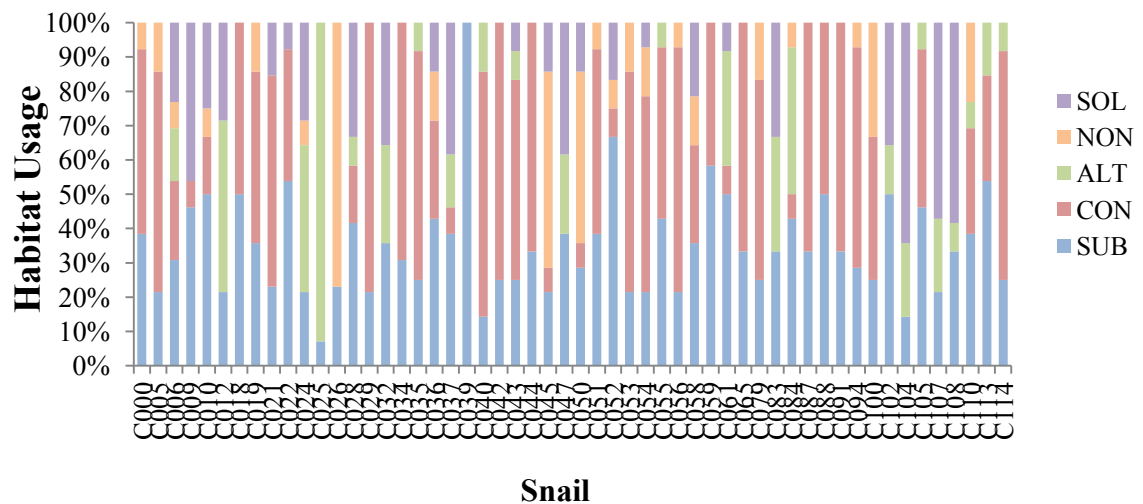


Figure 5.8 Percent of observations in each habitat type for 54 tagged snails that remained in the experimental area for at least three months. Habitat types include the four neighborhood treatments (SOL: solitary; NON: non-prey; ALT: alternative prey; CON: conspecific) and substrate (SUB).

Movement and Space Use

Examples of the movement path and home range estimators for a single snail are shown in Fig. 5.9. For the 100% MCP analysis, data were log₁₀ transformed prior to analysis to conform to the assumption of homogeneity of variances. All other data conformed to statistical assumptions. Results are reported in Table 5.4. Twenty six tagged snails, 15 male and 11 female, were recovered at the end of the experiment after a total of 129 days. There were, on average 11.54 ± 2.40 (SD) fixed location points per snail (range: 8-17). The number of fixes did not vary significantly between males and females (two-tailed t-test: $t_{24} = 1.71$, $P > 0.05$). Total linear distance traveled ranged from 0.13-32.43 m (mean: 12.34 ± 6.01). The 100% MCP estimator ranged from 0 - 37.32 m² (mean: 9.72 ± 7.8 m²), whereas the 95% and 50% kernel estimators ranged from 0.82 - 4.27 m² and 0.1 - 0.51 m², respectively (95% mean: 2.18 ± 0.89 ; 50% mean: 0.22 ± 0.11). The TLD and 100% MCP estimates were significantly different between sexes (TLD: $t_{24} = 2.063$, $P = 0.04$; 100% MCP: $t_{24} = 4.67$, $P < 0.001$), whereas the kernel estimates did not vary significantly ($P > 0.05$; Table 5.4).

