

10-1-2010

Reproductive Isolation and Hybridization Dynamics in Threatened Caribbean Acroporid Corals

Nicole D. Fogarty

Florida State University, fogartyn@uncw.edu

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THE FLORIDA STATE UNIVERSITY
COLLEGE OF ARTS AND SCIENCES

REPRODUCTIVE ISOLATION AND HYBRIDIZATION DYNAMICS IN
THREATENED CARIBBEAN ACROPORID CORALS

By

NICOLE D. FOGARTY

A Dissertation submitted to the
Department of Biological Sciences
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Degree Awarded:
Fall Semester, 2010

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The members of the committee approve the dissertation of Nicole D. Fogarty defended on July 1, 2010.

Don Levitan
Professor Directing
Dissertation

Markus Huettel
University Representative

Joe Travis
Committee Member

Alice Winn
Committee Member

Janie Wulff
Committee Member

Approved:

P. Bryant Chase, Chair, Department of Biological Science

The Graduate School has verified and approved the above-named committee members.

I dedicate this dissertation to my fiancé Kevin, to my family, and to anyone who has followed through with a childhood dream.

PREVIEW

ACKNOWLEDGEMENTS

I extend my sincere gratitude to my committee members, Don Levitan, Joe Travis, Janie Wulff, Alice Winn, Tony Arnold and Markus Huettel. I very much appreciate their advice and support throughout my time at Florida State University. I particularly want to thank my advisor and mentor, Don Levitan. I have learned much from Don and he has given me so many wonderful opportunities, that words cannot express my gratitude. He has taught not only how to do good science, but to have fun while doing it. I will forever cherish the laughter and good times I had in the Levitan lab. Don is extremely well respected in the fields of evolutionary biology and fertilization ecology, yet has remained humble and approachable. It was an honor to be a part of Don's lab.

This research could not have been conducted without the generous support of my funding agencies. I would especially like to thank the National Geographic Society (8230-07) with their generous contribution to this research and five years of support that the Smithsonian Marine Science Network provided me while conducting my research on Carrie Bow Cay, Belize. Additional support came from the American Academy of Underwater Science, The PADI Foundation, PADI AWARE, Lerner-Gray Memorial Fund of the American Museum of Natural History, and the Florida State University's Short, Bennison, Gramling, and International Dissertation Research Fellowships.

There were many, many people who assisted me in the field, and I am grateful for their hard work. I would like to first thank the members of Carrie Bow "Team Spawn," Val Paul, Bob Steneck, Raphael Ritson-Williams, and Susie Arnold. I would like to thank them for the wonderful collaboration over the past five years and thank you for the many laughs. Every year I looked forward to going to "Nerd Camp" and working with you all. I appreciate everything you have done for me. Thank you for the

many others that have helped me collect field data: S. Vollmer, B. Biggs, C. terHorst, A. Szmant, M. Miller, W. Cooper, D. Ferrell, P. Bouwma, N. Jue, C. Safina, J. Brown, K. Morrow, L. Huebner, K. Lotterhos, T. Hitchins, R. Rojan, B. Stauffer, B. Brown, A. Baker, M. Vermeij, S. Pointek, B. Mason, R. Albright, C. David, B. David, J. Nolan, K. DeFosset, B. Fogarty, E. Bartels, S. Prosterman, M. McField, E. McRae, and T. Smith. Luisa Rubio also assisted with many hours of analyzing photographs. I also would like to thank the many field stations that have supported my research. Including Mote Marine Laboratory (Fl. Keys), Ellen Bay Cottages (Antigua), STRI (Bocas del Toro), Carrie Bow Caye (Belize), Sea Aquarium (Curacao), and CMES (St. Thomas).

Many government agencies allowed me to collect acroporid specimens for my research. I would like to thank the Antigua Fisheries Division particularly T. Lovell, P. James, S. Archibald, M. Appleton and C. Dyer at the Environmental Division Management Authority for CITES. Eric Newton of the Conservation Policy Advisor and Department of Environment and Nature assisted me with permits in Curacao. The Belize Fisheries Department was always helpful particularly B. Wade, J. Azueta and Hampton. In addition, Ruth Gomez at the Division of Fish and Wildlife in St. Thomas was extremely helpful in assisting me in obtaining permits.

