

AN ABSTRACT OF THE DISSERTATION OF

Glenn R. Almany for the degree of Doctor of Philosophy in Zoology presented on May 24, 2002.

Title: Role of Priority Effects and Habitat Complexity in Coral-Reef Fish Communities.

Redacted for privacy

Abstract approved: _____
Mark A. Hixon

Understanding the processes that influence the composition of animal communities is a central goal in ecology. Interactions between established residents and colonizing juveniles that affect the subsequent survival of juveniles may influence community composition. In a series of experiments on coral reef fish communities in the Bahamas and Australia, I tested whether and how interactions between colonizing juveniles and established residents, such as predators and territorial competitors, affected recruitment, and whether these interactions were modified by habitat complexity.

In the Bahamas, I factorially manipulated the presence and absence of resident piscivores and territorial damselfishes on 16 spatially isolated patch reefs and found that both groups had strong, species-specific effects on subsequent recruitment. In a second experiment, I tested whether the aforementioned effects of residents were due to direct interactions between residents and juveniles or were the result of differential juvenile settlement. This was accomplished by repeating the first experiment, except this time placing piscivores and damselfishes within cages to prevent direct interactions. I found no evidence for differential settlement, suggesting that effects of residents were due to direct interactions between residents and juveniles after settlement. In a third experiment, I cross-factored the presence and absence of piscivores and damselfishes with two levels of habitat complexity. I found that juvenile abundance was strongly influenced by prior residents and that

effects of residents did not differ with habitat complexity. In contrast, the abundance of adult fish was strongly influenced by habitat complexity but not residents.

In Australia, I factorially manipulated the presence and absence of resident predators and potential competitors on 20 reefs to determine whether these fish communities were influenced by resident-juvenile interactions comparable to those in the Bahamas. Results were similar to those obtained with the same experimental design in the Bahamas, indicating that priority effects may be a common feature of coral reef fish communities.

These studies illustrate the importance of both habitat complexity and interactions between resident fishes and newly settled juveniles in coral reef fish communities, and provide a means of qualitatively predicting the future composition of these communities based on their current structure.

©Copyright by Glenn R. Almany
May 24, 2002
All Rights Reserved

Role of Priority Effects and Habitat Complexity in Coral-Reef Fish Communities

by

Glenn R. Almany

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented May 24, 2002
Commencement June 2003

Doctor of Philosophy dissertation of Glenn R. Almany presented on May 24, 2002.

APPROVED:

Redacted for privacy

Major Professor, representing Zoology

Redacted for privacy

Chair of the Department of Zoology

Redacted for privacy

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Redacted for privacy

Glenn R. Almany, Author

ACKNOWLEDGMENTS

I have been fortunate to have a number of excellent people as friends and colleagues that have contributed immensely to my degree, and without whom my work would have been impossible. My advisor, Mark Hixon, has been a source of support and inspiration in many ways. I thank him for his insightful conceptual and experimental advice, the endless hours he spent revising my manuscripts and trying to help me become a respectable writer, his patience in entertaining all my wild ideas, and his untiring support during his tenure as my mentor. I also thank him for friendship.

I am especially grateful to Michael Webster, my good friend and fellow graduate student. Michael and I worked closely together on all the work that I report here, and I couldn't have asked for a better colleague and friend. We have spent more time together in the last six years than two people should who aren't married, and through all the endless hours in the field, his sense of humor, tolerance for my eccentricities, and true friendship made the experience a real joy. I am indeed fortunate beyond measure I had Michael to lean on throughout my time as a graduate student.

Although I didn't spend nearly as much time with the other members of my lab, Karen Overholtzer and Barb Byrne have both been important parts of my degree. Karen and I spent lots of time discussing why it all matters and where we fit in to the universe, as well as more mundane subjects like ecology. Somehow she survived all my needling and teasing. Barb was always ready to help me with statistics, and is one of the most generous, thoughtful, and kind-hearted people I know. Her giggle fits in the Bahamas are legendary.

Many other fellow graduate students made my time at Oregon State University a lot of fun, especially Tess Freidenburg and Kirsten Monsen. Tess made an important contribution to my work by keeping Michael from losing his mind, and by collecting data for me when I was ill. Kirsten loved to make her

students cry, and I loved to hear about it. I owe each of them a huge debt of gratitude for taking care of Kitka and Phil while I was in the field – Thank you both!

I thank my parents, Tom and Linda Almany, and the rest of my family, for all their love and support through my many years in the higher education system, even when they couldn't understand how someone could spend so much time studying fish. I thank Jeanine Stier for her support, patience, and love. She has made this all worthwhile.

I am grateful to the staff and interns at both the Caribbean Marine Research Center and the Lizard Island Research Station for their logistical support. I thank M. Hixon and M. Carr for the use of their experimental reefs (Chapters 2 and 4), and M. Hixon and G. Jones for the use of their reefs (Chapter 3). I also thank T. Anderson, K. Overholtzer, M. Webster, and my graduate committee for constructive reviews of my manuscripts.

Financial support for this work was provided by an NSF Graduate Predoctoral Fellowship, OSU Zoology Research Funds, a Sigma Xi Grant-in-Aid of Research, and a PADI grant to the author, and by NSF grants (OCE-96-17483 and OCE-00-93976) and NOAA-NURP grants (CMRC-95-3042 and CMRC-97-3109) to M. Hixon.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: GENERAL INTRODUCTION.....	1
CHAPTER 2: PRIORITY EFFECTS IN CORAL REEF FISH COMMUNITIES.....	5
ABSTRACT.....	5
INTRODUCTION.....	6
METHODS.....	9
Study site.....	9
Study species.....	11
Effects of prior residents.....	11
Mechanisms underlying prior-resident effects.....	13
Data analysis.....	15
RESULTS.....	16
Effects of prior residents.....	16
Timing of mortality.....	20
Mechanisms underlying prior-resident effects.....	21
DISCUSSION.....	24
How do resident piscivores and territorial damselfish affect recruitment?.....	24
Do larvae use piscivores or territorial damselfish as settlement or avoidance cues?.....	26
When does mortality occur during recruitment?.....	27
Conclusions: is future community structure predictable?.....	28
CHAPTER 3: PRIORITY EFFECTS IN CORAL REEF FISH COMMUNITIES: GENERALITIES BETWEEN AUSTRALIA AND THE BAHAMAS	30
ABSTRACT.....	30
INTRODUCTION.....	31
METHODS.....	34
Study site.....	34

TABLE OF CONTENTS (continued)

	<u>Page</u>
Study species.....	36
Experimental design.....	36
Data analysis.....	38
RESULTS.....	40
Recruitment	40
Final recruit abundance.....	41
Recruit mortality.....	46
Species richness of final recruit assemblages and measurements of habitat complexity.....	47
DISCUSSION.....	48
Priority effects on recruitment: comparison with Bahamian reefs.....	48
Are priority effects common in coral reef fish communities?.....	54
 CHAPTER 4: DIFFERENTIAL RESPONSES OF JUVENILE AND ADULT CORAL REEF FISHES TO HABITAT COMPLEXITY AND PRIOR RESIDENCY BY PREDATORS AND COMPETITORS	 56
ABSTRACT.....	56
INTRODUCTION.....	57
METHODS.....	60
Study site.....	60
Study species.....	62
Experimental design	63
Data analysis.....	65
RESULTS.....	67
Effects of habitat complexity alone	67
Effects of both habitat complexity and prior residents.....	68
Habitat complexity and fish body depth	73
DISCUSSION.....	76
Effects of habitat complexity and prior residents on recruits.....	76
Effects of habitat complexity and prior residents on adults	79

TABLE OF CONTENTS (continued)

	<u>Page</u>
Conclusions: ontogenetic shifts in predation risk.....	81
CHAPTER 5: GENERAL CONCLUSIONS.....	83
BIBLIOGRAPHY.....	89

LIST OF FIGURES

<u>Fig.</u>		<u>Page</u>
2.1	Study site.....	10
2.2	Fish enclosure used to examine mechanisms underlying prior-resident effects	14
2.3	Differential effects of prior residents on recruitment of four species	17
2.4	Mechanisms underlying effects of prior-residents on recruitment	22
3.1	Study site.....	35
3.2	Differential effects of prior residents on the abundance of damselfish (Pomacentridae) recruits.....	43
3.3	Differential effects of prior residents on butterflyfish (Chaetodontidae), surgeonfish (Acanthuridae), and rabbitfish (Siganidae) recruitment...	45
3.4	Effects of prior resident adult damselfish on mortality of damselfish recruits.....	46
4.1	Study site.....	61
4.2	Relationships between habitat complexity and abundance of adult fishes.....	67
4.3	Effects of habitat complexity and prior residency by piscivores and adult damselfishes on recruitment of the beaugregory damselfish, <i>Stegastes leucostictus</i>	69

LIST OF FIGURES (continued)

<u>Fig.</u>		<u>Page</u>
4.4	Effects of habitat complexity and prior residency by piscivores and adult damselfishes on mortality of beaugregory damselfish (<i>Stegastes leucostictus</i>) recruits.....	71
4.5	Comparison of frequency distributions of hole diameter and body depths of all adult squirrelfishes, parrotfishes, and goatfishes on low and high complexity reefs.....	73
4.6	Frequency distributions of hole diameter and body depths of resident piscivores and adult territorial damselfishes.....	75

LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1 Differential effects of prior residents on the recruitment of three species	19
3.1 Recruitment during the 50-day experiment	42

ROLE OF PRIORITY EFFECTS AND HABITAT COMPLEXITY IN CORAL-REEF FISH COMMUNITIES

CHAPTER 1: GENERAL INTRODUCTION

Understanding the processes that structure ecological communities has long been a goal of ecologists, in part because such understanding permits predictions about how communities will respond to natural and unnatural events. As anthropogenic threats to the environment increase in both frequency and intensity, efforts to preserve and protect natural communities are strengthened by an increased understanding of how these systems function. My research has focused on understanding the processes that determine the composition of coral reef fish communities. Studies of coral reef fishes have played a central role in the development of ecological theory, and continue to provide a wealth of research opportunities for ecologists.

Like most marine species, nearly all reef fishes produce planktonic larvae that spend weeks to months in the pelagic environment (Leis 1991, Victor 1991). Larvae disperse from their natal reefs in oceanic currents, although recent studies provide evidence that some larvae are locally retained at the scale of oceanic islands (Jones et al. 1999, Swearer et al. 1999). Larvae typically make a nocturnal transition from the plankton to reef or near-reef habitats, a process called "settlement" (Victor 1991). After settlement, counted juveniles are called "recruits", and the net process of settlement minus subsequent mortality is called "recruitment". Because reef fishes have two distinct phases in their life history, a pelagic larval stage and a sedentary juvenile and adult stage, processes that affect either stage can generate patterns of abundance and distribution.

The earliest theory about how reef fish communities are structured borrowed heavily from theories developed in terrestrial systems. Reef fish

populations were assumed to be at carrying capacity, and that competition among benthic adults for limited living space drove patterns of abundance, distribution, and diversity (Smith and Tyler 1972, Ehrlich 1975). In a series of papers, Sale (1974, 1977, 1978) proposed an alternative model, called the lottery hypothesis, which shifted attention to processes occurring during the pelagic larval stage. Sale retained the assumption that populations were at carrying capacity and that competition between benthic adults occurred, but suggested that patterns of change in reef fish communities were driven by variable and unpredictable larval supply rather than competition between benthic juveniles and adults. In Sale's view, the random provision of unoccupied living space combined with variable larval settlement to unoccupied patches resulted in a stochastic and unpredictable assemblage of species. Other theories challenged the assumption that reef fish populations were at carrying capacity, and thus suggested that competition among benthic fishes was less important. For example, intense predation on benthic juveniles and adults could prevent populations from ever reaching a size where competition is important (Talbot et al. 1978, review by Hixon 1991). Doherty (1981) and Victor (1983) proposed the "recruitment limitation hypothesis", which suggested that larval supply was generally insufficient to allow populations to reach carrying capacity. In summary, the development of theory in coral reef fish ecology has centered on the debate over the relative importance of processes occurring during the pelagic larval stage and those occurring during the benthic juvenile and adult stages (review by Jones 1991). More recently, empirical studies have demonstrated that the relative importance of various processes often changes from one location to another and from one time period to the next. As a result, many reef fish ecologists have rejected single-factor theories and called for multifactor studies to determine the relative importance of each process (reviews by Hixon 1991, Jones 1991).

The research contained in this dissertation focuses on how early postsettlement interactions between newly settled juveniles and resident fishes,

such as predation and competition, influence the composition of coral reef fish communities. By testing two or more factors at the same time in each experiment, I have attempted to determine whether processes act independently or together to generate patterns of abundance and distribution. I have thus attempted to maintain a multifactor perspective throughout my research.

In Chapter 2, I used two experiments to test whether and how prior residency by predators (groupers and moray eels) and interference competitors (territorial damselfishes) affected the subsequent recruitment of reef fishes on a matrix of patch reefs in the Bahamas. In the first experiment, I found that prior residency by predators inhibited recruitment of a damselfish and surgeonfish, and enhanced recruitment of a wrasse. In contrast, prior residency by interference competitors inhibited recruitment of the damselfish and wrasse, and enhanced recruitment of the surgeonfish. In the second experiment, I tested whether the aforementioned effects of residents were a result of direct interactions between newly settled recruits and residents (i.e., predation and competition), or the result of differential larval settlement among reefs with different resident assemblages. I found no evidence for differential settlement, and thus recruitment patterns appear to have been caused by direct interactions between recruits and residents. Furthermore, differences in recruitment were established rapidly, within 24 hours of settlement.

In Chapter 3, I examined the effects of prior residency by predators (groupers and dottybacks) and competitors (adult damselfishes) on a series of patch reefs on the Great Barrier Reef, Australia. My goal was to determine whether Australian reef fish communities were influenced by the same early postsettlement interactions between recruits and residents that influenced Bahamian reef fish communities. I found that prior residency by predators caused decreased recruitment of damselfishes, surgeonfishes, butterflyfishes, and rabbitfishes, increased recruit mortality, and decreased recruit species richness. In contrast, prior residency by competitors decreased recruitment of damselfishes and

rabbitfishes, but did not affect recruitment of butterflyfishes and surgeonfishes, recruit mortality, or recruit species richness. Furthermore, recruitment patterns were established rapidly, within 48 hours of settlement. Effects of prior residency by predators and competitors were qualitatively similar to those documented on Bahamian reefs, suggesting that resident-recruit interactions may be of general importance in coral reef fish communities.

In Chapter 4, I tested whether prior residency by resident predators and competitors affected the abundance of both recruit and adult fishes, and whether these effects differed among Bahamian patch reefs that were either low or high habitat complexity. Resident predators and competitors had strong negative effects on the abundance of recruits regardless of habitat complexity, while increased habitat complexity had a weak positive effect on recruit abundance. In contrast, increased habitat complexity had strong positive effects on the abundance of adult fishes, while resident predators and competitors had no effect on adult abundance.

The common theme in these studies is that early postsettlement processes play an important role in coral reef fish communities, and that interactions among processes are common. In addition, despite important differences between Australian and Bahamian coral reef fish communities, these communities appear to be affected by similar processes. By demonstrating that habitat complexity and prior residency by predators and competitors influence the dynamics of reef fish communities, and that the effects of these factors are species- or family-specific, these studies strengthen our ability to predict how coral reef fish communities are likely to respond to events that affect habitat complexity and the abundance of predators and competitors on coral reefs.

CHAPTER 2: PRIORITY EFFECTS IN CORAL REEF FISH COMMUNITIES

ABSTRACT

Predicting the future composition of demographically open communities is difficult because the total and relative abundance of colonizing juveniles is often unrelated to current community structure. However, if prior residents affect juvenile survival in species-specific ways, then understanding resident-juvenile interactions may permit such predictions.

Using 16 spatially isolated communities of coral reef fishes in the Bahamas, I conducted two experiments to determine how two guilds of resident fishes affect recruitment, and thus influence subsequent community structure. Each experiment examined the effects of the presence and absence of two factorially manipulated guilds: resident piscivores (groupers and moray eels) and interference competitors (territorial damselfishes). In the first experiment, guilds were manipulated via selective removals, and subsequent juvenile recruitment (larval settlement minus mortality) was monitored over 44 days. In the second experiment, guilds were placed within large cages to prevent direct resident-juvenile interactions, while allowing for any cues produced by enclosed fishes, thereby testing whether incoming larvae used resident-derived cues in selecting or avoiding reefs. Colonizing juveniles were collected from each reef over 42 days to prevent confounding resident- and recruit-derived cues.