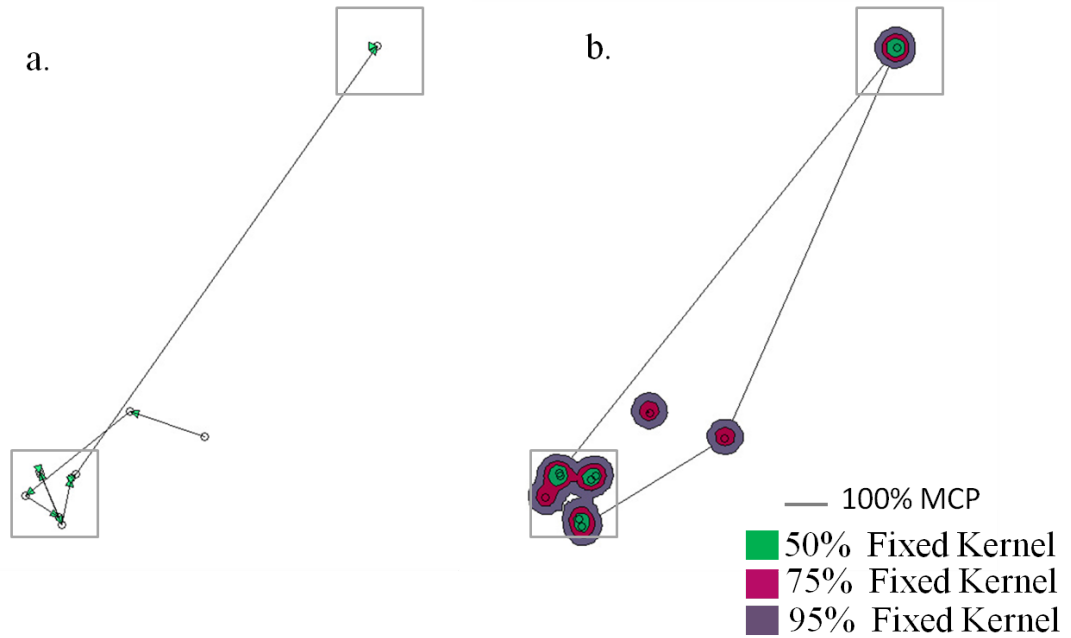


Figure 5.9 Example of movement path (a) and home range estimates (b) of an individual *Coralliophila abbreviata* snail. The solid line on the right image is the perimeter of 100% MCP area estimate. The 50% (core), 75%, and 95% (range) fixed kernel estimates are indicated. The grey boxes represent neighborhood plots; the bottom plot was a conspecific plot and the top plot was an alternative prey plot.

Table 5.4 Growth and movement data for male and female *Coralliophila abbreviata* recovered after a total of 129 days. SL: shell length; MCP: Minimum Convex Polygon.