The molecular work could not have been possible without the training of A. Plata-Stapper and the advice from I. Baums, M. Lowenberg, and N. Jue. *Acropora prolifera* samples were also supplied by D. Thornhill and I. Baums/D. Ruiz. I want to also thank S. Miller of the FSU sequencing facility for his assistance with genotyping and analyzing the microsatellites.

Lastly, I want to thank my friends, family and husband for their support throughout this long, arduous, and amazing journey. I am so fortunate to have wonderful friends and labmates that keep me smiling. I particularly want to thank M. Adreani, K. Lotterhos, J. Fierst, A. Plata-Stapper, B. Biggs, A. Strimaitis, C. Stahala, J. Banbury, D. Akob, P. Bouwma, P. Mungia, D. Ferrel, E. Franke, M. Lowenberg, B. Storz,

S. Storz, N. Jue, A. Kruse, H. Voegtle, S. McGauley, E. Vernon-Bell, T. Hitchins, C. Hitchins, J. Gregoire, M. Knowles, and the many other friends I am sure I am forgetting for their unconditional support and love. I am thankful to also have such amazing parents, brother, and sister-in-law that have supported me throughout this process. Lastly, I want to thank my husband for always being there for me, for supporting me and loving me (even though at times, I am sure this has been difficult).

PREVIEW

TABLE OF CONTENTS

List of Tables	viii
List of Figures	x
Abstract	xiv
1. Introduction	1
2. Weak prezygotic isolating mechanisms in threatened Caribbean <i>Acropora</i> corals.....	7
3. No evidence of postzygotic barriers to hybridization between threatened Caribbean acroporid corals.....	40
4. Variable genotypic diversity in the hybrid of threatened coral species, <i>Acropora palmata</i> and <i>A. cervicornis</i>	78
5. Conclusions	104
APPENDICES.....	106
REFERENCES	119
BIOGRAPHICAL SKETCH	131

LIST OF TABLES

Table 2.1. Dates attempted to observe and collect acroporid spawn throughout the Caribbean. If spawning did occur the time the gamete bundles were first observed in the mouth of the polyp was recorded as “bundle set time,” the range of spawning times was recorded below each species name, and the “bundle breakup” was the time in which the bundles dissipated. If no spawning occurred it was represented by and “ns,” and an “x” signifies that we did not monitor that species that night 34

Table 2.2. ANCOVA results testing differences in fertilization success as a function of cross type and sperm concentration. The dependent variable is the proportion of eggs fertilized (arcsine-transformed). The model consists of treatment group (conspecific vs. heterospecific cross) as the main effect, with sperm per milliliter (logistic transformation) as the covariate..... 36

Table 3.1. The abundance of each acroporid taxa and the wave environment in which they live at each site (H = high; M = moderate; L = low), and the experiment or assessment conducted at each site (LS = larval survival; SP = substrate preference; PS = post-settlement survival; AA = Adult affliction; RT = reciprocal transplant) 72

Table 3.2. Statistics describing patterns of settlement using a two-way ANOVA to explore differences in settlement between taxa and zone in which the tile was conditioned, and a two-way ANCOVA examining settlement using the amount of CCA covering a subset of tiles as a covariate and the zone in which the tiles were conditioned and taxa as the main effects..... 72

Table 3.3. Kruskal-Wallace analysis of afflictions across taxa..... 73

Table 3.4. P-values from Fisher Exact Test comparing affliction data collected in 2006 and 2007 at Director’s Bay, Curacao. Bold p-values indicate a significant difference..... 74

Table 3.5. P-values from Fisher Exact Test comparing affliction data collected in 2006 and 2009 at Carrie Bow Caye, Belize. Bold p-values indicate a significant difference..... 75

Table 3.6. P-values from Fisher Exact Test comparing affliction data collected in 2006 and 2007 at Sea Aquarium, Curacao. Bold p-values indicate a significant difference..... 76