In the first experiment, piscivores inhibited recruitment of a damselfish (Pomacentridae) and a surgeonfish (Acanthuridae), and enhanced recruitment of a wrasse (Labridae), perhaps because of the latter's role as a cleaner fish. In contrast, adult territorial damselfish caused lower recruitment of the damselfish and the wrasse, and enhanced recruitment of the surgeonfish, perhaps because the latter

was incidentally protected by damselfish aggression. Observations of early recruit mortality suggested that recruitment differences were established rapidly during the night or dawn periods shortly after settlement and before each daily census. In the second experiment, there was no evidence that larvae used resident-derived cues to select settlement sites, suggesting that recruitment differences in the first experiment were caused by direct resident-recruit interactions rather than differential larval settlement.

Besides demonstrating the importance of resident-recruit interactions, these results provide a means of qualitatively predicting future structure in these open communities because resident effects were species-specific. Thus, the present composition of coral reef fish communities can impose a previously undocumented degree of determinism on their future structure.

INTRODUCTION

A fundamental goal of ecology is predicting the future composition and relative abundance of species within a community (Morin 1999). In relatively closed and isolated communities where immigration and emigration are negligible, future structure is largely dependent on the present relative abundance of species, their reproductive output, and subsequent offspring survival. Consequently, understanding how abiotic factors and biotic interactions affect subsequent juvenile survival allows one to predict the future structure of these communities. In contrast, relatively open communities (e.g., most marine communities, as well as plant and insect communities with dispersive life-history stages) depend on external sources for most incoming juveniles (reviews by Sale 1991, Connolly and Roughgarden 1999, Knowlton and Jackson 2001). Juvenile supply is usually spatially and temporally unpredictable such that adjacent communities often receive different assemblages of incoming juveniles (reviews by Knowlton and

Jackson 2001, Morgan 2001). As a result, there is usually little relationship between the relative abundance of these juveniles and the current structure of the community (review by Morgan 2001).

Although the supply of juveniles may be unpredictable, various processes influence their survival after arriving and may strongly alter initial patterns of relative abundance. For example, established community residents may consume or compete with juveniles, thereby inhibiting their establishment in the community (e.g., Wilbur and Alford 1985, Lawler and Morin 1993, Ostfeld et al. 1997). Furthermore, if potential competitors arrive at different times, the interaction between them may shift from competition to predation as older, larger colonists consume smaller new arrivals (Blaustein and Margalit 1996). These "priority effects", in which established individuals affect those that arrive later, have been documented in plants (e.g., Huston and Smith 1987, Burrows 1990, Bertness and Shumway 1993), sessile marine organisms (e.g., Connell 1961, Sousa 1979, Menge and Sutherland 1987), coral reef fishes (e.g., Shulman et al. 1983, Sweatman 1985, Steele 1997), and amphibians (e.g., Alford and Wilbur 1985, Wilbur and Alford 1985, Lawler and Morin 1993). If these interactions are predictable, strong, and species-specific, a community's current structure can impose a level of determinism on its future structure.

Assemblages of coral reef fishes are classic examples of open communities (review by Sale 1991). Like most marine species, reef fishes produce planktonic larvae that spend weeks to months in the pelagic environment (Leis 1991, Victor 1991). Larvae disperse from their natal reefs in oceanic currents, although recent studies provide evidence that some larvae are locally retained at the scale of oceanic islands (Jones et al. 1999, Swearer et al. 1999). Larvae typically make a nocturnal transition from the plankton to reef or near-reef habitats, a process called "settlement" (Victor 1991). After settlement, counted juveniles are called "recruits", and the net process of settlement minus subsequent mortality until census is called "recruitment". A much-debated issue concerns the extent to which

patterns of relative abundance at settlement are reflected in future community structure (reviews by Doherty and Williams 1988, Hixon 1991, Jones 1991, Sale 1991, Ault and Johnson 1998b). That is, do initial patterns persist, or do processes modify them after settlement?

One prominent view of reef fish communities is that they are unpredictable assemblages driven by stochastic larval settlement (Sale 1980, Sale and Douglas 1984, Sale et al. 1994). However, the role of prior residents in determining subsequent community structure has seldom been explored, even though studies have demonstrated that residents can affect both settlement and recruitment. For example, some reef fish larvae select settlement sites based on the presence of conspecifics or particular types of habitat, which they detect via chemical or visual cues (Sweatman 1988, Booth 1992, Elliot et al. 1995, Danilowicz 1996). Settlement site selection in these studies occurred at the scale of individual coral heads, which could lead to distinct between-reef and within-reef patterns of recruitment. Effects of prior residents on subsequent recruitment appear to be common. For example, resident territorial damselfishes can inhibit heterospecific recruitment (Shulman et al. 1983, Sweatman 1983, 1985, Jones 1987, Risk 1998), and either facilitate (Sweatman 1983, 1985, Jones 1987, Booth 1992) or inhibit (Sale 1976) conspecific recruitment. Resident predators generally inhibit recruitment and cause increased recruit mortality (Shulman et al. 1983, Caley 1993, Carr and Hixon 1995, Beets 1997, Hixon and Carr 1997). However, in studies documenting effects of residents on recruitment, it was unclear whether effects were due to differential larval settlement or differential recruit mortality.

Here I present results from two related field experiments that tested whether and how prior residency by two guilds of fishes affected subsequent recruitment. I identified two guilds of residents likely to influence recruit survival: "resident piscivores", including groupers and moray eels, and "interference competitors", consisting of highly territorial damselfish. The first experiment addressed two questions: (1) does prior residence of these guilds affect recruitment, and (2) when

are recruitment patterns established? I found strong evidence that both guilds affected recruitment and that effects were species-specific. Recruitment differences among treatments were established rapidly by high recruit mortality during the night of settlement, or perhaps the following dawn, and before morning censuses. In the second experiment, I explored the mechanism by which residents affect recruitment. I tested whether settling larvae selected settlement sites based on the presence or absence of the two guilds. Specifically, I evaluated the hypotheses that (1) larvae select between reefs, (2) larvae select sites within reefs, and (3) larger larvae are more selective than smaller larvae. I found no evidence to support any of these hypotheses, indicating that prior residents affected recruitment via differential recruit mortality rather than differential larval settlement.

METHODS

Study site

The study was conducted near the Caribbean Marine Research Center at Lee Stocking Island, Bahamas. This site is located in the Exuma archipelago, which separates the shallow Great Bahama Bank to the west from the deep waters (> 2000 m) of the Exuma Sound to the east (Fig. 2.1A). All experiments were performed on a unique matrix of live-coral patch reefs that were translocated to a shallow sand flat on the leeward side of Norman's Pond Cay between 1991 and 1994 (Carr and Hixon 1995, Hixon and Carr 1997). The matrix included 32 reefs in five rows, at depths between 2 and 5 meters. Each reef consisted of 9 to 13 coral heads (mean = 10.8, SD = 1.5) of primarily three coral species: *Montastrea annularis*, *Porites asteroides*, and *Siderastrea siderea*. Average reef area was 6.6 m² (SD = 1.0 m²) and mean height was 0.5 m (SD = 0.07 m). Reefs supported fish communities indistinguishable from those on nearby (within 5 km) non-

manipulated patch reefs of similar size (*personal observation*). Each reef was separated from all others by 200 m of sand and seagrass and the closest naturally occurring reef was more than 1 km from the edge of the matrix. Therefore, the disappearance of any new recruit from a reef could be attributed only to mortality.

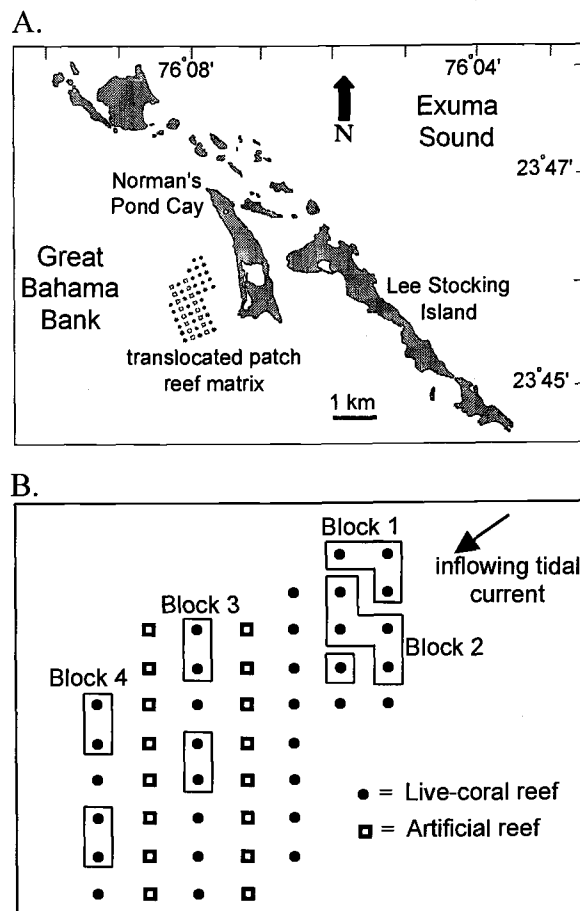


Figure 2.1: Study site. (A) Position of translocated patch reefs with respect to nearby islands. (B) Spatial arrangement of reefs and the blocking scheme of live-coral reefs used in both experiments. Unused artificial reefs were constructed of concrete blocks. Each reef is separated from its closest neighbor by 200 meters.

Study species

Tagging studies demonstrated that resident fish seldom moved between reefs in the matrix, with the exception of several transient predators (mostly jacks [*Caranx* spp.] and snappers [*Lutjanus* spp.]) (M. A. Hixon, *personal communication*). Therefore, each reef was considered an independent experimental unit. Resident piscivores were identified using two criteria: (1) a diet of at least 10% fishes by volume (Randall 1967) and (2) a strong tendency to retreat to the reef (as opposed to fleeing) when approached by a diver. The five resident piscivores included three diurnally active groupers (Serranidae: *Cephalopholis cruentata* [graysby], *C. fulva* [coney], and *Epinephelus striatus* [Nassau grouper]), and two nocturnally active moray eels (Muraenidae: *Gymnothorax moringa* [spotted moray] and *G. vicinus* [purplemouth moray]). There were two species of territorial damselfish: *Stegastes leucostictus* [beaugregory] and *S. partitus* [bicolor]. Adults of both species are aggressive towards nearly all other fishes (Robertson 1996). *Stegastes leucostictus* is omnivorous, consuming algae, detritus, polychaetes, and fish material, whereas *S. partitus* is primarily planktivorous (Randall 1967, Emery 1973).

Effects of prior residents

To determine the effects of resident piscivores and territorial damselfishes on subsequent recruitment, I factorially manipulated the presence and absence of these two guilds on 16 of the 32 translocated patch reefs during the 1997 summer settlement season. I selected four blocks of reefs, each block consisting of four reefs, using two criteria: (1) reefs within each block had similar naturally occurring communities of fishes, which minimized confounding effects of variable species composition, and (2) reefs within a block were close to each other, which

minimized confounding effects of variable larval supply. To meet these criteria, I compared the fish communities on all 32 reefs prior to any manipulation using Cluster Analysis (Bray-Curtis Distance and Group Average) and combined this analysis with reef location to select the best arrangement of reefs and blocks (Fig. 2.1B). Piscivore and damselfish densities varied among blocks, but were similar within blocks, and reflected the natural range of densities in the reef matrix prior to manipulations. Reefs were randomly assigned treatments within each block. There were four experimental treatments ($n = 4$ reefs each): piscivores and damselfish both present (P+D+); piscivores present, damselfish absent (P+D-); piscivores absent, damselfish present (P-D+); and both piscivores and damselfish absent (P-D-).

Using SCUBA, I manipulated resident piscivores and damselfish using the fish anesthetic quinaldine, hand nets, and a BINCKE net (Anderson and Carr 1998). After removing all recruits from each reef at the start of the experiment, I monitored subsequent cumulative recruitment by conducting a visual census of each reef approximately daily for 44 days. Recruits that had settled the previous night were identified by their incomplete pigmentation and small size and recorded as "new settlers." Mortality during the experiment was estimated by subtracting the number of disappearances from the number of observed new settlers. Settlement and mortality of wrasse were not estimated because newly settled wrasse could not be reliably distinguished from those that had settled the previous several days. During each census, I verified treatment conditions and removed any piscivore and adult damselfish immigrants. Immigration to the 16 reefs was negligible during the 44-day experiment (total of four piscivores and five adult damselfish).

To determine when recruitment patterns were established relative to nocturnal settlement events, I tested whether mortality was relatively high during the first few hours of daylight postsettlement by comparing the number of new settlers recorded during early (0800 – 0900) vs. late (1100 – 1200) morning censuses. I conducted recruitment censuses each day (ca. 15 min per reef) between

0800 and 1200. I divided the 16 reefs into four rows such that each row contained all four treatments to prevent confounding treatment with time-of-day. I systematically varied row censuses such that each row was censused in the early morning (0800 to 0900) every fourth day.

Mechanisms underlying prior-resident effects

The goal of the second experiment, conducted during the 1998 summer settlement season, was to determine whether recruitment differences observed in the first experiment were due to differential larval settlement or differential recruit mortality. The experimental design was identical to that of the first experiment except that piscivores and damselfish were placed in large plastic mesh enclosures in the center of the reef. Small coral heads and rubble were placed inside the enclosures to provide shelter for occupants, and coral heads that provided settlement habitat for recruits surrounded each enclosure. This manipulation eliminated direct interactions between enclosed fish and recruits outside cages, but retained any cues produced by enclosed fish that could be used by incoming larvae in selecting or rejecting a settlement site.

Each enclosure consisted of a cylindrical frame of metal re-bar (1.25-cm diameter) covered with plastic mesh (1.9-cm mesh "vexar"). New recruits could pass through this mesh. Enclosures had a diameter of 165 cm and a height of 65 cm (total volume = 1.4 m³) and each had an internal divider of vexar (Fig. 2.2). All enclosures were identical regardless of treatment.

I used the same reefs and blocks as in the first experiment and randomly re-assigned treatments (P+D+, P+D-, P-D+, or P-D-) to reefs within each block with the constraint that each reef's treatment differed from its treatment in the first experiment, thereby controlling for any location effects between experiments. Each

piscivore-present (P+) enclosure contained the average piscivore assemblage found on pre-manipulated reefs: two *Epinephelus striatus*, one *Cephalopholis cruentata*

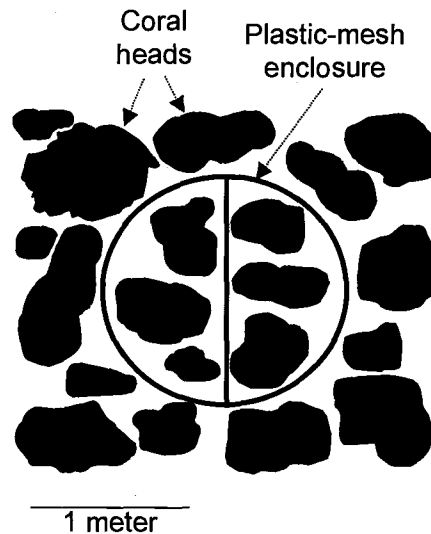


Figure 2.2: Fish enclosure used to examine mechanisms underlying prior-resident effects. View of a single reef showing the arrangement of the enclosure and coral heads. Each plastic-mesh enclosure had an internal divider to keep piscivores and damselfish separated in treatments where both were present, and each contained coral heads and rubble for shelter. Live coral heads outside enclosures served as settlement habitat for incoming larvae.

or *C. fulva*, and one *Gymnothorax moringa* or *G. vicinus*. Each damselfish-present (D+) enclosure contained the average damselfish assemblage on pre-manipulated reefs: two adult *Stegastes leucostictus* and two adult *S. partitus*. Where piscivores and damselfish occurred together (P+D+), each group occupied one half of the enclosure. Where piscivores occurred alone (P+D-), the two *E. striatus* were placed in one half and the *C. cruentata* or *C. fulva* and moray eel occupied the other. Where damselfish occurred alone (P-D+), each species occupied one half of the enclosure. Preliminary trials showed that this arrangement resulted in the

fewest antagonistic interactions between enclosed individuals. In most cases, prior residents from the same reef were used to stock the enclosure on that reef. Reefs where both piscivores and damselfish (P-D-) were removed had empty enclosures. Enclosed fishes generally showed no adverse effects of confinement and appeared to behave normally. During periods of predictably low settlement (i.e., full moon), I fed enclosed piscivores pieces of fish and small swimming crabs (Portunidae). Enclosed damselfish fed normally from enclosed coral heads or passing plankton.

I conducted a visual census of each experimental reef every other day for 42 days. During each census, I removed any recruits that had recently settled, using hand-nets and quinaldine, to eliminate any cues from recruits that might influence subsequent settlement and thus confound treatment effects. Prior to capture, I noted the position of each settler relative to the two sections of the enclosure on the two damselfish-present treatments (P+D+ and P-D+) to determine if there were any effects of enclosed fish on within-reef settlement location. I collected a random sample ($n = 25$ to 52 individuals per species) of newly settled recruits from the most abundant species in each family and measured each individual's total length (TL) to the nearest 0.1 mm using dial calipers.