| Snail | Sex | Initial SL (mm) | Final SL (mm) | Δ SL (mm) | # of fixes | Total Linear Dist. (m) | 100% MCP (m ²) | 95% Range Kernel (m ²) | 50% Core Kernel (m ²) |
|-------------------------|-----|-----------------|---------------|------------------|--------------|------------------------|----------------------------|------------------------------------|-----------------------------------|
| C005 | F | 18.6 | 18.6 | 0 | 11 | 5 | 1.27 | 1.09 | 0.12 |
| C015 | F | 20.9 | 21 | 0.1 | 10 | 13.52 | 9.62 | 3.17 | 0.24 |
| C019 | F | 24.5 | 24.5 | 0 | 14 | 13.51 | 5.86 | 3.58 | 0.31 |
| C024 | F | 19.5 | 20.7 | 1.2 | 11 | 6.27 | 4.32 | 1.43 | 0.12 |
| C025 | F | 17.5 | 19 | 1.5 | 13 | 0.13 | 0 | 1.07 | 0.4 |
| C045 | F | 20.7 | 21.5 | 0.8 | 13 | 15.34 | 6.36 | 1.76 | 0.1 |
| C053 | F | 18.8 | 19.6 | 0.8 | 12 | 5.77 | 2.16 | 1.05 | 0.1 |
| C056 | F | 24.4 | 24.9 | 0.5 | 12 | 9.52 | 9.1 | 1.51 | 0.15 |
| C098 | F | 21.6 | 21.7 | 0.1 | 6 | 12.76 | 4.93 | 1.41 | 0.1 |
| C104 | F | 17.7 | 18 | 0.3 | 14 | 10.45 | 4.32 | 2.96 | 0.17 |
| C105 | F | 19.7 | 19.9 | 0.2 | 10 | 12.17 | 9.93 | 1.98 | 0.2 |
| Mean F | | 20.35 | 20.85 | 0.50 | 11.45 | 9.49 | 5.26 | 1.91 | 0.18 |
| SD | | 2.40 | 2.24 | 0.51 | 2.30 | 4.66 | 3.35 | 0.91 | 0.10 |
| C012 | M | 15.8 | 17.8 | 2 | 17 | 15.63 | 15.59 | 3.52 | 0.15 |
| C021 | M | 17.9 | 19.4 | 1.5 | 11 | 11.67 | 5.62 | 2.42 | 0.37 |
| C029 | M | 15.9 | 17.3 | 1.4 | 13 | 10.04 | 5.88 | 1.93 | 0.19 |
| C032 | M | 16.5 | 17.2 | 0.7 | 11 | 12.78 | 11.39 | 2.74 | 0.44 |
| C036 | M | 17.1 | 17.3 | 0.2 | 12 | 9.01 | 8.01 | 2.3 | 0.17 |
| C040 | M | 16.6 | 17.4 | 0.8 | 14 | 16.62 | 14.62 | 2.16 | 0.11 |
| C050 | M | 22.9 | 22.8 | -0.1 | 11 | 12.25 | 5.78 | 0.82 | 0.1 |
| C055 | M | 16.7 | 18.1 | 1.4 | 9 | 32.43 | 19.06 | 2.05 | 0.22 |
| C058 | M | 16.7 | 17.3 | 0.6 | 11 | 11.93 | 16.99 | 2.55 | 0.23 |
| C084 | M | 16.6 | 18 | 1.4 | 9 | 19.16 | 37.32 | 2.62 | 0.22 |
| C094 | M | 20.4 | 22.2 | 1.8 | 9 | 6.11 | 1.32 | 1.57 | 0.19 |
| C102 | M | 17.3 | 19.3 | 2 | 16 | 19.78 | 15.7 | 4.27 | 0.51 |
| C107 | M | 17.8 | 20.8 | 3 | 12 | 12.47 | 10.06 | 1.59 | 0.13 |
| C022 | M | 16.3 | 16.1 | -0.2 | 8 | 11.88 | 10.34 | 1.91 | 0.2 |
| C054 | M | 17.7 | 18.6 | 0.9 | 11 | 14.76 | 19.06 | 3.33 | 0.35 |
| Mean M | | 17.48 | 18.64 | 1.16 | 11.60 | 14.43 | 13.12 | 2.39 | 0.24 |
| SD | | 1.87 | 1.94 | 0.87 | 2.56 | 6.16 | 8.59 | 0.86 | 0.12 |
| Mean overall | | 18.70 | 19.58 | 0.88 | 11.54 | 12.34 | 9.79 | 2.18 | 0.22 |
| SD | | 2.52 | 2.31 | 0.80 | 2.40 | 6.01 | 7.84 | 0.89 | 0.11 |
| <i>P</i> -value | | | | 0.03 | 0.88 | 0.04 | < 0.001 | 0.19 | 0.23 |
| (two-tailed t-test M:F) | | | | | | | | | |

Discussion

Prey preferences may drive community structure and dynamics. Although it has been presumed, based on growth and reproduction, that the acroporid corals are the preferred prey of *C. abbreviata*, prior attempts to quantify this preference have been inconclusive (Hayes 1990a). Furthermore, snails are often more abundant on non-acroporid corals on natural reefs (Miller 1981; Hayes 1990b; Baums et al 2003), suggesting other factors are contributing to the observed population structure and host-use patterns of *C. abbreviata*. Here, for the first time, I was able to quantify host preferences of *C. abbreviata* by calculating selection indices from the proportional use and abundance of each potential prey in the experimental area and implementing Neu's (Neu et al 1974) habitat selection analysis. These results validated our *a priori* quality rankings based on published life-history data and are fundamental to the observed neighborhood effects on foraging and impact of *C. abbreviata* reported here.

The resource concentration hypothesis (Root 1973) predicts that specialized microconsumers will be more likely to find and persist on hosts in monospecific stands than in mixed-species stands. Thus, heterospecific neighbors will provide associational resistance to consumption by specialists compared to conspecifics but may increase susceptibility to generalist consumers. Agrawal (2004) expanded this theory to incorporate the level of all resources utilized, including food quality and non-food resources such as oviposition sites and enemy free space. He hypothesized that the associational effect of neighbors on consumption by specialist and generalist consumers

will fall along a continuum from associational resistance (host facilitation) to associational susceptibility (host competition), depending on the sum of resources that the neighbors provide.