Table 3.7. P-values from Fisher Exact Test comparing affliction data collected in 2007 and 2009 at Sea Aquarium, Curacao. Bold p-values indicate a significant difference..... 76

Table 3.8. P-values from Fisher's exact test examining differences between 2006 and 2009 at Carrie Bow Cay, Belize. Bold values indicate statistical significance 76

Table 3.9. P-values from chi-square tests examining variation in the number of colonies showing signs of each affliction across all six sites. The data was pooled for those sites that were sampled across multiple years. Bold values indicate statistical significance..... 77

Table 4.1. The density and average volume of acroporids at a subset of sites across the Caribbean..... 102

Table 4.2. Genotypic indices for reefs where hybrids were sampled haphazardly. (N = number of samples; N_g/N = genotypic richness ; G_o/G_e = genotypic diversity; G_o/N_g = genotypic evenness; nd = no data; cb = co-occurring with both parental species; cc = co-occurring with a. palmata; np = nonparental habitat) 102

Table 4.3. Genotypic indices for reefs where nearly all hybrids were sampled (i.e. complete sampling). N = number of samples; N_g/N = genotypic richness ; G_o/G_e = genotypic diversity; G_o/N_g = genotypic evenness; nd = no data; cb = co-occurring with both parental species; cc = co-occurring with a. palmata; np = nonparental habitat) 103

Table 4.4. The average distance of nearest neighbors of the same genet and the maximum distance between ramets..... 103

LIST OF FIGURES

<p>Figure 2.1. The three Caribbean acroporids. a) <i>A. palmata</i>, b) hybrid, c) <i>A. cervicornis</i>.....</p>	30
<p>Figure 2.2. Map of Caribbean showing study sites.....</p>	31
<p>Figure 2.3. Spawning times for acroporid corals in Florida and the Caribbean taken from personal observations, publications, and postings on the coral-list server. Lines above the mean indicate the minimum and maximum spawn times for <i>A. palmata</i> (dashed lines) and <i>A. cervicornis</i> (solid lines)</p>	32
<p>Figure 2.4. Four separate spawning events where spawning was observed in both <i>A. palmata</i> and <i>A. cervicornis</i> on the same evening, a) Florida Keys 2005, b) Belize 2005, c) Belize 2008, d) Belize 2009.....</p>	33
<p>Figure 2.5. Fertilization success of (A) <i>A. palmata</i> eggs and (B) <i>A. cervicornis</i> eggs as a function of log sperm concentration per milliliter. Closed symbols and solid lines represent conspecific crosses and open symbols and dashed lines are heterospecific crosses.....</p>	37
<p>Figure 2.6. Average fertilization success of all possible crosses when gametes were fresh (30 minutes after bundle breakup) and aged (4-5 hours). Double letters represent conspecific crosses (p= <i>A. palmata</i> and c = <i>A. cervicornis</i>) and letters followed by an "e" or "s" represent eggs or sperm for each heterospecific cross. Numbers above bars represent p-values and error bars represent standard error. The inlay represents the individual conspecific <i>A. cervicornis</i> fertilization crosses, suggesting that a decrease in fertilization at high sperm concentrations (i.e polyspermy) may be biasing the result of lower fertilization when gametes were fresh.....</p>	38

Figure 2.7. The difference in the observed and the expected values for competitive crosses. Expected values were calculated based on sperm concentration. Values of 1 would signify 100% fertilization by conspecific male, -1 would signify 100% fertilization by heterospecific male and 0 represents no difference between the number of larvae sire and what is expected based on sperm concentration. Positive values denote conspecific sperm precedence, and negative values represent heterospecific sperm precedence. Closed symbols represent competitive trials when gametes were fresh. Squares represent the four crosses where competitive trials were conducted when gametes were fresh (closed squares) and gametes had aged four hours (open squares)..... 39