Data analysis

In the first experiment, designed to test for prior-resident effects, I compared differences in recruitment among treatments with two-way ANOVA (model terms: Blocks, Piscivores, Damselfish, and Piscivore-Damselfish interaction) (Sokal and Rohlf 1995). When interaction terms were significant ($P \leq 0.05$), I conducted a linear contrast of the means for each pairwise treatment comparison (Ramsey and Schafer 1997). When interaction terms had P -values ≥ 0.20 , I removed the interaction term and analyzed the additive model (model terms: Blocks, Piscivores, and Damselfish). When ANOVA F-tests were not significant

($P > 0.05$), I calculated the statistical power (θ) of the test to detect an actual difference of one fish among treatments. To analyze differences in recruitment, I compared the average number of recruits on each treatment on the last day of the experiment (day 44). I chose this response for three reasons: (1) final recruit density is logically the best predictor of future community structure, (2) recruitment patterns continued to diverge at the conclusion of the experiment, and (3) final recruit density was consistent with the recruitment trajectory observed throughout the study. In the second experiment, designed to test the underlying mechanisms of prior-resident effects, I used the same two-way ANOVA procedure to compare the total number of recruits collected from each treatment during the experiment. I compared the average total lengths (TL) of recruits among treatments with one-way ANOVA. When ANOVA F-tests were not significant ($P > 0.05$), I calculated the power of the test to detect an actual difference among treatments of 20% of the observed range of total length for each species. I analyzed within-reef differences in settlement location with a Binomial Test (Sokal and Rohlf 1995). To insure that ANOVA assumptions were met, I tested for homogeneity of variance using Levene's Test and examined normal probability plots (Ramsey and Schafer 1997). When ANOVA F-tests were significant ($P \leq 0.05$), I estimated effect sizes and calculated 95% confidence intervals (Zar 1999). All statistical analyses were conducted using SAS Institute statistical software (SAS version 6.12 and JMP version 4.0).

RESULTS

Effects of prior residents

During the 44-day duration of this experiment, I observed 340 new settlers representing 22 species, more than 90% of which were from three families:

Pomacentridae (130 damselfish recruits), Acanthuridae (28 surgeonfish recruits), and Labridae (150 wrasse recruits). Resident piscivores and territorial damselfish differentially affected recruitment of the most abundant species in each family.

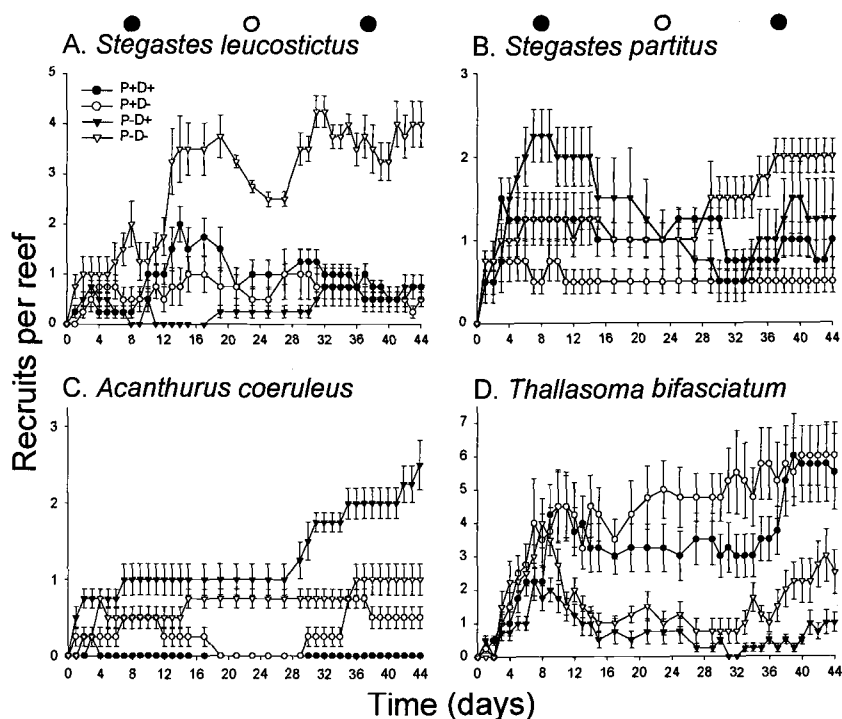


Figure 2.3: Differential effects of prior residents on recruitment of four species. Relationship between cumulative recruitment (larval settlement minus mortality) and experimental treatments ($n = 4$ reefs each) for the most abundant species in three families: (A) *Stegastes leucostictus* and (B) *Stegastes partitus* (Pomacentridae), (C) *Acanthurus coeruleus* (Acanthuridae), and (D) *Thalassoma bifasciatum* (Labridae). Treatments consisted of presence (+) or absence (-) of resident piscivores (P) and adult territorial damselfish (D). Error bars are \pm SE. The circles at the top of each column correspond to dates of the new moon (●) and full moon (○). Note that Y-axis scale varies among plots.

Damselfish recruitment – Most of the 130 newly settled damselfish were from two species: the beaugregory damselfish, *Stegastes leucostictus* (79 recruits), and the bicolor damselfish, *S. partitus* (42 recruits). Both piscivores and adult

territorial damselfish significantly affected *S. leucostictus* recruitment, and there was a significant interaction (Fig. 2.3A; two-way ANOVA: interaction $P = 0.021$). In the absence of adult damselfish, piscivores reduced recruitment by an average (\pm 95% CI) of 3.5 ± 2.0 recruits per reef (linear contrast: $P = 0.003$). In the absence of piscivores, adult damselfish reduced recruitment by 3.3 ± 2.0 recruits per reef (linear contrast: $P = 0.005$), while piscivores and adult damselfish together reduced recruitment by 3.3 ± 2.0 recruits per reef (linear contrast: $P = 0.005$). The number of observed new settlers was highest, and their subsequent mortality lowest, where both piscivores and adult damselfish had been removed (Table 2.1A). Recruitment of *S. partitus* was low, highly variable, and did not differ significantly among treatments (Fig. 2.3B; two-way ANOVA: $P = 0.590$, $\theta = 0.77$). The number of observed new settlers was highest where only adult damselfish were present (Table 2.1B). Low recruitment precluded comparisons of recruit mortality.

Table 2.1: Differential effects of prior residents on the recruitment of three species. The number of observed new settlers and their subsequent mortality during the experiment (44 days) for (A) *Stegastes leucostictus*, (B) *Stegastes partitus*, and (C) *Acanthurus coeruleus*.

Species	Treatment ¹	Number of observed new settlers	Number of disappearances (% mortality) ²
<i>A. S. leucostictus</i>	P+D+	18	15 (83.3)
	P+D-	14	12 (85.7)
	P-D+	9	6 (66.7)
	P-D-	38	22 (57.9)
<i>B. S. partitus</i>	P+D+	9	5 (55.6)
	P+D-	4	2 (50.0)
	P-D+	16	11 (68.8)
	P-D-	13	5 (38.5)
<i>C. A. coeruleus</i>	P+D+	1	1 (100.0)
	P+D-	5	3 (60.0)
	P-D+	10	0 (0.0)
	P-D-	5	1 (20.0)

¹P = predators, D = damselfish, + = present, - = absent.

²Note: Total % mortality = (total deaths/total new settlers) X 100.

Surgeonfish recruitment – Of 28 newly settled surgeonfish, 21 were *Acanthurus coeruleus* (blue tang). Piscivores and adult territorial damselfish both significantly affected recruitment of *A. coeruleus*, and there was a significant interaction (Fig. 2.3C; two-way ANOVA: interaction $P = 0.020$). In the absence of piscivores, adult damselfish increased recruitment by an average ($\pm 95\%$ CI) of 1.5 ± 0.8 recruits per reef (linear contrast: $P = 0.015$). In the absence of adult damselfish, piscivores decreased recruitment by 0.5 ± 0.8 recruits per reef (linear contrast: $P = 0.343$). There was no surgeonfish recruitment where both piscivores and adult damselfish were present. The number of observed new settlers was

highest where only adult damselfish were present (Table 2.1C). Low recruitment precluded comparisons of recruit mortality.

Wrasse recruitment – Of 150 newly settled wrasse, 127 were *Thalassoma bifasciatum* (bluehead wrasse). Recruitment of *T. bifasciatum* was significantly influenced by piscivores, independent of adult damselfish, and differed among blocks (Fig. 2.3D; two-way ANOVA: piscivores $P = 0.004$, damselfish $P = 0.371$, blocks $P = 0.011$). Piscivores increased recruitment by an average (\pm 95% CI) of 4.0 ± 2.4 recruits per reef. The average (SD) number of recruits per reef in each block was as follows: block 1 = 6.8 (4.9), block 2 = 1.0 (2.0), block 3 = 2.0 (2.2), and block 4 = 5.3 (2.2). The number of observed new settlers, and their subsequent mortality, was not estimated due to the difficulty in distinguishing newly settled wrasse from those that had settled the previous several days.

Timing of mortality

The number of new settlers observed between early (8 am - 9 am) and late (11 am - noon) morning was similar for each category of recruits (early morning counts: all species = 50, *S. leucostictus* = 21, *S. partitus* = 10, *A. coeruleus* = 4; late morning counts: all species = 60, *S. leucostictus* = 20, *S. partitus* = 10, *A. coeruleus* = 6), indicating that mortality was negligible between these two periods.

Comparisons of early and late morning counts of wrasse were again precluded by the difficulty in distinguishing newly settled wrasse from those that had settled the previous several days.

Mechanisms underlying prior-resident effects

During the 42-day duration of this experiment, I collected 488 recruits from 25 species, more than 90% of which were from four families: Pomacentridae (153 damselfish recruits), Acanthuridae (53 surgeonfish recruits), Labridae (164 wrasse recruits), and Pomacanthidae (72 angelfish recruits).

Damselfish recruitment – Of 153 damselfish recruits, 105 were *Stegastes leucostictus* (beaugregory) and 28 were *S. partitus* (bicolor). The average number of recruits per reef did not differ significantly among treatments for either species (Fig. 2.4; two-way ANOVA: *S. leucostictus*, $P = 0.560$, $\theta = 0.48$; *S. partitus*, $P = 0.180$, $\theta = 0.66$). Average total length of *S. leucostictus* recruits did not differ among treatments (one-way ANOVA: $P = 0.328$, $\theta = 0.90$).

Within-reef location with respect to enclosed fishes was noted for all *S. leucostictus* and *S. partitus* recruits collected from the two treatments where adult damselfish were present (P+D+ and P-D+). On P+D+ reefs, *S. leucostictus* recruits were evenly distributed (near piscivores = 12, near damselfish = 13). On P-D+ reefs, more than twice as many *S. leucostictus* recruits were collected adjacent to adult *S. leucostictus* (near *S. leucostictus* = 17, near *S. partitus* = 8), a difference that was marginally significant (Binomial Test: $P = 0.054$). On P+D+ reefs, *S. partitus* recruits were evenly distributed (near piscivores = 6, near damselfish = 5), while recruitment to P-D+ reefs was low (near *S. leucostictus* = 0, near *S. partitus* = 1).

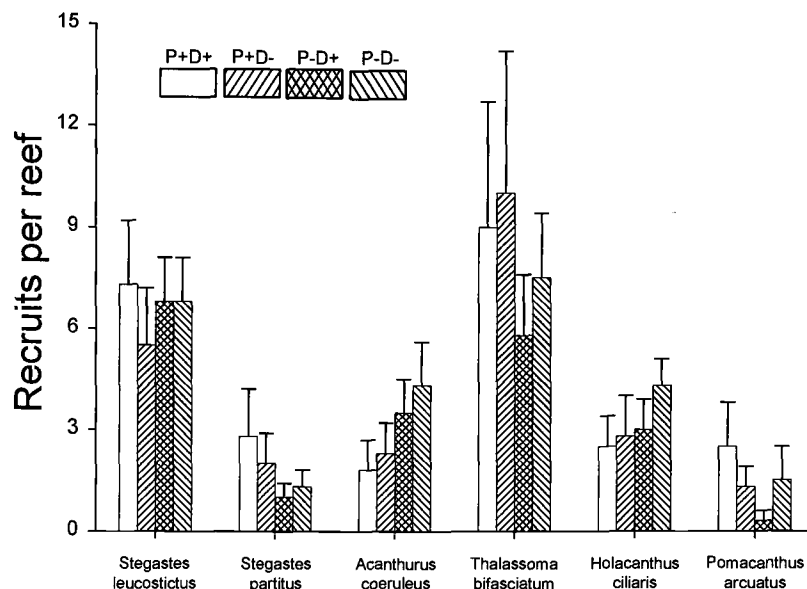


Figure 2.4: Mechanisms underlying effects of prior-residents on recruitment. Relationship between the average (+ SE) number of recruits collected per reef over 42 days in each experimental treatment ($n = 4$ reefs each) for the most abundant species in four families: *Stegastes leucostictus* and *Stegastes partitus* (Pomacentridae), *Acanthurus coeruleus* (Acanthuridae), *Thalassoma bifasciatum* (Labridae), and *Holacanthus ciliaris* and *Pomacanthus arcuatus* (Pomacanthidae). Treatments consisted of plastic mesh enclosures that contained (+) or did not contain (-) resident piscivores (P) and adult territorial damselfish (D). There were no significant differences among treatments, indicating no differential settlement due to prior-resident cues (see text).

Surgeonfish recruitment – Of 53 surgeonfish recruits, 47 were *Acanthurus coeruleus* (blue tang). The average number of *A. coeruleus* recruits per reef did not differ significantly among treatments (Fig. 2.4; two-way ANOVA: $P = 0.525$, $\theta = 0.41$). Average total length of *A. coeruleus* recruits did not differ significantly among treatments (one-way ANOVA: $P = 0.576$, $\theta = 0.94$). The high mobility of surgeonfish recruits immediately after settlement prevented comparison of their within-reef settlement locations.

Wrasse recruitment – Of 164 wrasse recruits, 129 were *Thalassoma bifasciatum* (bluehead). The average number of *T. bifasciatum* recruits per reef did not differ significantly among treatments, although the statistical power of this test was low (Fig. 2.4; two-way ANOVA: $P = 0.293$, $\theta = 0.10$). Average (SD) total length of *T. bifasciatum* recruits did not differ significantly among treatments (one-way ANOVA: $P = 0.325$, $\theta = 1.00$). The high mobility of wrasse recruits immediately after settlement prevented comparison of their within-reef settlement locations.

Angelfish recruitment – Of 73 angelfish recruits, 50 were *Holacanthus ciliaris* (queen) and 22 were *Pomacanthus arcuatus* (gray). For each species, the average number of recruits per reef was independent of both piscivores and adult damselfish (Fig. 2.4; two-way ANOVA: *H. ciliaris*, piscivores $P = 0.170$, damselfish $P = 0.293$; *P. arcuatus*, piscivores $P = 0.156$, damselfish $P = 0.418$). For *H. ciliaris*, recruitment differed significantly among blocks (two-way ANOVA: blocks $P = 0.028$), and the average (SD) number of recruits per reef in each block was as follows: block 1 = 2.8 (2.1), block 2 = 3.3 (1.7), block 3 = 5.0 (0.8), and block 4 = 1.5 (0.6). Average total length of *H. ciliaris* recruits did not differ significantly among treatments (one-way ANOVA: $P = 0.339$, $\theta = 0.90$).

Within-reef location with respect to enclosed fishes was noted for all *H. ciliaris* and *P. arcuatus* recruits collected from the two damselfish-present treatments (P+D+ and P-D+). Location did not differ significantly for *H. ciliaris* on either P+D+ (near piscivores = 3, near damselfish = 3) or P-D+ reefs (near *S. leucostictus* = 6, near *S. partitus* = 4), while *P. arcuatus* settlement was generally low (P+D+: near piscivores = 3, near damselfish = 1; P-D+: near *S. leucostictus* = 0, near *S. partitus* = 1).

DISCUSSION

Factorial removal of resident predators and interference competitors clearly demonstrated that these guilds strongly affected the recruitment of other reef fishes and thereby dramatically influenced community structure. A subsequent experiment further suggested that reef fish larvae do not select or reject settlement sites based on the presence or absence of either piscivores or territorial damselfish. Thus, recruitment differences were due to differential recruit mortality among treatments caused directly or indirectly by resident piscivores and territorial damselfish, and not the result of larvae avoiding settlement to reefs inhabited by these two guilds. Resident piscivores and territorial damselfish each affected the survival of newly settled juveniles in a species-specific manner and thereby significantly altered initial patterns of settlement.

How do resident piscivores and territorial damselfish affect recruitment?