Here, I tested this theory in a coral reef ecosystem by assessing the associational effects of three coral taxa, representing a range of prey quality, on the dynamics and impact of a generalist coral-eating gastropod. My results show that the sum of all resources available did indeed accurately predict snail colonization and initial impact of predation on focal *A. cervicornis* colonies. There was a significant positive relationship between neighborhood quality and both the numerical response of snails and subsequent mortality of focal *A. cervicornis* colonies due to predation over the first nine weeks. Furthermore, implementation of habitat selection analysis revealed significant effects of neighborhood treatment on habitat use by snails throughout the experiment. I was thus able to reject the null hypothesis that snail colonization and habitat use would be independent of neighborhood treatment and reject the null hypothesis that the performance (growth and survival) of focal *A. cervicornis* colonies would be independent of neighborhood treatment.

Associational susceptibility of the focal colony occurred with conspecific neighbors (density dependent mortality) and with alternative prey neighbors (apparent competition) compared to solitary colonies. The initial colonization as well as the overall use of alternative prey plots was intermediate between that of conspecific and solitary plots. However, because snails exhibited a strong feeding preference for and greater impact on *A. cervicornis* over *M. faveolata*, mortality rate of focal colonies in alternative prey plots was similar overall to that in conspecific plots where some level of prey

dilution occurred (Fig. 5.10). Thus, *M. faveolata* neighbors had a negative effect on *A. cervicornis* colonies through asymmetrical apparent competition. This is among the first evidence of predator-mediated associational susceptibility or apparent competition occurring between scleractinian corals.

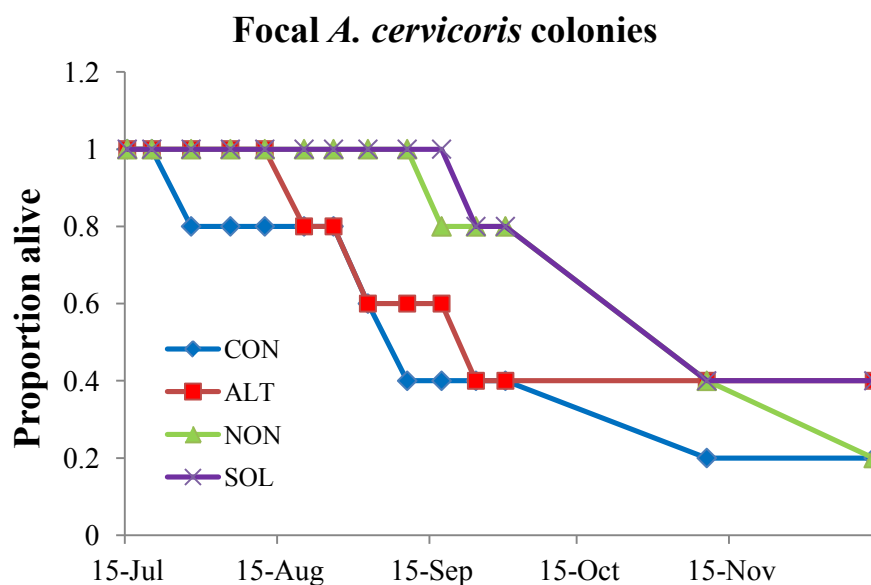


Figure 5.10 Mortality of focal *Acropora cervicornis* colonies in each neighborhood treatment through time.

The initial colonization, overall use, and performance of focal colonies for non-prey plots were not significantly different than solitary plots. However, based on the habitat selection analysis, there was significant negative selection (avoidance) for non-prey plots throughout most of the experiment whereas there was neutral selection for solitary plots after the first month. These results suggest that non-prey neighbors may provide some level of resistance to predation through physical or chemical means. Similar refuges due to physical sheltering by non-preferred, structurally complex

neighbors (Kayal et al 2011) and/or biotically defended neighbors (Glynn 1985) have been demonstrated for prey coral of the crown of thorns sea star, *Acanthaster planci*, in the Indo-Pacific. In addition, non-prey neighbors could provide association resistance in natural populations by taking up space that could otherwise be colonized by prey species that would subsequently increase risk of predation. Of course, trade-offs might also exist between reduced predation and growth and reproduction in natural populations.