Figure 3.1. Size frequency distribution of each taxon at sites a) E. Rocks, Antigua, b) Flat Key, St. Thomas, c) Sea Aquarium, Curacao, d) N. Caye Caulker, Belize, and e) Carrie Bow, Belize. Volume is an estimate of biomass and calculated by multiplying length, width, and height measurements (cm) of each colony 63

Figure 3.2. A comparison of larval survival in Caribbean acroporids during the planktonic period until becoming competent. Bars are standard error... 65

Figure 3.3. Mean acroporid settlement eight days after fertilization on tiles that had been seasoned in the shallow hybrid zone and slightly deeper parental species zone. Bars are standard error 66

Figure 3.4. Mutlidimensional scaling plot examining the similarities and dissimilarities in the severity of each affliction for individuals of each taxa. Overgrowth = over; Disease = dis; Paling/Bleaching = pal/bl; Predation = pred; Parasitism = para 67

Figure 3.5. A comparison across taxa of the proportion of colonies afflicted by a) all afflictions, b) disease, c) predation, c) paling or bleaching, parasitism, and f) overgrowth 68

Figure 3.6. Mean proportion of transplants surviving (including broken colonies) over time 69

Figure 3.7. The proportion of colonies alive, broken, and dead at two, six, twelve, and twenty-three months. (P= *A. palmata*; H = hybrid; C= *A. cervicornis*) at four time steps a) 2 mo, b) 6mo, c) 12 mo, and d) 23 mo.

(white bars = alive, gray = broken, black = dead) 70

Figure 3.8. The mean amount of growth (mm) of transplants from a) 2006-2007 and b) 2006-2008 for the shallow, intermediate, and deep habitats..... 71

Figure 4.1. Map of Caribbean showing hybrid sampling sites at six different localities. (1) Caye Caulker North, (2) Caye Caulker South, (3) South Carrie Bow, (4) Southwater, (5) Sea Aquarium, (6) Director's Bay, (7) North Rocks, (8) East Rocks, (9) Bolongo Bay, (10) Flat Key, (11) Botany Bay, (12) Hans Lolick, (13) San Cristobal, (14) Palmata Reef 94

Figure 4.2. Frequency distribution of the number of ramets per genet (genet size) for a) haphazard sampling and b) complete sampling methods 95

Figure 4.3. Rarefaction curves showing the expected number of genets detected for various sample sizes a) up to 30 samples and b) for the fewest number of samples (i.e. 5) collected at a site. This analysis could not be conducted for sites that were solely composed of a single genet. * Sites where complete sampling was conducted. ER (East Rocks); bot (Botany Bay); ccs (Caye Caulker South); flk (Flat Key); aqu (Sea Aquarium); bah (Bahamas); pr (Puerto Rico); bol (Bolongo Bay); scb (South Carrie Bow); han (Hans Lolick); sw (Southwater) 96

Figure 4.4. Combination of genotypic diversity (G_o/G_e) and evenness (G_o/N_g) across Caribbean sites. Closed symbols denote sites that were haphazardly sampled while open symbols represent sites that were completely sampled. When values approach 1 for genotypic diversity and evenness the population is more sexual, but when the values approach zero the population is dominated by only a few clones. Although counterintuitive, when a reef is composed of only one genet a value of 1 for genotypic evenness is assigned and therefore a predominately asexual population..... 97

Figure 4.5. The effect of wave action on the genotypic diversity. The same trend was seen with genotypic richness. (Bars = \pm S.E.)..... 98

Figure 4.6. Hybrid map of the South Carrie Bow Reef looking at clonal structure over three years a) 2005, b) 2006, c) 2007..... 99

Figure 4.7. Hybrid map of the Sea Aquarium Reef looking at clonal structure over three years a) 2006, b) 2007, c) 2008..... 100

Figure 4.8. A frequency distribution comparing the genotypic richness (N_g/N) between the three Caribbean taxa across Caribbean sites. Only those sites that were sampled haphazardly were included in this analysis..... 100

Figure A1. The frequency of corals in each percent afflicted category at Director’s Bay, Curacao. Numbers after taxon names denotes sample size. Letters “a-e “are affliction data collected in 2006 and letters “f – j “are affliction data collected in 2007 106