Recruitment of beaugregory damselfish (*Stegastes leucostictus*) was significantly higher on reefs where both piscivores and adult territorial damselfish had been removed (P-D-), and was uniformly low where either group was present alone (P+D- and P-D+), or where both groups were present (P+D+). Thus, the presence of either piscivores or adult damselfish resulted in high recruit mortality. That piscivores consume recruits and thus negatively affect recruitment is not surprising and has been demonstrated in several other studies (review by Hixon 1991, Carr and Hixon 1995, Hixon and Carr 1997, Planes and Lecaillon 2001, Webster 2002). Curiously, adult damselfish had the same effect as piscivores on damselfish recruitment. By what mechanism could adult damselfish affect juvenile survival? One possibility is that aggressive interactions between adults and juveniles make juveniles more susceptible to predation by resident piscivores (on

P+D+ reefs) and/or transient piscivores (on P-D+ reefs) such as schooling jacks (see Hixon and Carr 1997). Adults may chase juveniles away from shelter and thereby expose them to predation from resident piscivores, or force them to the edge of the reef where they would be more susceptible to passing transient piscivores. Another possibility is that adult damselfish directly consume newly settled juveniles. Although I know of no other studies that have explored this hypothesis, Randall's (1967) gut content analysis of 41 adult *S. leucostictus* revealed that they consume a considerable amount of fish material (7.1% by volume), but whether this material was scavenged from already-dead fishes or resulted from direct predation is unknown. Consistent with this hypothesis, I have observed adults of both *S. leucostictus* and *S. partitus* attack and consume disoriented conspecific and congeneric recruits that had been captured for tagging or measuring and released. This observation suggests that adults at least recognize recruits as potential food items and will consume them opportunistically. Consumption of conspecific and congeneric recruits may have additional benefits in that it would result in the elimination of future competitors before they became a serious threat.

In contrast to damselfish, recruitment of surgeonfish (*Acanthurus coeruleus*) was highest on reefs where only adult damselfish were present (P-D+) and lowest on reefs with resident piscivores (P+D+ and P+D-). Why piscivores have strong negative effects on surgeonfish recruitment seems clear. At settlement, surgeonfish recruits are slow-swimming and approximately three times the length of damselfish and wrasse recruits, and may therefore be attractive targets to larger resident piscivores (see Rice et al. 1993, Sogard 1997). How do adult damselfish enhance surgeonfish recruitment? In the absence of resident piscivores, the primary source of recruit mortality would most likely be transient piscivores (Hixon and Carr 1997). Because Caribbean *Stegastes* species will attack transient piscivore intruders, juvenile surgeonfish may obtain anti-predator benefits from damselfish aggression, especially if damselfish are not also strongly aggressive

toward surgeonfish. This scenario appears to be the case in this system, and in other systems damselfish and surgeonfish actually share territorial defense (Robertson and Polunin 1981, Roberts 1985).

In contrast to both damselfish and surgeonfish, wrasse recruitment (*Thalassoma bifasciatum*) was highest on reefs with resident piscivores (P+D+ and P+D-). Why would piscivores have a positive effect on *T. bifasciatum* recruitment? Juvenile *T. bifasciatum* are facultative cleaners that remove ectoparasites from other fishes (Itzkowitz 1979). Each piscivore treatment included several Nassau grouper (*Epinephelus striatus*) that were 20 to 40 cm TL and were the largest fishes on these reefs. Because parasite load is correlated with host fish size (Arnal et al. 2000), juvenile *T. bifasciatum* would have had access to a greater food supply on reefs with piscivores, thereby increasing recruit survival. In addition, mortality from predation is often greatly reduced for cleaners because predators benefit from their cleaning services (Poulin and Vickery 1995). Carr and Hixon (1995) also found that resident piscivores did not have a negative effect on survival of newly settled *T. bifasciatum*.

Do larvae use piscivores or territorial damselfish as settlement or avoidance cues?

Results from the enclosure experiment do not support the hypothesis that reef fish larvae use the presence of resident piscivores and territorial damselfish to select or reject settlement sites. First, unlike the first experiment, when resident piscivores and territorial damselfish were caged, there was no significant difference in recruit abundance among treatments for any species. Second, there was no significant difference in average recruit size among treatments for any species, indicating that selectivity is unrelated to recruit size. Third, except for one case, there was no evidence that larvae avoided or selected within-reef settlement sites based on the location of piscivores or damselfish. The single exception was a

suggestive pattern for newly settled beaugregory damselfish on reefs with enclosed adult damselfish (P-D+): more than twice as many recruits were found adjacent to the half of the enclosure containing adult *S. leucostictus* relative to the other half containing adult *S. partitus*.

Although Sweatman (1988) and Booth (1992) demonstrated that settlers of other damselfish (*Dascyllus* spp.) could detect conspecifics through chemical and visual cues, there is no unequivocal evidence that reef fish larvae can detect heterospecific residents. *Dascyllus* are typically found in dense conspecific or congeneric aggregations on a few species of highly branched corals. Newly settled juveniles have enhanced survival in the presence of adults, perhaps because adults are aggressive towards predators or increase group vigilance (Forrester 1990, Booth 1995). When juveniles derive benefits from associating with conspecifics, the ability to detect adults before settling would clearly be beneficial. However, this ability would most likely evolve in species that live in dense social groups because chemical or visual signals would be sufficiently strong due to the high concentration of individuals. For species that do not live in dense aggregations, such as the piscivores and damselfish in this study, chemical or visual cues are probably relatively weak or diffuse, thereby preventing the development of a reliable means to detect their presence. This is despite the fact that this ability would seem to be beneficial given the results of this study. It appears that most larvae simply settle on any suitable reef (Sale et al. 1994).

When does mortality occur during recruitment?

Several observations suggest that recruitment patterns were established shortly after nocturnal settlement. First, because the first few daylight hours postsettlement are thought to be a critical mortality period for recruits (Leis 1991, Schmitt and Holbrook 1999), one would expect to observe fewer newly settled

fishes in the late morning relative to the early morning. However, there were no differences in the number of new settlers observed during these two periods. This result suggests that recruitment patterns were already established before censusing began at 8:00 am each day. Second, a recent study on bicolor damselfish (*Stegastes partitus*) in this system compared daily and weekly recruit censuses to determine whether estimates of recruitment varied with sampling frequency (M. A. Hixon, *personal communication*). Results indicated that daily and weekly censuses were equivalent, which again suggests that recruitment patterns were established before each daily census. Finally, another study demonstrated that recruit mortality within 36 hours of settlement was significantly higher when prior residents, including predators, were present relative to reefs where all residents had been removed (Planes and Lecaillon 2001).

If settlement was uniform among reefs and recruitment differences were established prior to daily censuses, then substantial differential recruit mortality must have occurred in the first few hours postsettlement among the different experimental treatments. Such mortality most likely occurred at dawn when low, changing light levels confer an advantage to visual piscivores (Hobson 1991, McFarland 1991). Newly settled fish may be especially vulnerable to predation during this period due to unfamiliarity with their new surroundings and the consequent difficulty in finding adequate, unoccupied shelter.

Conclusions: is future community structure predictable?

Priority effects occur when early-colonizing individuals affect the recruitment of later colonists. These effects have been well documented in a variety of systems, and when they are species-specific and predictable, they introduce a level of determinism to the dynamics of a community. The present study documents how resident predators and interference competitors affect the

survival of recruiting reef fish. Coral reef fish communities are dynamic, open systems that depend on a spatially and temporally variable supply of planktonic larvae for new colonists. Because reefs are unlikely to ever be completely denuded of inhabitants, larvae entering the community must interact with a variety of reef residents. As these experiments show, interactions between prior residents and newly settled recruits can influence recruit survival in ways that substantially modify initial patterns of relative abundance established at the time of larval settlement. Because these interactions were species-specific, one may be able to use the current composition of a community to predict its future structure. For example, based on the results of this study and assuming larvae of all families settle, one could predict that reefs with both resident piscivores and territorial damselfish would experience relatively low recruitment of damselfishes and surgeonfishes, and high recruitment of wrasses that act as cleaners. Understanding whether and how other types of residents affect juvenile survival would increase the predictability of community structure in reef fishes.

CHAPTER 3: PRIORITY EFFECTS IN CORAL REEF FISH COMMUNITIES: GENERALITIES BETWEEN AUSTRALIA AND THE BAHAMAS

ABSTRACT

Priority effects occur when established community residents influence the colonization success of individuals entering the community. When priority effects are strong and taxon-specific, they can determine which taxa successfully enter the community, and thus provide a means of qualitatively predicting the future structure of a community based on its current composition. Using 20 spatially isolated patch reefs at Lizard Island on the Great Barrier Reef, I factorially manipulated the presence and absence of two guilds of resident fishes, predators (groupers and dottybacks) and potential competitors (damsel-fishes), to determine whether and how they affect the subsequent recruitment, mortality, and species richness of newly settled fishes. During the 50-day experiment, prior residency by predators dramatically reduced recruitment of damselfishes, surgeonfishes, butterflyfishes, and rabbitfishes, increased recruit mortality, and decreased recruit species richness. In contrast, prior residency by competitors decreased damselfish and rabbitfish recruitment, but did not affect either recruit mortality or recruit species richness. Effects of competitors on recruitment were likely due to aggressive interactions between residents and juveniles that either caused mortality directly (e.g., via injury or consumption) or indirectly by increasing the susceptibility of juveniles to predators. Effects of prior residents were strongest within 48 hours of settlement, resulting in the rapid establishment of recruitment patterns that persisted to the conclusion of the experiment. The results of the present study are qualitatively similar to those from a study I conducted in the Bahamas that also factorially manipulated resident predators and competitors on

patch reefs, suggesting that priority effects may be generally important determinants of coral reef fish community structure.

INTRODUCTION

Predicting the future structure of demographically open communities (e.g., most marine communities, as well as plant and insect communities with dispersive life-history stages) is often difficult because these communities depend on recruitment from external sources (Connolly and Roughgarden 1999). Due to a variety of factors, such as variability in reproductive output, larval survival, and dispersal mechanisms, there is often little relationship between the relative abundance of colonizing juveniles and current residents, resulting in a seemingly spatially and temporally unpredictable assemblage of species (reviews by Knowlton and Jackson 2001, Morgan 2001). However, when established community residents influence the colonization success of incoming juveniles in taxon-specific ways, understanding these interactions may permit predictions of future community structure based on the current composition of the community. Such priority effects have been documented in a variety of organisms, including plants (e.g., Burrows 1990, Bertness and Shumway 1993), sessile marine organisms (e.g., Sousa 1979, Menge and Sutherland 1987), amphibians (e.g., Wilbur and Alford 1985, Lawler and Morin 1993), and fishes (e.g., Shulman et al. 1983, Steele 1997). When priority effects occur, they introduce a level of determinism, and thus predictability, to the dynamics of a community.

Coral reef fish communities rely on a spatially and temporally unpredictable supply of larvae for colonizing juveniles, and are thus classic examples of demographically open communities (review by Sale 1991). Like most other marine species, reef fishes produce planktonic larvae that spend days to months developing in the pelagic environment away from natal reefs (Leis 1991, Victor 1991). Larvae

typically make a nocturnal transition to reef habitats in a process called settlement, and the net process of settlement and early postsettlement mortality is called recruitment. Although some have argued that stochastic larval supply results in unpredictable assemblages of coral reef fishes (Sale 1980, Sale and Douglas 1984, Sale et al. 1994), several studies have found evidence for deterministic settlement and recruitment processes. For example, settling larvae may choose settlement sites based on the presence or absence of conspecifics or certain types of habitat (Sweatman 1988, Booth 1992, Elliot et al. 1995, Danilowicz 1996). In addition, observational studies have documented strong relationships between the presence and/or abundance of some reef fish species and particular reef zones or coral types, suggesting that habitat selection may be important at both small and large spatial scales (reviews by Williams 1991, Booth and Wellington 1998).

Other potentially deterministic processes may operate after settlement and thus influence recruitment, such as competitive and predatory interactions between recently settled fish and established residents. There is growing evidence that recruitment patterns are strongly influenced by such interactions, often shortly after settlement. For example, predators typically cause decreased recruitment of most species, presumably because relatively naïve newly settled juveniles are especially vulnerable to predation (Webster 2002, Hixon and Webster *in press*, Almany *in review-b*), although the presence of large predatory fishes may have positive effects on recruitment of some cleaner fishes, perhaps because these large fishes are rich sources of ectoparasites (Almany *in review-b*). Furthermore, predators appear to have particularly strong negative effects on recruitment of species that settle at relatively large sizes (Almany *in review-b*, Webster and Almany *in review*). Prior residency by interference competitors, such as territorial damselfishes, can result in both positive and negative effects on recruitment. For example, damselfishes have been shown to either inhibit (Shulman et al. 1983, Sweatman 1983, 1985, Jones 1987, Risk 1998, Almany *in review-b*) or facilitate (Almany *in review-b*) heterospecific recruitment, and either inhibit (Sale 1976, Almany *in review-b*) or

facilitate (Sweatman 1983, 1985, Jones 1987, Booth 1992) conspecific recruitment. When established residents influence subsequent recruitment in a predictable taxon-specific manner, the recent recruitment history of a community can influence its future structure by setting the stage for interactions between residents and newly settled fishes.

Studies of coral reef fishes have typically been conducted in either the western Pacific, especially the Great Barrier Reef in Australia, or in the western Atlantic and Caribbean, and comparative studies between the two regions are rare (review by Thresher 1991). Two dominant hypotheses have emerged regarding the relative importance of processes structuring fish communities on coral reefs: (1) stochastic larval supply is the major determinant of community structure, and (2) postsettlement interactions, such as competition and predation, primarily determine community structure (review by Jones 1991). Thresher (1991) argued that much of the evidence supporting the first hypothesis comes from western Pacific studies, while evidence supporting the second hypothesis comes primarily from western Atlantic studies. This geographic difference has led to speculation that western Pacific and western Atlantic reef fish communities differ in fundamental ways, such as the relative importance of pre- and postsettlement processes. Because researchers in the western Pacific and Atlantic often use different experimental methodologies, the search for general principles would benefit from conducting similarly designed studies in both systems (reviews by Hixon 1991, Jones 1991).

I present the results of a field experiment conducted on the Great Barrier Reef that used the same design as an experiment I previously conducted in the Bahamas (Almany *in review-b*). I factorially manipulated the presence and absence of two guilds of resident fishes that were likely to influence subsequent reef fish recruitment, mortality, and species richness: predators, consisting of piscivorous groupers and dottybacks, and potential competitors, consisting of several species of damselfishes. I subsequently monitored the effects of these treatments over 50 days. I addressed the following questions: (1) does prior residency by predators

and competitors affect recruitment, mortality, and recruit species richness (2) are these effects similar between the Great Barrier Reef and the Bahamas, and (3) how quickly are recruitment patterns established? I found strong evidence that both predators and competitors negatively influence recruitment, and that predators also negatively affect recruit mortality and species richness. There was convincing evidence that recruitment patterns were established rapidly, within the first 48 hours following settlement. Importantly, the results of this study were qualitatively similar to those documented in the Bahamian study, indicating general patterns common to different geographical regions.

METHODS

Study site

This study was conducted from November 1999 to January 2000 at Lizard Island on the northern Great Barrier Reef, Australia (14°40'S, 145°28'E). In 1993, researchers consolidated live patches of coral (*Porites cylindrica*) into an array of 54 reefs on the sandy bottom of the southeastern section of the lagoon (Fig. 3.1A; Hixon and Jones *in preparation*). On average (SE), each reef was 3.2 m (0.05 m) long by 0.6 m (0.01 m) wide with a surface area of 2.0 m² (0.05 m²). Reefs were separated from neighboring reefs and the main platform reef by 30 meters of sand (Fig. 3.1B). Because similar isolation distance has been shown to inhibit the movement of most small reef fishes (Doherty 1982, Hixon and Beets 1989), the disappearance of a recruit in this study was attributed to mortality, and each reef was considered an independent experimental unit.