Movement rates, foraging range and area utilized may be affected by the identity, abundance, and spatial distribution of all available prey as well as social factors and energetic requirements that may change with age or reproductive stage (MacArthur and Pianka 1966; Krebs and Davies 1978; Bernstein et al 1988a). In this study, individual snail foraging behavior was characterized by periods of residence in neighborhood plots followed by travel to new plots (see Fig. 5.9). Individual snails, on average, spent more time in conspecific plots than other neighborhood treatments, indicating that *C. abbreviata* forage in a hierarchical manor, in which higher quality patches are colonized first and utilized until resources are diminished. Over a period of 129 days, snails traveled, on average (\pm SD), 12.34 ± 6.01 m (TLD) over an area of 9.72 ± 7.8 m² (100% MCP). The TLD and 100% MCP home range estimates varied significantly between males and females, with males traveling farther and using more space than females. Growth rate was also greater for males than females over the course of the experiment, suggesting differential foraging behavior may be a result of varying energetic requirements between the sexes. These results indicate that males may play a bigger role in snail dispersal on a reefs scale. The factors that affect the movement of snails between coral colonies, within and among coral prey taxa, will affect the distribution of snails

across a reef and thus the potential spatial scale and magnitude of direct tissue consumption and disease transmission. This is the first report of individual movement and resource use patterns for *C. abbreviata*. These data are thus useful for informing conservation and management strategies.

Prior to the mass die-off over the last three decades, the acroporid corals in the Caribbean were considered competitively dominant due to fast growth rates and a high rate of asexual reproduction through fragmentation. On these 'robust' coral reefs, the direct and indirect effects of predation observed in this study might have been negligible or even contributed to coral diversity and species coexistence by reducing strong interspecific competition for space (Chesson 2000). However, in the wake of perturbations that have severely reduced the density and abundance of acroporid corals throughout the region, predation by *C. abbreviata* may have shifted to represent a profound threat to the persistence and recovery of remnant populations. The results presented here suggest that apparent competition and other associational effects may be important mechanisms contributing to the decline of threatened coral populations.

However, this manipulative experiment represents only the first step in understanding the complex interactions among *C. abbreviata* and their coral hosts. The presence, abundance, size, and specific spatial structure of coral colonies in natural communities will undoubtedly influence the identity, strength and outcome of predator-prey interactions. Furthermore, the predator population may vary across space and time due to a variety of other biotic and abiotic factors. Thus, the impact of snail predation will likely vary among heterogeneous coral reef communities.

CHAPTER 6: SUMMARY AND SYNTHESIS

Summary

The direct and indirect interactions associated with predation often contribute to the stability, diversity, and productivity of natural ecosystems (Paine 1966; Connell 1970b; Chesson 2000; Shea et al 2004). These interactions have generally been continually shaped over evolutionary time as part of an arms race between the interacting species in a given environment. The scale and rate of change that humans have imposed on natural communities in recent times has, in many cases, destabilized these interactions, resulting in unforeseen trophic cascades and alternate, less desirable stable states (Knowlton 2004). Thus, an understanding of the mechanistic drivers of predator-prey dynamics, including the feedbacks between prey community structure and predator population structure in space and time is important for the management and conservation of natural ecosystems.

Coral reef ecosystems are often compared to terrestrial rainforests due to the biogenic nature of the structural habitat and the vast diversity of organisms supported. However, although the evolutionary ecology of plant-herbivore systems is the subject of a vast literature, very little is known about the direct and indirect interactions among foundational scleractinian coral species and their natural enemies (Rotjan and Lewis 2008). This is especially true in the Caribbean where, historically, corallivory was not considered a strong ecological force (Ott and Lewis 1972). However, there are indications that as coral cover declines due to a variety of natural and anthropogenic stressors, corallivores will have an increasingly important role in shaping coral community structure and function in the Caribbean and globally (Rotjan and Lewis 2008; Fabricius et al 2010). For this dissertation, I used the corallivorous gastropod,

Coralliophila abbreviata, as a case study to investigate coral-corallivore interactions on coral reefs in Florida and the Caribbean.