Figure A2. The frequency of corals in each percent afflicted category at South Carrie Bow Cay, Belize. Numbers after taxon names denotes sample size. Letters a-e are affliction data collected in 2006 and letters f – j are affliction data collected in 2009..... 108

Figure A3. The frequency of corals in each percent afflicted category at East Rocks, Antigua in 2007. Numbers after taxon names denotes sample size. 110

Figure A4. The frequency of corals in each percent afflicted category at North Caye Caulker, Belize in 2007. Numbers after taxon names denotes sample size. 112

Figure A5. The frequency of corals in each percent afflicted category at Flat Key, St. Thomas in 2009. Numbers after taxon names denotes sample size. 114

Figure A6. The frequency of corals in each percent afflicted category at Director’s Bay, Curacao. Numbers after taxon names denotes sample size. Letters “a-e “are affliction data collected in 2006, letters “f – j “are affliction data collected in 2007, letters “k – o“ are affliction data collected in 2009.. 116

ABSTRACT

The Caribbean corals, *Acropora palmata* and *A. cervicornis*, are abundant in fossil records but have recently undergone drastic declines primarily as a result of disease. *Acropora prolifera*, a hybrid of these species, has no fossil record and was previously considered rare and to occupy nonparental habitats. Now, hybrids have equivalent or greater abundance than the parental species and have expanded into the parental habitat at some sites. Previous molecular studies have demonstrated regional variability in unidirectional introgression of *A. palmata* genes into *A. cervicornis*. The goals of this dissertation are **(1) to determine the strength of prezygotic mechanisms and to establish the likelihood of density dependent reproductive isolation, (2) to determine the strength of intrinsic and extrinsic postzygotic barriers, and (3) to ascertain if hybrid populations are composed of rare hybridization events that have asexually fragmented, or if colonies are genotypically distinct suggesting separate hybrid events.** Overall barriers to hybridization in this genus are weak, and the efficacy of these semipermeable isolating mechanisms may depend on density. In addition, hybrids are as viable as the parental species at a variety of life history stages and are less or equally susceptible to the typical afflictions that have led to their decline. Most hybrid populations do not seem to be composed of a single hybridization event that has asexually propagated, but rather the genotypic diversity varies across sites with up to 17 different distinct genets in one population. Taken together, it appears that hybridization in a threatened Caribbean genus is evolutionarily significant with a range of possible outcomes from the benefit of novel alleles to the swamping of *A. cervicornis*' genome. These outcomes may hinge on the ability of the Caribbean acroporids to withstand the onslaught of threats that currently faces this genus (i.e.

Allee Effect, disease, predation, increased sea temperature, ocean acidification, and increased disturbances).

PREVIEW

CHAPTER 1

INTRODUCTION

Botanists have long realized the importance of introgressive hybridization (i.e. gene flow between genetically different species via hybridization) as a key evolutionary process (Anderson 1949; Stebbins 1959; Grant 1981); however, only recently has the importance of introgressive hybridization been considered in animals (reviewed in Arnold 1997, 2007, Willis 2006). Outcomes of introgressive hybridization can vary from the exchange of novel alleles to the genetic swamping of one or both of the parental species. The likelihood of this outcome is dependent upon the strength of selection and direction of introgression. If there is sufficient selection against introgressed alleles, then ecological and morphological identity of the species will be maintained. Weak selection coupled with extensive hybridization, may result in genetic swamping driving one species, via unidirectional introgression, or both species to extinction through the fusion of both parental species genomes (Levin et al. 2002; Rhymer and Simberloff 1996). If introgressed alleles are favored by selection, it may lead to adaptive shortcuts for the recipient species (Stebbins 1959; Martinsen et al. 2001; Arnold 2006). Lastly, if hybrid populations stabilize and become reproductively isolated from the parental species, a new species may form (Riesberg 1997; Salzburger et al. 2002; Arnold 2006; Willis et al. 2006).