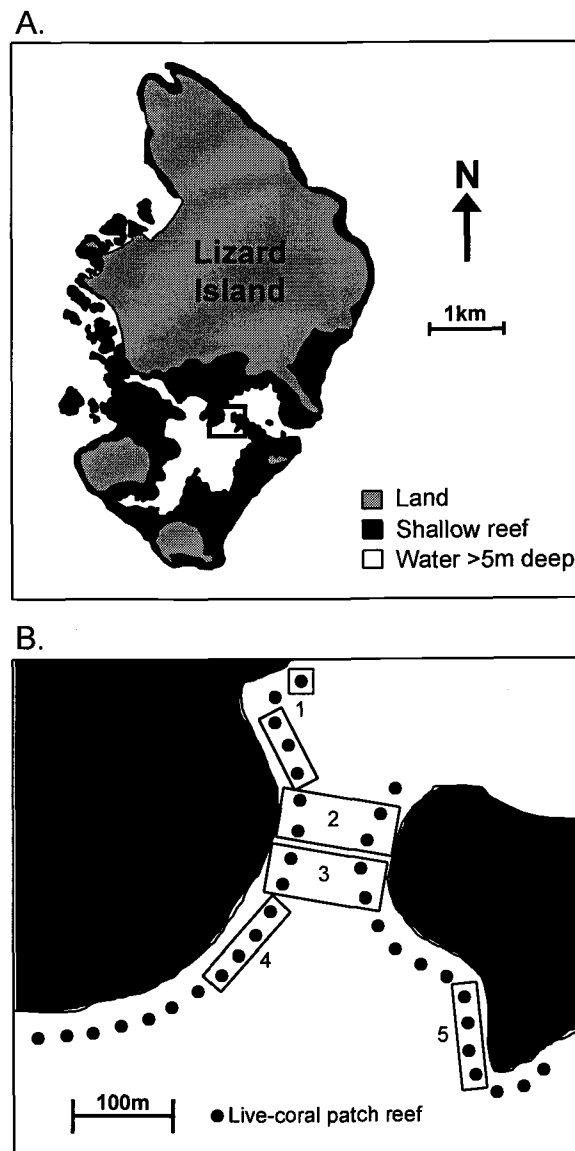


Figure 3.1: Study site. (A) Location of experimental patch reefs in the lagoon at Lizard Island. (B) Spatial arrangement of reefs and the blocking scheme used in the experiment. Each reef was separated from its closest neighbor and the main reef by 30 meters of featureless sand.

Study species

I manipulated the presence and absence of two groups of resident fishes: piscivores and adult damselfishes. Resident piscivores consisted of two common, highly piscivorous species: the chocolate hind (Serranidae: *Cephalopholis boenak*) and the brown dottyback (Pseudochromidae: *Pseudochromis fuscus*) (Blaber et al. 1990, Beukers and Jones 1997). All resident piscivores in this study were less than 10 cm TL (total length). Adult damselfishes (Pomacentridae) consisted primarily of six species: the planktivore *Neopomacentrus cyanomos* (regal demoiselle), and the omnivores *Pomacentrus amboinensis* (Ambon damsel), *P. nagasakiensis* (Nagasaki damsel), *P. pavo* (blue damsel), *P. moluccensis* (lemon damsel), and *Dascyllus aruanus* (humbug dascyllus) (Allen 1991).

Experimental design

To determine whether prior residency by piscivores and adult damselfishes influenced recruitment, recruit mortality, and recruit species richness, I factorially manipulated the presence and absence of these two guilds on 20 patch reefs. To minimize confounding effects of variable juvenile supply, I selected five blocks of reefs, each block containing four reefs, such that reefs within a block were close to each other (Fig. 3.1B). Within each block, I randomly assigned reefs to four treatments: (1) resident piscivores and adult damselfishes both present (P+D+), (2) resident piscivores present, adult damselfishes removed (P+D-), (3) resident piscivores removed, adult damselfishes present (P-D+), and (4) resident piscivores and adult damselfishes both removed (P-D-). On each piscivore-occupied (P+) reef, I standardized piscivore abundance via removals and additions until each reef had 4-6 *Cephalopholis boenak* and 1-2 *Pseudochromis fuscus* per reef, which was between the average density observed during an initial census of all reefs (3.0 C.

boenak and 1.7 *P. fuscus*) and the maximum (9 *C. boenak* and 3 *P. fuscus*). Prior to manipulations, average (SE) adult damselfish abundance was 118.1 (5.1) fish per reef (range: 79 to 163). On each damselfish-occupied (D+) reef, I selectively removed adult damselfishes to achieve a standard abundance of approximately 80 fish with a relative abundance of approximately 35% *Neopomacentrus cyanomos*, 30% *Pomacentrus amboinensis*, 15% *P. nagasakiensis*, 10% *P. pavo*, 5% *P. moluccensis*, and 5% *Dascyllus aruanus*. All other damselfish species were removed. Fish manipulations were conducted using clove oil as a fish anesthetic (Munday and Wilson 1997), hand nets, and a BINCKE net (Anderson and Carr 1998).

After establishing treatment conditions, I removed any recruits from each reef. Thereafter, I monitored subsequent recruitment by conducting a visual census of each reef every other day for 50 days. Due to the interval between censuses, recruitment was defined as the observation of a newly settled fish within 48 hours of settlement. During each census, I noted any newly settled fishes, which could be identified by their small size and incomplete pigmentation, previously recruited fishes, and any disappearances. The location of each newly settled fish was marked with a small piece of flagging tape, which was removed if the recruit disappeared. During each census, I counted resident piscivores on each P+ reef, and searched for and removed any immigrant piscivores on P- reefs and adult damselfishes on D- reefs. Piscivore and damselfish immigration during the 50-day experiment was low (16 *C. boenak*, 3 *P. fuscus*, and 16 adult damselfish).

During initial reef censuses, there was considerable variation in the abundance of cardinalfishes (Apogonidae: *Apogon fragilis* and *A. doederleini*) among reefs, with some reefs supporting more than 2000 individuals, while others were devoid of cardinalfishes. Because *C. boenak* frequently consumes cardinalfishes (Blaber et al. 1990, Stewart 1998), cardinalfishes represented a potentially important alternative prey source. Thus, variation in cardinalfish abundance among P+ reefs could cause between-reef variation in the effect of

resident piscivores on other species (see Webster and Almany *in review*). I therefore removed cardinalfishes from each reef prior to the start of the experiment, and thereafter once per week, to minimize such confounding effects.

To obtain quantitative measures of habitat complexity to compare with measures from patch reefs used in the Bahamian study, I randomly selected 8 of the 20 experimental reefs and established two transects on each reef, each transect extending across the entire reef. Along each transect, I measured: (1) topographic complexity, defined as the ratio between the length of a fine-link chain allowed to conform to the coral topography along the transect and the straight-line length of each transect (Risk 1972), (2) number of potential shelter holes, (3) depth of each hole, and (4) diameter of each hole (Roberts and Ormond 1987). I combined measurements from the two transects on each reef to obtain a reef average for measures (1), (3), and (4), and summed the number of holes on both transects to obtain a total estimate of potential shelter hole abundance (2).

Data analysis

I limited my analyses to recruits that were conspicuous and could therefore be reliably and easily censused. These included damselfishes, butterflyfishes (Chaetodontidae), surgeonfishes (Acanthuridae), and rabbitfishes (Siganidae). For damselfishes, I analyzed differences among treatments for the three most abundant species as well as for the entire family. For butterflyfishes, surgeonfishes, and rabbitfishes, all analyses were conducted at the family level because (1) overall recruitment was low relative to damselfishes, and (2) surgeonfish and rabbitfish recruits could not be identified to species. Family-level analyses assume that each species within the family responded similarly to experimental manipulations. Within each of the four families, recruits were of similar size and trophic status, and appeared to use the reef in similar ways. Two exceptions were the

damselishes *Neopomacentrus cyanomos* and *Chromis viridis*; recruits of these species remained well above the reef rather than within the coral, as was typical of all other recruit species. Because these differences in behavior likely have important demographic consequences (Webster 2002), I analyzed *N. cyanomos* separately from all other damsselfishes and did not include this species in damsselfish family-level comparisons. Recruitment of *C. viridis* was low ($N = 3$ new settlers) and therefore unlikely to influence family-level comparisons.

I compared differences in recruitment, final recruit abundance at the end of the experiment (day 50), recruit mortality, and species richness of final recruit assemblages among treatments with two-way ANOVA (model terms: Blocks, Piscivores, Damsselfishes, and Piscivore-Damsselfish interaction) (Sokal and Rohlf 1995). When interaction terms were significant ($P \leq 0.05$), I conducted a linear contrast of the means for each pairwise treatment comparison (Ramsey and Schafer 1997). When interaction terms were not significant ($P \geq 0.10$), I removed the interaction and analyzed the additive model. When ANOVA F-tests were significant ($P \leq 0.05$), I estimated effect sizes and calculated 95% confidence intervals (Zar 1999). When data were transformed (\ln) to correct heterogeneous variance, resulting confidence intervals were asymmetric and I report both the upper and lower limits of the confidence interval. When ANOVA F-tests were not significant ($P > 0.05$), I calculated the statistical power (θ) of the test to detect an actual difference of five fish among treatments (number of observed new settlers and final recruit abundance) or 5% (recruit mortality). To insure that ANOVA assumptions were met, I tested for homogeneity of variance using Levene's Test and examined normal probability plots (Ramsey and Schafer 1997). All statistical analyses were conducted using SAS Institute statistical software (JMP version 4.0).

RESULTS

Recruitment

Damselfishes – The dominant family of fish recruiting to the experimental reefs was damselfishes (Pomacentridae). There was a significant interactive effect of resident piscivores and adult damselfishes on the subsequent recruitment of damselfishes (Table 3.1; two-way ANOVA: interaction $P=0.005$). In the absence of adult damselfishes, piscivores reduced recruitment by an average (\pm 95% CI) of 42.0 ± 8.2 fish per reef (linear contrast: $P<0.0001$). In the presence of adult damselfishes, piscivores reduced recruitment by 23.6 ± 8.2 fish per reef (linear contrast: $P<0.0001$). In the absence of piscivores, adult damselfishes reduced recruitment by 19.8 ± 8.2 fish per reef (linear contrast: $P=0.0002$), while in the presence of piscivores, adult damselfishes had no effect on recruitment (linear contrast: $P=0.715$). Of the 598 recruits, more than 70% were from two species: *Pomacentrus amboinensis* (254 recruits) and *Pomacentrus nagasakiensis* (173 recruits). There was a significant interactive effect of resident piscivores and adult damselfishes on recruitment of *P. amboinensis* (Table 3.1; two-way ANOVA: interaction $P=0.020$). On reefs where adult damselfishes had been removed, piscivores reduced recruitment by 16.0 ± 3.9 fish per reef (linear contrast: $P<0.0001$). Where adult damselfishes were present, piscivores reduced recruitment by 9.2 ± 3.9 fish per reef (linear contrast: $P=0.0003$). On piscivore removal reefs, adult damselfishes reduced recruitment by 5.2 ± 3.9 recruits per reef (linear contrast: $P=0.014$), and where piscivores were present, adult damselfishes had no effect on recruitment (linear contrast: $P=0.391$). For *P. nagasakiensis*, recruitment was significantly influenced by both piscivores and adult damselfishes (Table 3.1; two-way ANOVA: piscivores $P<0.0001$; damselfishes $P=0.008$). Piscivores reduced recruitment by 10.9 ± 3.0 fish per reef, while adult damselfishes reduced recruitment by 4.3 ± 3.0 fish per reef. For *Neopomacentrus cyanomos*, there was

no effect of either piscivores or adult damselfishes on recruitment (Table 3.1; two-way ANOVA: piscivores $P=0.115$; damselfishes $P=0.279$; $\theta = 1.00$).

Butterflyfishes, Surgeonfishes, and Rabbitfishes – For butterflyfishes (Chaetodontidae) and surgeonfishes (Acanthuridae), recruitment was strongly influenced by piscivores, but independent of adult damselfishes (Table 3.1; Butterflyfishes: two-way ANOVA: piscivores $P<0.0001$; damselfishes $P=0.449$. Surgeonfishes: two-way ANOVA: piscivores $P=0.0002$; damselfishes $P=0.863$). Piscivores reduced butterflyfish recruitment by 8.0 fish per reef (95% CI: 6.0 to 10.7), and surgeonfish recruitment by an average (\pm 95% CI) of 5.8 ± 2.5 fish per reef. For rabbitfishes (Siganidae), there was a marginally significant interactive effect of piscivores and damselfishes on recruitment (two-way ANOVA: interaction $P=0.040$). No recruits were observed on treatments where piscivores were present (Table 3.1; P+D+ and P+D-). In the absence of resident piscivores, adult damselfishes reduced recruitment by an average (\pm 95% CI) of 3.4 ± 2.3 fish per reef (linear contrast: $P=0.007$).

Final recruit abundance

Damselfishes – There was a significant interactive effect of resident piscivores and adult damselfishes on the final abundance of damselfish recruits (Fig. 3.2A; two-way ANOVA: interaction $P=0.0039$). Where adult damselfishes had been removed, piscivores reduced final abundance by an average (\pm 95% CI) of 37.0 ± 6.2 fish per reef (linear contrast: $P<0.0001$), and where adult damselfishes were present, piscivores reduced final abundance by 22.6 ± 6.2 fish per reef (linear contrast: $P<0.0001$). Where piscivores had been removed, adult damselfishes reduced final abundance by 14.2 ± 6.2 fish per reef (linear contrast: $P=0.0003$), and

Table 3.1: Recruitment during the 50-day experiment. Total number of new recruits observed on each. A new recruit was defined as a newly settled fish observed within 48 hours of settlement. Within a family, species are listed from most abundant to least abundant.

Species	Family	Number of new recruits per treatment ¹ (SE)			
		P+D+	P+D-	P-D+	P-D-
	Damselfishes (Pomacentridae)	63 (1.9)	73 (2.9)	180 (1.5)	282 (2.9)
<i>Pomacentrus amboinensis</i>		36 (1.5)	28 (1.8)	82 (1.0)	108 (0.5)
<i>Pomacentrus nagasakiensis</i>		9 (0.6)	23 (1.4)	56 (1.8)	85 (1.1)
<i>Hemiglyphidodon plagiometopon</i>		9 (1.1)	11 (0.7)	21 (0.5)	42 (3.0)
<i>Dischistodus perspicillatus</i>		1 (0.2)	5 (0.3)	5 (0.3)	27 (1.2)
<i>Pomacentrus pavo</i>		7 (0.9)	1 (0.2)	6 (0.4)	9 (0.9)
<i>Pomacentrus moluccensis</i>		0	2 (0.2)	2 (0.2)	2 (0.4)
<i>Amblypomacentrus breviceps</i>		0	0	0	5 (0.4)
<i>Pomacentrus wardi</i>		1 (0.2)	1 (0.2)	1 (0.2)	1 (0.2)
<i>Dascyllus aruanus</i>		0	0	3 (0.4)	0
<i>Dischistodus prosopotaenia</i>		0	0	1 (0.2)	2 (0.2)
<i>Chromis viridis</i>		0	2 (0.2)	0	1 (0.2)
<i>Amblyglyphidodon curacao</i>		0	0	2 (0.4)	0
<i>Dascyllus trimaculatus</i>		0	0	1 (0.2)	0
<i>Neopomacentrus cyanomos</i> ²		49 (5.4)	20 (2.4)	66 (5.9)	51 (4.0)
	Butterflyfishes (Chaetodontidae)	1 (0.2)	1 (0.2)	38 (1.0)	47 (0.9)
<i>Chaetodon ephippium</i>		1 (0.2)	1 (0.2)	24 (0.6)	33 (0.5)
<i>Chaetodon auriga</i>		0	0	7 (0.2)	10 (0.8)
<i>Chaetodon lunula</i>		0	0	3 (0.4)	1 (0.2)
<i>Heniochus acuminatus</i>		0	0	2 (0.4)	1 (0.2)
<i>Chaetodon melannotus</i>		0	0	1 (0.2)	1 (0.2)
<i>Chaetodon ulietensis</i>		0	0	1 (0.2)	1 (0.2)
	Surgeonfishes (Acanthuridae)				
<i>Acanthurus</i> spp.		8 (1.6)	3 (0.2)	33 (1.4)	36 (1.0)
	Rabbitfishes (Siganidae)				
<i>Siganus</i> spp.		0	0	11 (0.9)	28 (1.1)

¹ Treatments consisted of the presence (+) or absence (-) of resident piscivores (P) and adult damselfishes (D). There were five reefs in each treatment.

² This species was treated separately from all other damselfishes due to differences in ecology and behavior (see text).