Host Effects on Life-History and Fitness

Coralliophila abbreviata snails live in close association with coral hosts that provide both food and habitat. Variation in individual fitness across hosts may have important ecological and evolutionary consequences. Here, I identified remarkable variation in life-history traits for *C. abbreviata* across coral host taxa in the Florida Keys that is likely driven by host-specific nutritional and mortality regimes. Based on estimates of fitness correlates such as growth, longevity, and female reproductive output, *A. palmata* appears to be a superior host for *C. abbreviata*. However, the patterns of variation in size and age at sex change across hosts suggest that snails on *A. palmata* might experience relatively high juvenile mortality. Theoretically, when predation pressure is high for juveniles or small individuals and there is an escape in size later in life, net fitness of the population is maximized when individuals mature later at larger sizes (Stearns and Koella 1986; Beckerman et al 2010). My data showed that snails on *A. palmata* changed sex later at much larger sizes than snails on the other two coral hosts. Based on these and previously published data viewed in the context of the theory of life-history evolution, I hypothesize that a host-associated trade-off exists for *C. abbreviata* between early survival and later reproductive potential. Such a trade-off would promote the evolution and maintenance of a generalist strategy across a heterogeneous environment (Singer et al 2004).

Overall, these data demonstrate that coral community composition will influence the structure and productivity of snail populations, affecting the overall feedback between the coral community structure and subsequent snail impact on the coral populations.

Furthermore, by characterizing the host-specific life-history traits of *C. abbreviata*, I was able to develop testable hypotheses about the selective forces acting on snails on different coral hosts. An understanding of how individuals and populations are affected by environmental variation is crucial to understanding the distribution of organisms and species.

Microsatellite Development

Both past and present demographic and evolutionary processes play a role in shaping the patterns of genetic variation found in contemporary populations. Thus, due to major advances in technology and theory over the last three decades, researchers in the fields of population genetics and phylogenetics have been able to shed light on demographic, ecological, and evolutionary processes that were previously unrecognized or unsubstantiated. Microsatellites, in particular, have emerged as powerful molecular tools for studying the ecology and evolution of populations (Selkoe and Toonen 2006).

Microsatellites are short sections of DNA that contain tandem nucleotide repeats, generally of di-, tri-, or tetranucleotide motifs. These repetitive DNA units are abundant and ubiquitous across all eukaryotic genomes (Hamada et al 1982; Tautz and Renz 1984). They occur mainly in non-coding regions and are, therefore, assumed to evolve neutrally. They are also co-dominant and have a relatively high rate of mutation (on average: 5×10^{-4}) leading to high allelic diversity and heterozygosity in populations (Schlötterer 2000). Due to these characteristics, microsatellites can be used to assess genetic structure at a finer scale of resolution than most other molecular markers (Avice 1994). For instance, they can be used to identify individuals (i.e. “DNA fingerprinting”) and to assess the relationships and patterns of genetic exchange within and among family groups,

subpopulations, populations, and closely related species. Furthermore, because events such as population bottlenecks and expansions leave characteristic signatures in the patterns of genetic variation at neutral markers, microsatellites can be used to elucidate the demographic history of populations (Kimmel et al 1998; Luikart et al 1998; King et al 2000).

Here, I developed a set of polymorphic microsatellite markers that are suitable to assess the population genetic structure, connectivity, and patterns of gene flow among populations of *C. abbreviata*. Specifically, eight polymorphic microsatellite loci were isolated and characterized for *C. abbreviata*, and tested for cross-amplification in the congener, *C. caribaea* (Abbott 1958). The loci were screened using 60 *C. abbreviata* from two geographically disparate populations (Key Largo, FL USA and St. Vincent and the Grenadines). All loci were highly polymorphic with an average number of alleles per locus of 24 (range 13-34). Observed and expected heterozygosity values ranged from 0.375 - 0.969 and 0.877 - 0.981, respectively. Three loci deviated significantly from Hardy-Weinberg equilibrium in both populations, presumably due to null alleles. Loci were not well conserved in the congener *C. caribaea*, with only one locus amplifying consistently in this species. These are the first microsatellite markers developed for *C. abbreviata* and thus constitute a valuable tool set that can be used to address a multitude of ecological and evolutionary questions for this species. The microsatellite sequences have been deposited in GenBank and are publicly available for future research (accession numbers HM156485-HM156492).