Another way of viewing introgression is that hybrids act as an evolutionary filter where selection will allow the introgression of beneficial alleles but prevent many deleterious alleles from introgressing (Martinsen et al. 2001). This balance of selection can be disrupted by ecological changes (i.e. species introductions, habitat destruction,

abiotic fluctuations, and disease, predation, or parasitism outbreaks) that lead to high mortality in the parental species and a reduction in the efficacy of reproductive isolating barriers (Levin et al. 2002; Rhymer and Simberloff 1996; Dowling and Secor 1997). When this occurs, it is often the rarer of the two hybridizing species that suffers increased introgression and is threatened by genetic swamping (Hubbs 1955; Levin et al. 2002; Rhymer and Simberloff 1996; Wirtz 1999; Lepais et al. 2009). Endangered taxa are particularly vulnerable to genetic swamping; yet, these taxa are at risk of inbreeding depression and may actually benefit from the acquisition of genetic variation through introgression. In such a system, a sister species is sometimes introduced to enhance the genetic variation of the rare species as a conservation strategy (reviewed in Rhymer and Simberloff and Arnold 2006).

Reticulate evolution can be the result of extensive introgressive hybridization in a genus, where species undergo repeated fusion and separation over time. Reticulate evolution is well established as an evolutionary process in many plant species, but occurs to a lesser extent or at least understudied in animal species (Arnold 1992; Arnold 2006). Corals are one of the best known animal examples of introgressive hybridization. Corals share many life history characteristics with plants (e.g. sessile adults, broadcasting of gametes, lack of mating behavior, common hermaphroditism, and effective means of asexual propagation –Willis et al. 2006) and therefore appear to undergo similar evolutionary processes such as introgressive hybridization and reticulate evolution (Veron 1995; Hatta et al. 1999; Willis et al. 2006). The main evidence of reticulation of corals comes from their longevity in the fossil record, their ability to hybridize, their extensive diversity, their biogeographic patterns, and coral's mode of reproduction and long distant dispersal (Veron 1995). The genus *Acropora* is the most well studied coral genus likely because of its evolutionary success with more than 100 species, its dominance in shallow water reefs (Wallace 1999; Veron 2000), and its remarkable ability of effective clonal reproduction (Tunncliffe 1981, 1983). Evidence

from several molecular studies on Indo-Pacific acroporids species found high levels of gene pool sharing and suggest these species should belong to a syngameon (i.e. a complex of interbreeding species). These findings are consistent with expectations of reticulate evolution (Hatta et al. 1999; van Oppen et al. 2001, 2002).

The Caribbean acroporid system is only composed of two species, *A. palmata* and *A. cervicornis* that form a hybrid, previously called *A. prolifera* (van Oppen et al. 2000; Vollmer and Palumbi 2002). Although *A. cervicornis* and *A. palmata* have been found in the fossil record for 6.6 (Budd and Johnson 1999) and 3.6-2.6 million years, respectively, the hybrid has no fossil record (Budd et al. 1994). Unidirectional introgression of genes from *A. palmata* to *A. cervicornis* occurs at varying frequencies across loci and across geographic sites (van Oppen 2000; Vollmer and Palumbi 2002, 2007; Hemond and Vollmer 2010). The role hybridization and reticulation play in this system has been controversial. Some scientist believe that these hybrids have little evolutionary significant but will persist through asexual fragmentation and the occupation of nonparental niches (Cairns 1982; Vollmer and Palumbi 2002), while others believe that even small amounts of introgression may increase genetic diversity needed for the resilience of these declining coral species (Miller and van Oppen 2003; Willis et al. 2006). It has also been suggested that although reticulation is an important evolutionary force in the Indo-Pacific, the Caribbean is likely too uniform for reticulate pathways be created (Veron 1995).