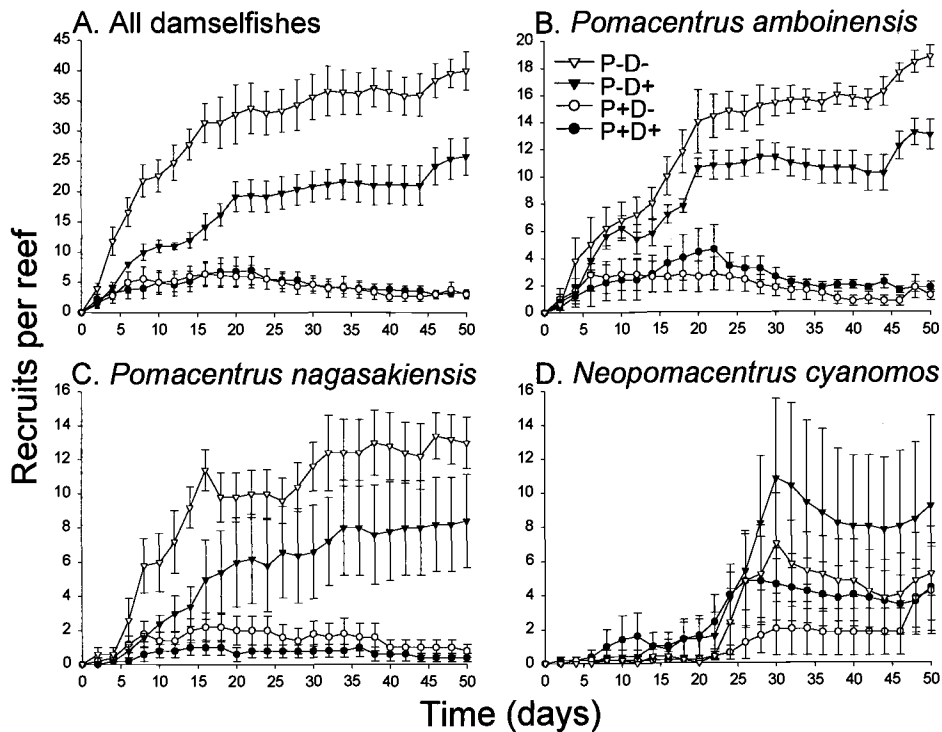


Figure 3.2: Differential effects of prior residents on the abundance of damselfish (Pomacentridae) recruits. Relationship between cumulative recruitment (larval settlement minus mortality) and experimental treatments ($n = 4$ reefs each) for (A) all damselfish species combined (excluding *Neopomacentrus cyanomos*) and the three most abundant species (B) *Pomacentrus amboinensis*, (C) *P. nagasakiensis*, and (D) *Neopomacentrus cyanomos*. Treatments consisted of factorial combinations of the presence (+) and absence (-) of both resident piscivores (P) and adult damselfishes (D). Error bars are \pm SE. Note that Y-axis scale varies among plots.

where piscivores were present, adult damselfishes had no effect on final abundance (linear contrast: $P=0.945$). Similarly, there was a significant interactive effect of resident piscivores and adult damselfishes on the final abundance of *P. amboinensis* recruits (Fig. 3.2B; two-way ANOVA: interaction $P=0.011$). In the absence of adult damselfishes, piscivores reduced final abundance by 9.6 fish per

reef (95% CI: 7.0 to 13.3; linear contrast: $P < 0.0001$), and where adult damselfishes were present, piscivores reduced final abundance by 5.1 fish per reef (95% CI: 3.7 to 7.1; linear contrast: $P < 0.0001$). Where piscivores had been removed, adult damselfishes reduced final abundance by 1.4 recruits per reef (95% CI: 1.0 to 2.0; linear contrast: $P = 0.035$), and where piscivores were present, adult damselfishes weakly increased final abundance (linear contrast: $P = 0.088$). Final abundance of *P. nagasakiensis* recruits was strongly influenced by resident piscivores, but independent of adult damselfishes (Fig. 3.2C; two-way ANOVA: piscivores $P < 0.0001$; damselfish $P = 0.109$). Piscivores reduced final abundance by 10.1 ± 3.1 recruits per reef. For *Neopomacentrus cyanomos*, final abundance was independent of both resident piscivores and adult damselfishes (Fig. 3.2D; two-way ANOVA: piscivores $P = 0.331$; damselfishes $P = 0.433$; $\theta = 0.85$).

Butterflyfishes, Surgeonfishes, and Rabbitfishes – Final abundance was strongly influenced by resident piscivores, but independent of adult damselfishes for butterflyfishes (Fig. 3.3A; two-way ANOVA: piscivores $P < 0.0001$; damselfishes $P = 0.122$), surgeonfishes (Fig. 3.3B; two-way ANOVA: piscivores $P = 0.0004$; damselfishes $P = 0.440$), and rabbitfishes (Fig. 3.3C; two-way ANOVA: piscivores $P = 0.007$; damselfishes $P = 0.173$). Piscivores reduced final abundance of butterflyfish by an average (\pm 95% CI) of 5.7 ± 1.2 recruits per reef, surgeonfish by 4.1 ± 1.9 recruits per reef, and rabbitfish by 2.2 ± 1.5 recruits per reef.

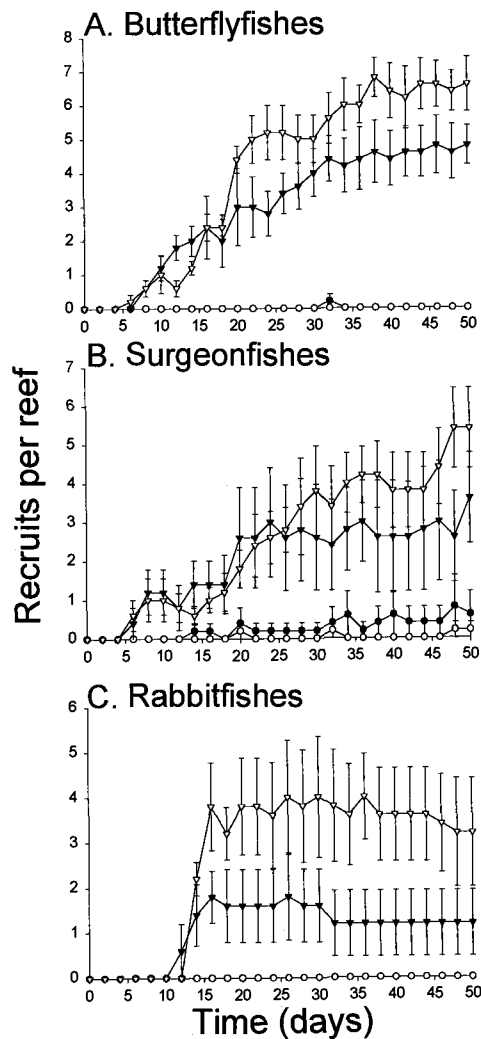


Figure 3.3: Differential effects of prior residents on butterflyfish (Chaetodontidae), surgeonfish (Acanthuridae), and rabbitfish (Siganidae) recruitment. Relationship between cumulative recruitment (larval settlement minus mortality) and experimental treatments ($n = 4$ reefs each) for (A) all butterflyfish species combined, (B) all surgeonfish species combined, and (C) all rabbitfish species combined. Treatments consisted of factorial combinations of the presence (+) and absence (-) of both resident piscivores (P) and adult damselfishes (D). Error bars are \pm SE. Note that Y-axis scale varies among plots, and that recruitment was often zero on P+D+ and P+D- treatments.

Recruit mortality

Damselfishes – Recruit mortality was strongly influenced by resident piscivores, but independent of adult damselfishes (Fig. 3.4A; two-way ANOVA: piscivores $P < 0.0001$; damselfishes $P = 0.968$). Piscivores increased recruit mortality

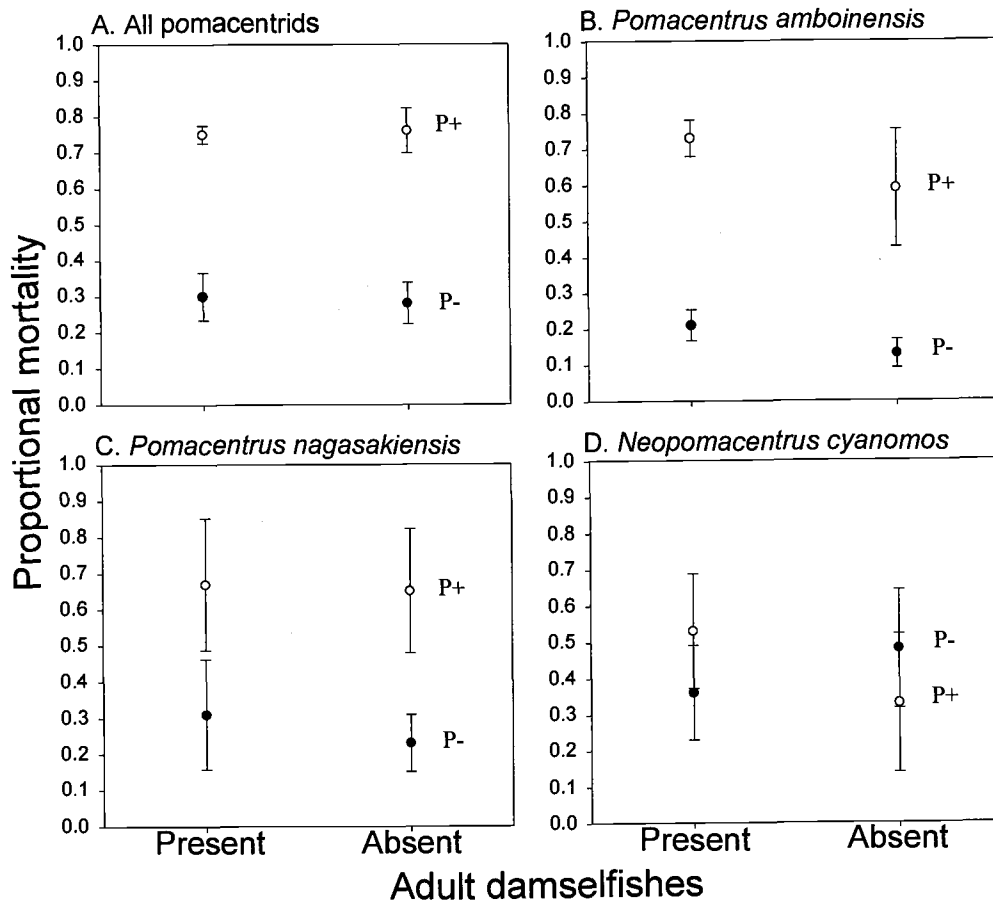


Figure 3.4: Effects of prior resident adult damselfish on mortality of damselfish recruits. Relationship between average recruit mortality and experimental treatments ($n = 4$ reefs each) for (A) all damselfish species combined (excluding *Neopomacentrus cyanomos*), and the three most abundant species, (B) *Pomacentrus amboinensis*, (C) *P. nagasakiensis*, and (D) *Neopomacentrus cyanomos*. Treatments consisted of the presence (P+) or absence (P-) of resident piscivores, and the presence or absence of adult damselfishes. Error bars are \pm SE.

by an average (\pm 95% CI) of $46.1\% \pm 8.0\%$. Similarly, recruit mortality for the two most abundant species was strongly influenced by resident piscivores, but independent of adult damselfishes (*P. amboinensis*: Fig. 3.4B; two-way ANOVA: piscivores $P < 0.0001$; damselfishes $P = 0.215$. *P. nagasakiensis*: Fig. 3.4C; two-way ANOVA: piscivores $P = 0.002$; damselfishes $P = 0.641$). For *P. amboinensis* recruits, piscivores increased mortality by an average (\pm 95% CI) of $49.1\% \pm 18.6\%$, while for *P. nagasakiensis* recruits, piscivores increased mortality by $38.9\% \pm 21.4\%$. For *Neopomacentrus cyanomos*, recruit mortality was independent of both resident piscivores and adult damselfishes (Fig. 3.4D; two-way ANOVA: piscivores $P = 0.950$; damselfishes $P = 0.806$; $\theta = 0.09$).

Butterflyfishes, Surgeonfishes, and Rabbitfishes – Recruitment of these three families was low where resident piscivores were present (P+D+ and P+D-), which prevented comparing recruit mortality among the four treatments. However, comparisons of recruit mortality on the remaining two treatments (P-D+ and P-D-) indicated that adult damselfishes did not influence recruit mortality (t-test: butterflyfish $P = 0.103$; surgeonfish $P = 0.497$; rabbitfish $P = 0.399$).

Species richness of final recruit assemblages and measurements of habitat complexity

Recruit Species Richness – At the conclusion of the experiment (day 50), average recruit species richness was strongly influenced by resident piscivores, but independent of adult damselfishes (two-way ANOVA: piscivores $P < 0.0001$; damselfishes $P = 0.872$). Piscivores reduced average (\pm 95% CI) richness by 6.9 ± 1.3 species per reef. Average (SE) final recruit species richness on each treatment was as follows: P+D+ = 3.4 (0.7); P+D- = 3.4 (0.4); P-D+ = 10.4 (0.5); P-D- = 10.2 (1.1). Of the 14 damselfish species that recruited during the experiment, only the five most abundant were present on piscivore-occupied reefs (*Neopomacentrus cyanomos*, *Pomacentrus amboinensis*, *P. nagasakiensis*, *Hemiglyphidodon*

plagiometopon, and *Dischistodus perspicillatus*). In contrast, on reefs where piscivores had been removed, six relatively rare damselfish species were present (*Pomacentrus moluccensis*, *P. wardi*, *Dascyllus aruanus*, *D. trimaculatus*, *Dischistodus prosopotaenia*, and *Amblyglyphidodon curacao*) in addition to the five most abundant species. Butterflyfish and rabbitfish recruits were completely absent from piscivore-occupied reefs. Three butterflyfish species recruited to reefs where piscivores had been removed (*Chaetodon ephippium*, *C. auriga*, and *C. lunula*).

Habitat Complexity – Average (SE) topographic complexity on eight randomly selected reefs was 2.0 (0.05), and there were an average of 65.5 (3.5) potential shelter holes per reef. Holes had an average diameter of 1.8 cm (0.08) and an average depth of 6.3 cm (0.4).

DISCUSSION

Priority effects on recruitment: comparison with Bahamian reefs

The results of the present study are qualitatively similar to those obtained from a comparable 44-day experiment on similarly-sized patch reefs in the Bahamas (Almany *in review-b*). Both experiments factorially manipulated the presence and absence of resident piscivores and adult damselfishes. Bahamian resident piscivores consisted of two species of small grouper (Serranidae: *Cephalopholis cruentata*, and *C. fulva*), one species of large grouper (*Epinephelus striatus*), and two moray eels (*Gymnothorax moringa* and *G. vicinus*). Adult damselfishes consisted of two highly territorial species (Pomacentridae: *Stegastes leucostictus* and *S. partitus*). Thus, the suites of predators and damselfishes manipulated were quite different between the Great Barrier Reef and the Bahamas. In the Bahamian study, resident piscivores had strong negative effects on the

recruitment and final recruit abundance of damselfishes and surgeonfishes, and positive effects on the final abundance of wrasse (Labridae) recruits. Adult damselfishes had strong negative effects on the final abundance of damselfishes that were indistinguishable from the negative effects of resident piscivores, and positive effects on the final abundance of surgeonfish recruits.

In the Australian study, resident piscivores and adult damselfishes had similar effects on both the recruitment and final abundance of all families except rabbitfishes. For all damselfishes except *Neopomacentrus cyanomos*, resident piscivores had strong negative effects on recruitment and final abundance, while adult damselfishes had weaker negative effects. Piscivores had strong negative effects on butterflyfish, surgeonfish, and rabbitfish recruitment and final abundance. In contrast, adult damselfishes had negative effects on rabbitfish recruitment, but did not influence the final abundance of rabbitfish recruits, or the recruitment and final abundance of butterflyfishes and surgeonfishes.

By what mechanism(s) do piscivores and adult damselfishes influence recruitment? The two most likely mechanisms in both the Bahamian study and the Australian study were (1) differential settlement among treatments and/or (2) differential recruit mortality among treatments. In the first scenario, settling larvae simply avoided reefs with resident piscivores and/or adult damselfishes. The underlying assumption is that larvae somehow detected residents prior to settling, perhaps through chemical, visual, or auditory cues, and then selected reefs based on the presence or absence of piscivores and/or damselfishes. Although Sweatman (1988) and Booth (1992) demonstrated that some newly settled damselfishes (*Dascyllus* spp.) select settlement sites by detecting conspecifics through chemical and visual cues, there is little evidence that larvae can detect heterospecific residents. Almany (*in review-b*) demonstrated that settling damselfish, surgeonfish, and wrasse in the Bahamas do not select among reefs based on the presence or absence of either resident piscivores or adult territorial damselfishes. If settling larvae are generally not able to detect heterospecific residents prior to settling, then

differential settlement is unlikely to explain recruitment patterns in either the Bahamian or present study.

The most likely cause of differences in recruitment among treatments was differential postsettlement mortality. Because the effects of resident piscivores and adult damselfishes on both recruitment and final recruit abundance were generally similar in the Australian study, differences among treatments were largely established within 48 hours of settlement. Similarly, in the Bahamian study there was strong evidence that recruitment patterns were established even more rapidly after settlement, within 24 hours, by high differential recruit mortality. These results suggest that pattern-forming processes occurred rapidly, and that there was high differential recruit mortality immediately after settlement. Consistent with this hypothesis, several recent studies have demonstrated that settling larvae and newly settled juveniles are subject to high mortality 24 to 48 hours after settlement (Planes and Lecaillon 2001, Webster 2002, Webster and Almany *in review*). Newly settled fishes may be especially vulnerable to predation immediately after settlement due to an unfamiliarity with their new surroundings and consequent difficulty in finding adequate shelter. Moreover, predation on new settlers is likely highest during dawn following settlement, when low, changing light levels favor piscivorous fishes that hunt by sight (Hobson 1991, McFarland 1991).