Population Genetic Structure and Demographic History

Populations of *C. abbreviata* associated with the threatened acroporid corals, *Acropora palmata* and *A. cervicornis*, display different behavioral, morphological, demographic, and life-history characteristics than those that inhabit other coral host taxa. Because of this variation, I hypothesized that host-associated adaptation has led to genetic differentiation of these snail populations. Host-associated adaptation is thought to be largely responsible for the vast diversity of phytophagous insects on land (reviewed in: Berlocher and Feder 2002; Janz et al 2006) and is increasingly being reported in the marine environment (Knowlton 1993; Sotka 2005a; Krug 2011). The presence of population structure or cryptic species will greatly affect predator-prey dynamics and community interactions. Isolated populations or cryptic species that specialize on specific coral host taxa will be tightly linked to local and regional population fluctuations of their host corals. A single, generalist species that is highly connected across populations, however, will be buffered numerically from fluctuations of any one prey species. Predator-mediated indirect interactions among multiple prey species in these cases often have important impacts on community structure.

Using microsatellite markers and mtDNA sequence data, I found no evidence of genetic differentiation among snail populations feeding on different coral host taxa or from locations separated by up to 3000 km. Instead, *C. abbreviata* populations constitute a single large, well-connected metapopulation across the Caribbean. Demographic analyses consistently supported a scenario of population expansion during the Pleistocene, a time of major carbonate reef development in the region. The evolution and maintenance of a generalist strategy for *C. abbreviata* might be a result of the combined

effects of colonization history, high dispersal, and local and meta-population scale environmental heterogeneity. Overall, the lack of host specialization and the high connectivity among locations translate into continuous predation pressure on severely declining stands of the preferred but threatened *Acropora* spp. corals.

Foraging Behavior and Indirect Coral-Coral Interactions

Individual foraging behavior and habitat use of a consumer may be influenced by factors such as the abundance, quality, and spatial distribution of resources, social cues, and physiological requirements that may vary in space and time (MacArthur and Pianka 1966; Krebs and Davies 1978; Bernstein et al 1988a). Patterns of resource use will in turn determine the likelihood of direct and indirect interactions among organisms. In the case of rare and imperiled species, such interactions may affect the persistence and recovery of local populations (Holt 1977; Holt and Lawton 1994; DeCesare et al 2010).

In this study, I examined the effects of coral neighborhood composition on the foraging behavior and subsequent impact of *C. abbreviata* on focal colonies of the threatened coral prey, *A. cervicornis*. Additionally, I analyzed the movements, habitat use, and foraging behavior of tagged snails through time as neighborhood patches were depleted.

I found that the density and identity of neighboring corals indirectly affected predation pressure on focal *A. cervicornis* colonies. Snails exhibited a strong feeding preference for *A. cervicornis* during the experiment. They responded numerically to overall neighborhood quality and subsequently had the greatest negative impact on focal *A. cervicornis* colonies surrounded by conspecifics. The presence of alternative prey also contributed to predator abundance in experimental plots, thus *M. faveolata* neighbors had

a negative effect on *A. cervicornis* colonies through apparent competition. Furthermore, this indirect interaction was asymmetrical as *C. abbreviata* had a preference for and greater impact on, *A. cervicornis* colonies. This is the first evidence, to my knowledge, of predator-mediated associational susceptibility or apparent competition occurring between scleractinian corals. These results suggest that apparent competition may be an important mechanism contributing to the decline of threatened coral populations.

Individual snail foraging behavior was characterized by periods of residence in neighborhood plots followed by travel to new plots. Individual snails appear to forage in a hierarchical manner, in which higher quality patches are colonized first and utilized until resources are diminished. Over a period of 129 days, snails traveled, on average (\pm SD) 12.34 ± 6.01 m (TLD) within an area of 9.72 ± 7.8 m² (100% MCP). The TLD and 100% MCP home range estimates varied significantly between males and females, with males traveling farther and using more space than females. Growth rate was also greater for males than females over the course of the experiment, suggesting differential foraging behavior may be a result of varying energetic requirements between the sexes. These results indicate that males may play a bigger role in snail dispersal on a reef scale.

The factors that affect the movement of snails between coral colonies, within and among coral prey taxa, will affect the distribution of snails across a reef and thus the potential spatial scale and magnitude of direct tissue consumption and disease transmission. This is the first report of individual movement and resource use patterns for *C. abbreviata*. These data are thus useful for informing conservation and management strategies. For instance, this information could be incorporated into an out-planting design for nursery reared corals to reduce the impact of predation.