Because a paucity of information exists on the ecology of the hybrid, the reproductive ecology of the parental species, and the strength of the reproductive isolating barriers, it is difficult to assess the evolutionary significance of hybridization in the Caribbean acroporids. Understanding the current ecology of the Caribbean acroporid system is particularly important because drastic ecological changes have occurred recently. In the past 30 years, *A. palmata* and *A. cervicornis* have undergone drastic declines of over 97% in abundance and coral cover (*Acropora* biological review

team). This decline is primarily the result of white-band disease (Aronson and Prect 2001; Patterson et al. 2002; Williams and Miller 2006; Pandolfi and Jackson 2006), but predation, coral bleaching, disturbances, and other diseases (i.e. white pox) are factors that have also contributed to the dramatic loss of acroporids (Bruckner 2002). The loss of the parental species may have changed their reproductive success in two ways: (1) an overall decrease in the fertilization rates because gamete concentrations are too dilute (i.e. the Allee Effect Levitan and McGovern 2002), or (2) if eggs are not immediately swamped by conspecific sperm, they may drift unfertilized for longer periods of time increasing the probability of encountering heterospecific sperm. Understanding the level of compatibility between *A. palmata* and *A. cervicornis* will elucidate the probability of increased hybridization as a function of decreased parental species abundance.

If *A. palmata* and *A. cervicornis* are compatible, there may be postzygotic mechanisms that prevent the proliferation of the hybrid. Postzygotic mechanisms that may act on hybrids are intrinsic (i.e. hybrid sterility and hybrid inviability) or extrinsic (i.e. ecological inviability; Coyne and Orr 2004). For unidirectional introgression to occur between these species (*A. palmata* genes flowing into *A. cervicornis*), *A. cervicornis* must mate with hybrids demonstrating that hybrids are not sterile and therefore hybrid sterility can be ruled out as a possible postzygotic mechanism. Hybrid inviability could take place at a variety of different life cycle stages (i.e. larval, settlement, post-settlement, and adult). To summarize these stages, Caribbean acroporids are hermaphroditic corals that broadcast spawn gamete bundles full of eggs and sperm on a few nights in late summer (Szmant 1986). Fertilization takes place at the water's surface and the resulting larvae are competent (i.e. having the ability to settle) after four days (Fogarty pers.obs) but may not settle for a week or two (Szmant 1986). Settlement involves finding appropriate substrate through which chemical cues are used (Ritson-Williams et al. 2010). Because of their small size and slow growth rates, corals are particularly vulnerable during the post-settlement period (Ritson-Williams 2010) and

take at least four years to reach sexual maturity (Wallace 1985). As adults, acroporids face numerous threats such as predation, disease, overgrowth, parasitism, coral bleaching, and disturbances. In order to adequately assess the hybrid inviability as a source of postzygotic selection, all of these stages should be assessed. Finally, ecological viability occurs when hybrids suffer lower fitness because they fail to find an appropriate ecological niche. Acroporid hybrids were thought to live in only nonparental niches (Carins 1982; Vollmer and Palumbi 2002; Willis et al. 2006); however, recently hybrids have also been observed to co-occur with both parental species (N.D. Fogarty pers. obs) which may suggest the expansion of their habitat range.

Not only might hybrids be expanding their range, but they may also be expanding their numbers. Although documented as rarer than the parental species, currently hybrid abundance is equivalent or greater than one or both parental species at some sites (N.D. Fogarty pers. obs.). A recent increase in hybrid abundance may be a result of an increase in the number of hybrid embryos formed, an increase in asexual fragmentation, and/or higher resistance of the hybrids to the factors that have led to the decline of the parental species.

Through use of field experiments and observations, laboratory experiments, and molecular techniques, this dissertation focused on the importance of hybridization in broadcast spawning clonal organisms. The goals of this dissertation are **(1) to determine the strength of prezygotic mechanisms and to establish the likelihood of density dependent reproductive isolation, (2) to determine the strength of intrinsic and extrinsic postzygotic barriers, and (3) to ascertain if hybrid populations are composed of rare hybridization events that have asexually fragmented, or if colonies are genotypically distinct suggesting separate hybrid events.**