The negative effects of piscivores on recruitment and recruit mortality in both the Australian study and the Bahamian study were almost certainly due to piscivores directly consuming recruits. On Australian reefs, recruit mortality was significantly higher for all species where resident piscivores were present, with the exception of *Neopomacentrus cyanomos*. Piscivores in both studies had strong negative effects on species that settle at relatively large sizes, such as surgeonfish, rabbitfish, and butterflyfish, perhaps because piscivores disproportionately targeted these larger recruits (see Rice et al. 1993, Sogard 1997). In contrast, in the Bahamian study piscivores had a significant positive effect on recruitment of wrasse. Most Bahamian wrasse recruits were *Thalassoma bifasciatum* (bluehead),

and juveniles of this species are facultative cleaners that remove ectoparasites from other fishes (Itzkowitz 1979). It is likely that juvenile *T. bifasciatum* had higher survival in the presence of large Bahamian piscivores (*Epinephelus striatus*) due to a greater access to ectoparasites (see also Carr and Hixon 1995).

Importantly, because mortality estimates on both Australian and Bahamian reefs were based on following the fates of recruits, they underestimated actual mortality because they did not account for any mortality that occurred during the hours between settlement and censusing by divers. Since piscivores increased recruit mortality in both studies, they likely had similar, if not greater, negative effects on mortality between settlement and censusing (Hixon and Carr 1997, Schmitt and Holbrook 1999, Planes and Lecaillon 2001, Webster 2002). Even in the absence of resident piscivores, recruit mortality was always greater than zero in both studies, which indicates that recruits were subject to predation from transient predators or cryptic resident predators. Common transient predators in both studies included jacks (Carangidae), which frequently move among reefs, and lizardfishes (Synodontidae), which were common in the sand surrounding reefs. Such transient predators represent a significant source of recruit mortality (Sweatman 1984, Hixon and Carr 1997).

High habitat complexity may ameliorate negative effects of predators on prey (e.g., Murdoch and Oaten 1975, Hixon and Menge 1991). In an additional Bahamian study, I manipulated habitat complexity to determine whether increased complexity mediated the aforementioned negative effects of resident piscivores and territorial damselfishes on recruits (Almany *in review-a*). I found no evidence for any effect of increased habitat complexity. Using the same methods to quantify complexity as in the present study, high complexity Bahamian reefs had an average of 4 holes per 1 m of reef surface, 22 potential shelter holes, and holes had an average entrance diameter of 2.8 cm (Almany *in review-a*). In contrast, Australian reefs had an average of 10.0 holes per 1 m, 65 potential shelter holes, and holes had an average entrance diameter of 1.8 cm. Thus, Australian reefs provided a greater

abundance of shelter and were structurally more complex than their Bahamian counterparts. Because predator foraging efficiency is often negatively influenced by increased habitat complexity (e.g., Greenberg et al. 1995, Beukers and Jones 1997), I expected to find that recruitment on Australian reefs was relatively less affected by resident piscivores than on Bahamian reefs. However, results clearly demonstrate that resident piscivores had strong negative effects on recruitment and recruit mortality. I hypothesize that the resident piscivores manipulated in both the Bahamian and Australian study are relatively unaffected by structural complexity because they are primarily ambush predators, which are often not adversely affected by increased habitat complexity (James and Heck 1994, Flynn and Ritz 1999).

How did adult damselfishes influence damselfish recruitment and final recruit abundance? On both Australian and Bahamian reefs, effects of adult damselfish occurred early, within 48 hours of settlement. If adult damselfishes are aggressive towards recruits, such aggression could cause direct mortality or make recruits more susceptible to predation from resident and/or transient piscivores, especially if aggression excludes recruits from shelter (see also Carr et al. *in press*). Additionally, the relatively small size of newly settled damselfishes may have allowed adults of omnivorous species to prey on new settlers shortly after settlement when they are most vulnerable. In the Bahamian study, there was correlative evidence that adult damselfishes opportunistically consumed recruits; on several occasions I observed adults attack and consume disoriented recruits that had been captured for tagging or measuring and released. However, on Australian reefs, the negative effect of adult damselfishes on rabbitfish recruitment was most likely due to damselfish aggression and not damselfish predation because of the large size of newly settled rabbitfishes. After a few days on the reef, recruits were larger, more mobile, and had presumably found shelter, which could explain the absence of effects of adult damselfish on subsequent recruit mortality.

An important difference between the Australian study and the Bahamian study is that the negative effects of Bahamian damselfishes was identical to that of Bahamian piscivores, whereas on Australian reefs, negative effects of adult damselfishes were weaker than those of resident piscivores. Bahamian damselfishes likely had greater negative effects than their Australian counterparts, despite the fact that adult damselfishes were approximately 10 times more abundant in the present study, because Bahamian damselfishes were more aggressive and territorial (Williams 1980, Robertson 1996). Aggression by Bahamian damselfishes was more likely to have resulted in recruit mortality, either directly or indirectly, than the weaker aggression by Australian damselfishes. However, increased damselfish aggression may indirectly benefit some species. For example, Bahamian damselfishes had significant positive effects on the abundance of surgeonfish recruits in the absence of resident piscivores. Where resident piscivores had been removed, transient piscivores were the most likely source of recruit mortality. I frequently observed aggressive interactions between Bahamian damselfishes and jacks, and surgeonfish recruits may have benefited if foraging by transient piscivores was inhibited by damselfish aggression. There were no positive effects of adult damselfishes on other species in the present study, perhaps because of the weaker aggression by Australian damselfishes.

On Australian reefs, recruitment and mortality of the damselfish *Neopomacentrus cyanomos* was independent of both resident piscivores and adult damselfishes. While recruits of all other species and families were closely associated with the coral substrate, *N. cyanomos* recruits remained well above the reef where they fed on passing plankton with other planktivorous damselfishes and cardinalfishes. These differences in behavior likely caused *N. cyanomos* recruits to be relatively unaffected by reef-associated residents and more influenced by transients, such as jacks, which often feed on planktivorous fishes above reefs (Hixon and Carr 1997, Webster 2002).

Species richness of final recruit assemblages on Australian reefs was negatively influenced by resident piscivores but independent of adult damselfishes. Butterflyfish and rabbitfish recruits were completely absent from piscivore-occupied reefs, suggesting that successful recruitment of these families may depend on the availability of piscivore-free patches. Similarly, Bahamian resident piscivores negatively influenced the species richness of recruit assemblages. In both studies, it appeared that resident piscivores prevented establishment of rare species, most likely through non-selective predation, or perhaps by disproportionately consuming rare species (Van Valen 1974, Hixon 1986).

Are priority effects common in coral reef fish communities?

Factorial removal of resident piscivores and adult damselfishes demonstrated that prior residency by these fishes strongly influenced the recruitment of other species on Bahamian and Australian reefs. Because priority effects were strong and taxon-specific, these effects likely influenced the subsequent structure of both fish communities and may therefore provide a means of predicting future community structure based on current community composition. The qualitative similarity between the results of both studies suggests that priority effects may be widespread and of general importance in coral reef fish communities (see also Shulman et al. 1983). This conclusion seems especially warranted given that the studies were conducted in systems that represent opposite ends of the global spectrum of coral reef ecosystems. In general, western Atlantic coral reefs are orders of magnitude less diverse than Indo-Pacific reefs (Thresher 1991). Within the western Atlantic, Bahamian reefs are less diverse than most other sites, perhaps because the Bahamas are primarily subtropical and highly seasonal (Bohlke and Chaplin 1993). In contrast, the northern Great Barrier Reef is tropical,

relatively non-seasonal, and highly diverse. Despite these substantial differences, similar priority effects influenced the reef fish communities at both sites.

CHAPTER 4: DIFFERENTIAL RESPONSES OF JUVENILE AND ADULT CORAL REEF FISHES TO HABITAT COMPLEXITY AND PRIOR RESIDENCY BY PREDATORS AND COMPETITORS

ABSTRACT

Greater habitat complexity is often associated with greater abundance of organisms. More complex habitats may ameliorate negative interactions (competition and predation) between individuals, thereby allowing more individuals to occupy a given area. Using 16 spatially isolated reefs in the Bahamas, I conducted two experiments that examined how juvenile (recruit) and adult reef fishes respond to differences in habitat complexity, and whether negative effects of resident predators and interference competitors are modified by habitat complexity. In the first experiment, manipulating the relative abundance of low and high complexity corals on each reef created two levels of habitat complexity. One month later, both new recruits and adult fishes were more abundant on high complexity reefs. In a second 60-day experiment, habitat complexity treatments were cross-factored with the presence or absence of two guilds of resident fishes: predators (groupers and moray eels) and interference competitors (territorial damselfishes). Resident predators and competitors had strong negative effects on the abundance of recruits regardless of habitat complexity, but had no effect on adult abundance. Increased habitat complexity had a weak positive effect on recruit abundance and a strong positive effect on the abundance of adult fishes. Various lines of evidence suggest that the differential response of recruits and adults to differences in habitat complexity and prior residents is related to the differential effects of habitat complexity on the primary predators of recruits and adults. Newly settled recruits, which are typically strongly reef-associated, are likely to be most influenced by smaller resident predators, while larger adult fishes

that forage beyond the reef and use reefs primarily for shelter are likely most influenced by larger transient predators, such as barracudas. Increased structural complexity appeared to inhibit foraging by larger transient predators that actively chase their prey, but not smaller resident predators, which primarily use ambush tactics to capture prey. These results underscore the importance of habitat complexity in coral reef fish communities, which is of growing concern given the accelerated loss of structurally complex corals worldwide.

INTRODUCTION

Structural complexity is a major determinant of the local abundance of organisms in that relatively highly complex habitats typically support more individuals (Bell et al. 1991). One mechanism proposed to explain this general pattern is that complex habitats ameliorate negative biotic interactions, especially predation and competition (Holt 1987, Hixon and Menge 1991, O'Conner 1991). Structurally complex habitats can reduce predation by both providing more prey refuges and reducing encounter rates between predators and prey (Murdoch and Oaten 1975, Sih 1987). Numerous studies have demonstrated that complex habitats reduce predation risk in a wide range of taxa, including insects (Pierce 1988), fishes (Lindholm et al. 1999), amphibians (Babbitt and Tanner 1998), birds (Schneider 1984), and mammals (Dickman 1992). Prey often increase their use of structurally complex habitats as refugia in the presence of predators (Holbrook and Schmitt 1988, Sih et al. 1992, Candolin and Voigt 1998), and predators tend to be less efficient foragers in complex habitats (Greenberg et al. 1995, Tatrai and Herzig 1995, Beukers and Jones 1997). Importantly, the influence of habitat complexity on predation may depend on a predator's foraging tactics. For example, predators that actively pursue prey are often less efficient in high complexity habitats, while

sit-and-wait predators may be unaffected by increased habitat complexity (James and Heck 1994, Flynn and Ritz 1999).

Structurally complex habitats may also ameliorate competition between individuals and species because they provide a greater spectrum of discrete resources (e.g., food and shelter) and microhabitats, and thus allow for enhanced niche partitioning (MacArthur and Levins 1964). Although this mechanism has typically been proposed to explain the general pattern of higher species diversity in complex habitats (e.g., Kohn 1967, Pianka 1967, Luckhurst and Luckhurst 1978), an implicit prediction is that the overall abundance of organisms pooled across species will also be greater in high complexity habitats.

Coral reefs are structurally heterogeneous environments, which consist of many different microhabitats that vary in their complexity depending on coral architecture (Jones and Syms 1998). Several studies of coral reef fishes have suggested that habitat complexity is a major determinant of abundance. For example, abundance is often positively associated with high habitat complexity (Luckhurst and Luckhurst 1978, Hixon and Beets 1993, Grigg 1994, McCormick 1994; but see Robertson and Sheldon 1979, Booth and Beretta 1994), increases as the number of potential shelter sites increases (e.g., Shulman 1984, Roberts and Ormond 1987, Friedlander and Parrish 1998), and the availability of suitably-sized shelter can influence both the abundance and size distribution of fishes (Hixon and Beets 1989, review by Williams 1991). Furthermore, reef fish are known to compete for shelter (Shulman 1985a, Buchheim and Hixon 1992) although shelter may not always limit abundance (Robertson and Sheldon 1979). These patterns illustrate the potential importance of habitat complexity in coral reef fish communities, although most studies have not identified the causative mechanisms responsible for these relationships (Shulman 1985b, Caley and St. John 1996, Ault and Johnson 1998a).

Relationships between habitat complexity and abundance could arise from several processes, such as habitat selection by settling larvae, postsettlement

immigration and emigration, and differential mortality. For example, many studies have reported positive relationships between recruit abundance and the availability of particular microhabitats, inferring that settling larvae actively choose specific microhabitats as settlement sites (e.g., Booth and Beretta 1994, Tolimieri 1995, Caselle and Warner 1996). However, correlations between recruit abundance and habitat type could also arise from differential mortality, and unequivocal demonstrations that such patterns are caused by larvae actively selecting settlement sites is rare (but see Elliot et al. 1995, Danilowicz 1996). Patterns of abundance may also be established and modified by the postsettlement movement of both juvenile fish (e.g., Frederick 1997, Lewis 1997) and adults (e.g., Zeller 1997, Chapman and Kramer 2000). For example, many species of reef fish undergo ontogenetic shifts in habitat (e.g., Lirman 1994, Dahlgren and Eggleston 2000) and frequently change home range locations (e.g., Bartels 1984, van Rooij et al. 1996). Additionally, differential postsettlement mortality can generate and modify relationships between abundance and habitat complexity (Jones 1988). For example, Beukers and Jones (1997) found that a highly complex coral reduced the feeding efficiency of small predatory fishes preying on damselfish recruits, resulting in higher recruit abundance on that coral.

Independent of habitat complexity, patterns of abundance can be influenced by postsettlement predation and competition. For example, the presence of reef-associated (resident) predators typically results in lower recruit abundance of most species, presumably because newly settled fishes are especially vulnerable to predation (Shulman et al. 1983, Carr and Hixon 1995, Hixon and Carr 1997, Webster 2002, Almany *in review-b*). Resident predators may also influence the abundance of adult fishes (review by Hixon 1991). Furthermore, predation by widely ranging non-resident (transient) predators, such as jacks, snappers, and barracudas, can negatively affect recruit abundance (Hixon and Carr 1997). Prior residency by interference competitors, such as territorial damselfishes, can result in both positive and negative effects on recruit abundance. For example, damselfishes

have been shown to either depress (Shulman et al. 1983, Sweatman 1983, 1985, Jones 1987, Risk 1998, Almany *in review-b*) or enhance (Almany *in review-b*) heterospecific recruit abundance, and either depress (Sale 1976, Almany *in review-b*) or enhance (Sweatman 1983, 1985, Jones 1987, Booth 1992) conspecific recruit abundance. Additionally, the presence of territorial damselfishes can negatively affect the adult abundance of other species (Robertson 1996).

Although these examples demonstrate that predation and competition can influence abundance, we know relatively little about whether and how these processes are influenced by habitat complexity. Here I report the results from two related field experiments that tested how, first, habitat complexity, and second, the interaction between habitat complexity and prior residency by predators and interference competitors influenced the abundance of both recruit and adult fishes on isolated patch reefs in the Bahamas. Specifically, I addressed the following questions: (1) does altering habitat complexity influence recruit and adult abundance, and (2) do effects of resident predators and interference competitors change with differences in habitat complexity?