Synthesis: Implications for Imperiled Caribbean Corals

In this dissertation, I investigated three major components of the predator-prey dynamics of the corallivore, *Coralliophila abbreviata*, and its scleractinian coral prey/hosts: 1.) The effects of coral host taxon on the demographic structure and life-history of *C. abbreviata*, 2.) The regional and host-specific population genetic structure, connectivity, and demographic history of *C. abbreviata*, and 3.) The effects of coral community structure on the foraging behavior and subsequent impact of *C. abbreviata*. These processes drive the feedbacks between coral community structure and corallivore population structure on local and regional scales. Understanding them is thus crucial for predicting the impacts of corallivory on a changing coral community.

A major finding of this research is that *C. abbreviata* constitute a single large population throughout the greater Caribbean characterized by high gene flow and host-associated life-history characteristics. A consequence of this in regards to coral community interactions is that snail populations are decoupled demographically from local and regional population fluctuations of any one prey population. Local snail populations may be supplied from distant locations and maintained on alternative coral prey. However, the per capita reproductive output of females reported here was substantially greater for females found on *A. palmata* compared to the other two common coral prey taxa investigated. Thus, populations of *C. abbreviata* may be disproportionately linked to fluctuations of acroporid coral populations. However, *A. palmata* form two regionally isolated populations in the eastern and western Caribbean (Baums et al 2005) and are therefore decoupled at large scales from predator populations; although robust coral populations in one region will not supplement conspecific

populations in the other, they may supplement predator populations across regions. Furthermore, the degree to which the demographic numerical response of *C. abbreviata* tracks fluctuations in the abundance of acroporid corals will depend on the occurrence and strength of host-specific life-history trade-offs. Trade-offs will also act to decouple the predator-prey relationship. The weaker the demographic link between predator and prey populations, the more vulnerable the acroporid corals are to predation as their populations decline, leading to compensatory mortality due to predation and population instability.

On a reef scale, the aggregative response of *C. abbreviata* to overall prey abundance and quality may lead to apparent competition between prey species in areas where their populations overlap. Such apparent competition will have a greater negative impact on acroporid corals due to a strong feeding preference and greater tissue consumption rates by *C. abbreviata* on these corals. The same aggregative response, however, may provide refuges in space for acroporid corals in low density/quality patches. Furthermore, in the experiment reported here, the mortality rate of the acroporid corals declined through time as the density of acroporid corals declined and snails began to switch to less preferred prey (Fig. 5.8; Table 5.3). This data suggests that *C. abbreviata* may exhibit a Type III functional response to declining acroporid populations. In this case, corals will have a refuge from predation at low densities. Such low densities, however, might make the acroporid populations extremely vulnerable to Allee effects and stochastic disturbances.

Historically, the effects of predation on robust acroporid coral populations in the Caribbean might have been negligible or may have even contributed to species

coexistence by reducing strong interspecific competition for space in some areas. However, in the wake of perturbations that have severely reduced the density and abundance of *Acropora* spp. corals throughout the region, predation by *C. abbreviata* may have profound negative effects on the persistence and recovery of remnant populations. Understanding and managing this threat is thus crucial for reef conservation in the region. Relative to the other major contemporary stressors affecting *Acropora* spp. corals in the Caribbean, including disease and hurricanes, predation by *C. abbreviata* may be the single most manageable threat. Furthermore, targeted snail removal may be imperative to ensure the persistence and/or recovery of particularly vulnerable *Acropora* colonies such as small fragmented or remnant colonies, nursery transplanted colonies and new recruits. However, removal efforts will be constantly mitigated by input from other local and regional sources. Control strategies, therefore, need to be designed accordingly.

In general, although corallivory is not the ultimate cause of coral reef decline, it may be a proximate cause, responsible for continued coral population declines after acute disturbances, maintaining alternate stable states, or even local extinctions. Managing this stressor may help increase the resilience of vulnerable coral populations, promoting recovery and allowing local populations more time to adapt to large scale environmental changes.

In addition to the conservation implications, the research presented here provides valuable insights into the demographic and ecological processes that shape the evolution of life-history strategies and interactive behaviors of coral associated organisms. These data provide a solid framework for future empirical and theoretical studies of this system.

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