Chapter one is, in part, collaboration with Dr. Steve Vollmer and Dr. Don Levitan. Dr. Vollmer's contribution to chapter one is: (1) genotyping the parental

species prior to the 2005 spawning session, (2) assisting during the 2005 spawning trip to Carrie Bow,(3) genotyping the larvae from 2005 choice experiment, (4) conducting backcross and F2 crosses in Puerto Rico, (5) reviewing drafts of the manuscript (Chapter 2). Dr. Levitan contributed (1) training me how to conduct fertilization experiments, (2) monitoring hybrids for spawning at Carrie Bow in 2005, (3) helped with analyses, and (4) reviewed various stages of the manuscript (Ch. 2). I contributed by writing the grants that made this work possible and by conducting the bulk of the fieldwork, analysis, and writing. Over a five year period, I collected spawning data during 13 trips to five sites, genotyped the 2008 choice experiments, conducted the analyses and wrote the manuscript. I was the sole contributor to chapters 3 and 4.

PREVIEW

CHAPTER 2

WEAK PREZYGOTIC ISOLATING MECHANISMS IN THREATENED CARIBBEAN *ACROPORA* CORALS

2.1 ABSTRACT

The Caribbean corals, *Acropora palmata* and *A. cervicornis*, recently have undergone drastic declines primarily as a result of disease. Previous molecular studies have demonstrated that these species form a hybrid, formerly called *A. prolifera*, and that variability in unidirectional introgression of *A. palmata* genes into *A. cervicornis* exist across loci and across sites. Hybrid abundance varies from rare to locally abundant with no obvious geographic pattern. Here we examine the effectiveness of prezygotic reproductive isolating mechanisms within the Caribbean acroporid system including choice and no-choice fertilization crosses. We show that these species have subtle difference in mean spawning times, but overlapping ranges in spawning time and species-specific differences in gametic incompatibilities. *Acropora palmata* eggs were relatively resistant to hybridization, especially when conspecific sperm are available to outcompete heterospecific sperm. *Acropora cervicornis* eggs demonstrated no evidence for gametic incompatibility. This asymmetry in compatibility matches the genetic data on unidirectional introgression. Our data also suggest that these incomplete prezygotic isolating mechanisms may be density dependent. Under low abundances, eggs may remain unfertilized for longer periods, reducing the effectiveness of conspecific sperm precedence and subtle differences in spawning time in isolating these species.

2.2 INTRODUCTION

Although well established in plants, the evolutionary significance of introgressive hybridization is becoming more widely accepted in animals (Dowling and Secor 1997; Mallet 2005; Arnold 1997, 2006; Arnold and Fogarty 2009). Depending upon the strength of selection and the rate of introgression across loci, the outcome of introgressive hybridization may vary (Hunt and Selander 1973; Harrison 1986; Arnold et al. 1990; and Martinsen et al. 2001). If selection is weak and hybridization rates are high, then genetic swamping may eliminate one or both species, depending upon the directionality of introgression (Rhymer and Simberloff 1996). If there is sufficient selection against deleterious introgressed alleles, however, then the ecological and morphologic identity of the species will be maintained despite some low levels of gene exchange (Barton and Hewitt 1985; Martinsen et al. 2001). Increased genetic diversity from low levels of introgressed alleles may also lead to adaptive shortcuts for the recipient or may lead to reproductive isolation from the parental species resulting in a new species (Grant 1981; Dowling 1997; Riesberg 1997; Arnold 2006).

When ecological conditions change, the balance of selection and introgression may shift, become unstable, and lead to genetic swamping (Rhymer and Simberloff 1996). Anthropogenic activities (i.e. introduced species, excessive killing, and habitat alterations) are often the primary culprits that lead to destabilization of hybrid systems and increased introgression (Rhymer and Simberloff 1996; Dowling and Secor 1997). Natural declines in adult density from disease and predator outbreaks can also affect the degree of hybridization, as can environmental fluctuations that create an inhospitable environment for the parental species or a hospitable zone in which hybrids can thrive (Barton and Hewitt 1985). In many cases, reproductive isolation itself can be density-dependent such that the rarer species of a hybridizing pair is overwhelmed by abundant heterospecifics (Hubbs 1955; Rhymer and Simberloff 1996; Wirtz 1999). Thus