METHODS

Study site

This study was conducted near the Caribbean Marine Research Center at Lee Stocking Island, Bahamas. Lee Stocking Island is part of the Exuma archipelago, which separates the deep waters (>2000 m) of Exuma Sound to the east from the shallow (<5 m) Great Bahama Bank to the west (Fig. 4.1A). Experiments were performed on a unique matrix of live-coral patch reefs that were

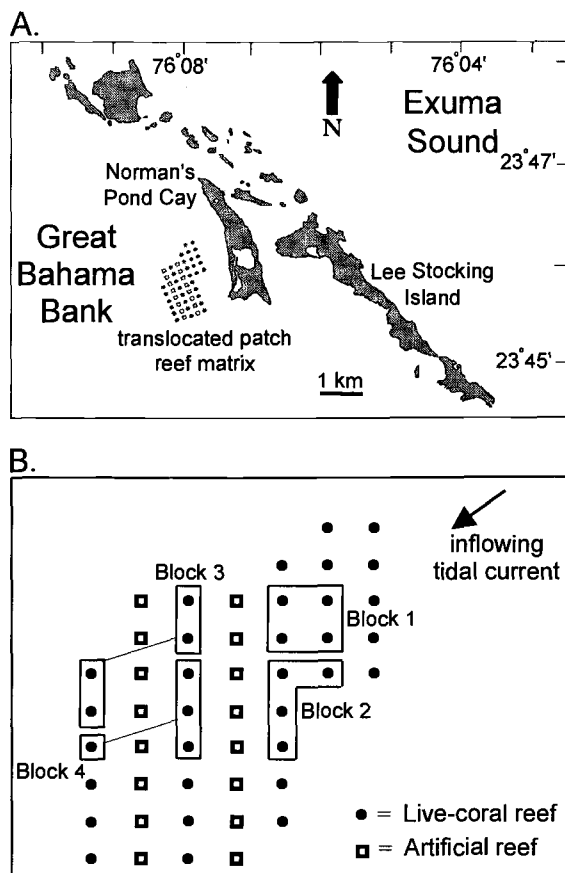


Figure 4.1: Study site. (A) Position of translocated patch reef matrix with respect to nearby islands. (B) Spatial arrangement of reefs and the blocking scheme used in experiment 2, cross-factoring habitat complexity with the presence and absence of resident piscivores and territorial damselfishes. Unused artificial reefs were constructed of concrete blocks. Each reef is separated from its closest neighbor by 200 meters of sand and seagrass.

translocated to a featureless sandy seagrass bed on the leeward side of Norman's Pond Cay between 1991 and 1994 (Carr and Hixon 1995, Hixon and Carr 1997). The matrix included 32 reefs in five rows. Water depth varied between 2 and 5 meters. Each reef was separated from its nearest neighbor by 200 m, and the closest naturally occurring reef was >1 km from the edge of the matrix (Fig. 4.1B). Prior to manipulation, each reef consisted of 9 to 13 coral heads ($\bar{x} = 10.8$, SD =

1.5) of primarily three species: *Montastrea annularis*, *Porites asteroides*, and *Siderastrea siderea*. The average (SD) reef footprint was 6.6 m² (1.0 m²) and height was 0.5 m (0.07 m). A tagging study demonstrated that resident fishes seldom moved between reefs in the matrix, although transient predators, such as jacks (*Caranx* spp.), snappers (*Lutjanus* spp.), and barracudas (*Sphyraena barracuda*) did so (M. A. Hixon, *personal communication*). Therefore, the disappearance of any newly settled recruit was attributed to mortality, and each reef was considered an independent experimental unit.

Study species

I manipulated the presence and absence of two guilds of resident fishes: predators and interference competitors. Resident predators were identified using two criteria: (1) a diet of $\geq 10\%$ fishes by volume (Randall 1967) and (2) a strong tendency to retreat to the reef (as opposed to fleeing the reef) when approached by a diver. Resident predators consisted of seven species of piscivorous fishes: four diurnally active groupers (Serranidae: *Cephalopholis cruentata* [graysby], *C. fulva* [coney], *Epinephelus striatus* [Nassau grouper], and *Serranus tigrinus* [harlequin bass]), one nocturnally active grouper (Serranidae: *Rypticus subbifrenatus* [spotted soapfish]), and two nocturnally active moray eels (Muraenidae: *Gymnothorax moringa* [spotted moray] and *G. vicinus* [purplemouth moray]). Interference competitors consisted of two species of territorial damselfish (Pomacentridae): *Stegastes leucostictus* (beaugregory), and *S. partitus* (bicolor). Adults of both species are aggressive towards nearly all other fishes (Robertson 1996). *Stegastes leucostictus* is omnivorous, consuming algae, detritus, polychaetes, and fish material, whereas *S. partitus* is primarily planktivorous (Randall 1967, Emery 1973).

Experimental design

Experiment 1 – To test for effects of habitat complexity on recruit and adult abundance (for both experiment 1 and 2, "adults" were defined as individuals that had settled during the prior year or previously), I conducted experiments on 16 of the 32 translocated patch reefs during the 1999 summer settlement season. I selected the 16 reefs that had the most similar fish communities prior to any manipulation based on Cluster Analysis (Bray-Curtis Distance and Group Average). I then increased habitat complexity on eight randomly selected reefs and decreased habitat complexity on the remaining eight reefs. On reefs assigned to the "high complexity" treatment, I removed half of the existing coral heads and replaced them with an equal volume of *Agaricia tenuifolia*, a highly branched foliaceous coral. On reefs assigned to the "low complexity" treatment, I removed half of the existing coral heads and replaced them with an equal volume of relatively low complexity massive coral of three different species: *M. annularis*, *S. siderea*, and *Porites porites*. After habitat manipulations, I estimated each reef's volume assuming a cylindrical shape. To obtain quantitative measures of habitat complexity, I established two perpendicular transects across each reef. Along each transect, I measured: (1) topographic complexity, defined as the ratio between the length of a fine-link chain allowed to conform to the coral topography along the transect and the straight-line length of the transect (Risk 1972), (2) depth of each potential shelter hole, (3) diameter of each hole, and (4) number of holes (cf. Roberts and Ormond 1987). I averaged data collected from the two transects on each reef to obtain a reef average for complexity measures (1-3), and the total number of potential shelter holes on each reef was estimated by summing hole counts from the two transects on that reef. After habitat manipulations, I conducted a complete census of each reef and removed any existing recruits. Thirty-two days later, I conducted another complete census of each reef.

Experiment 2 – To test for the combined effects of (1) habitat complexity and (2) prior residency by predators and interference competitors on recruit and adult abundance, I cross-factored the previously established habitat complexity treatments (high or low) with the presence or absence of piscivores and territorial damselfishes (both guilds present or both guilds absent). The goal of this second experiment was to determine whether habitat complexity modifies the effects of predators and interference competitors. I selected four blocks of reefs, each block containing four reefs (two high complexity and two low complexity), using two criteria: (1) reefs within each block had similar communities of fishes before the experiment began, thereby minimizing potential confounding effects of variable species composition, and (2) reefs within each block were close to each other to minimize possible confounding effects of patchy larval supply (Fig. 4.1B). To meet the first criterion, I manipulated the fish communities on each of the 16 reefs via selective removals such that the relative and total abundance of each species was similar among reefs. Within each block, high and low complexity reefs were randomly assigned to one of two resident fish treatments, creating a total of four treatments ($n = 4$ reefs each): (1) piscivores and damselfishes present, low habitat complexity; (2) piscivores and damselfishes absent, low habitat complexity; (3) piscivores and damselfishes present, high habitat complexity; and (4) piscivores and damselfishes absent, high habitat complexity. All fish manipulations were conducted using the fish anesthetic quinaldine, hand nets, and a BINCKE net (Anderson and Carr 1998). Piscivore and damselfish densities varied between blocks (3 to 6 piscivores and 2 to 4 damselfishes per reef), but were similar within blocks, and reflected the natural range of densities in the matrix prior to manipulations. After removing any existing recruits from each reef, I monitored subsequent cumulative recruitment by conducting a visual census of each reef every three days for 60 days. “New settlers”, recruits observed for the first time, were identified by their incomplete pigmentation and small size. Mortality rates for each treatment over the 60-day period were calculated in two ways: (1) number of

Disappearances (D) divided by the number of Observed New Settlers (ONS), and (2) by assuming that the average number of new settlers observed on the two treatments where predators and competitors had been removed, the Estimated Number of Settlers (ENS), also settled to the two treatments where predators and competitors were present. I estimated mortality on the two treatments where residents were present as $[(ENS-ONS + D) / ENS]$. At the conclusion of the experiment, two divers conducted a complete, independent census of each reef and estimated the total length (TL) of each fish. Length estimates were averaged between the two independent censuses. To determine the long-term effects of habitat manipulations, I conducted another complete census of each reef one year after the start of this experiment.

To determine whether potential shelter holes on low and high complexity reefs were likely to provide refuges from predation and/or interference competition, I compared the distribution of body depths of all resident predators and interference competitors with the distribution of hole diameters on both low and high complexity reefs. I converted total length estimates to body depths using the ratio between these two measures obtained from five specimens of each resident piscivore and damselfish species. Similarly, for those fish families whose adult abundance differed in response to habitat complexity treatments, I converted the total length estimate for each adult to body depth and compared body depth distribution with hole diameter distribution on both low and high complexity reefs.

Data analysis

In the first experiment, I compared differences in recruit abundance, adult abundance, reef volume, topographic complexity, number of potential shelter holes, hole depth, hole diameter, and changes in adult abundance of each fish family on high and low complexity reefs using two-sample t-tests. In the second experiment,

I compared changes in adult abundance of each fish family on low and high complexity reefs with two-sample t-tests, and differences in recruit abundance, adult abundance (excluding manipulated residents), and recruit mortality among the four treatments with two-way ANOVA (model terms: Blocks, Complexity, Prior Residents, and Complexity x Prior Residents interaction) (Sokal and Rohlf 1995). When interaction terms were significant ($P \leq 0.05$), I calculated effect sizes and 95% confidence intervals, and conducted linear contrasts of the means for each possible comparison. When interaction terms were not significant ($P\text{-value} \geq 0.20$), I removed the interaction term, refit the additive model, and calculated effect sizes and 95% confidence intervals (Zar 1999). All interaction terms had P -values that were either ≤ 0.05 or ≥ 0.20 . I compared recruit abundance on the last day of each experiment because final recruit abundance is logically the best predictor of future community structure. Additionally, in the second experiment, recruitment patterns both continued to diverge at the conclusion of the experiment and were consistent with the trajectories observed throughout. In most cases, I limited analyses to family-level comparisons since most species in each family utilize resources similarly in this system and major guilds occur at the family level (e.g., Randall 1967, Gladfelter and Johnson 1983, McAfee and Morgan 1996, Tilghman et al. 2001). To insure that ANOVA assumptions were met, I tested for homogeneity of variance using Levene's Test and examined normal probability plots (Ramsey and Schafer 1997). I compared differences in recruit abundance and adult abundance on low and high complexity reefs after one year using two-sample t-tests. All statistical analyses were performed using SAS Institute statistical software (SAS version 8.0 and JMP version 4.1).

RESULTS

Effects of habitat complexity alone

Recruit Abundance – Thirty-two days after habitat manipulations, total abundance of new recruits was significantly greater on high complexity reefs (t-test: $P = 0.032$; mean [SE]: low complexity = 4.3 [1.8], high complexity = 12.1 [2.7]). High complexity reefs had a greater abundance of damselfish recruits (mean [SE]: low complexity = 1.9 [1.3], high complexity = 3.5 [0.8]) and wrasse recruits (Labridae; mean [SE]: low complexity = 1.3 [0.8], high complexity = 4.5 [2.3]). After one year, there was no difference in the number of recruits present on low and high complexity reefs (t-test: $P = 0.736$; mean [SE]: low complexity = 11.0 [2.5] recruits, high complexity = 12.5 [3.6] recruits).

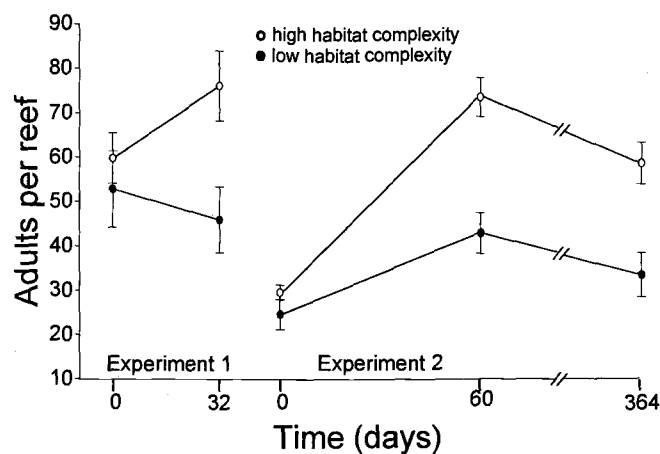


Figure 4.2: Relationships between habitat complexity and abundance of adult fishes. Habitat complexity treatments consisted of high and low complexity reefs ($n = 8$ reefs each). (A) Change in abundance during experiment 1 (32 days). (B) Change in abundance during experiment 2 (60 days). Between the end of experiment 1 and beginning of experiment 2, relative and total abundance of adult fishes was standardized among reefs via selective removals. (C) Change in abundance approximately one year after the end of experiment 2. Error bars are ± 1 SE. Note that the scale of both axes varies between plots.

Adult Abundance – Immediately after habitat manipulations, total abundance of adult fish did not differ between low and high complexity reefs (Fig. 4.2; t-test: $P = 0.510$; mean [SE]: low complexity = 52.8 [8.6], high complexity = 59.8 [5.7]). Thirty-two days after habitat manipulations, abundance had increased on high complexity reefs and decreased on low complexity reefs, such that the difference between them was significant (Fig. 4.2; t-test: $P = 0.040$; mean [SE]: low complexity = 42.1 [6.9], high complexity = 64.4 [7.0]). Changes in abundance on high and low complexity reefs were significantly different for three families: grunts (Haemulidae; t-test: $P = 0.004$; mean [SE]: low complexity = 3.3 [1.4], 27% decrease; high complexity = 4.0 [1.5], 24% increase), surgeonfishes (Acanthuridae; t-test: $P = 0.011$; mean [SE]: low complexity = 1.8 [0.8], 41% decrease; high complexity = 1.1 [0.5], 21% increase), and parrotfishes (Scaridae; t-test: $P = 0.017$; mean [SE]: low complexity = 1.6 [0.8], 54% decrease; high complexity = 1.0 [0.5], 29% increase). Approximately one year later, adult fish remained significantly more abundant on high complexity reefs (Fig. 4.2; t-test: $P = 0.004$; mean [SE]: low complexity = 22.8 [4.7], high complexity = 45.6 [4.7]).

Effects of both habitat complexity and prior residents

In the following sections, (L) = low habitat complexity, (H) = high habitat complexity, (–) that piscivores and damselfishes had been removed, and (+) that piscivores and damselfishes were present, such that the four experimental treatments were L–, L+, H–, and H+.

Recruit Abundance – I observed a total of 268 new settlers of 17 species during the 60-day experiment. Final recruit abundance was significantly influenced by habitat complexity, strongly influenced by prior residents (two-way ANOVA: complexity $P = 0.016$, prior residents $P < 0.0001$), and there was no evidence for an interactive effect of the two factors (two-way ANOVA: interaction $P = 0.437$).

Independent of habitat complexity, removing prior residents increased final recruit abundance (\pm 95%CI) by 11.0 ± 3.3 recruits per reef, primarily due to higher damselfish recruit abundance in the absence of prior residents (mean [SE]: without prior residents = $13.6 [1.1]$ recruits; with prior residents = $2.8 [0.7]$ recruits). Independent of prior residents, high complexity reefs had 4.3 ± 3.3 more recruits per reef than low complexity reefs, also due to higher damselfish recruit abundance on high complexity reefs (mean [SE]: high complexity = $9.9 [2.3]$ recruits; low complexity = $6.5 [2.1]$ recruits). The average (SE) number of recruits per reef on each treatment at the end of the experiment was as follows: L- = $13.3 (1.1)$, L+ = $3.5 (1.5)$, H- = $18.8 (2.1)$, and H+ = $6.5 (1.6)$.

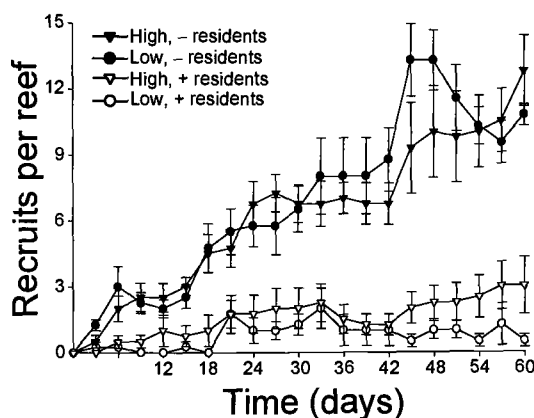


Figure 4.3: Effects of habitat complexity and prior residency by piscivores and adult damselfishes on recruitment of the beaugregory damselfish, *Stegastes leucostictus*. Relationship between cumulative recruitment (larval settlement minus mortality) and experimental treatments ($n = 4$ reefs each). Treatments consisted of two levels of habitat complexity (low and high) cross-factored with the presence (+) or absence (-) of resident piscivores and adult territorial damselfish. Error bars are ± 1 SE.

Of the 268 new settlers, 174 were *Stegastes leucostictus*, the beaugregory damselfish, by far the most abundant species. Final recruit abundance was

marginally affected by habitat complexity, strongly affected by prior residents (Fig. 4.3; two-way ANOVA: complexity $P = 0.053$, prior residents $P < 0.0001$), and there was no evidence for an interactive effect between the two factors (two-way ANOVA: interaction $P = 0.822$). Independent of habitat complexity, removing prior residents increased recruit abundance ($\pm 95\%CI$) by 10.0 ± 2.3 recruits per reef. Independent of prior residents, high habitat complexity increased recruit abundance by 2.3 ± 2.3 recruits per reef. The total number of new settlers observed on each treatment during the 60-day experiment was: L- = 77 recruits, L+ = 22 recruits, H- = 62 recruits, and H+ = 22 recruits.

There was a significant interactive effect of prior residents and habitat complexity on the mortality of beaugregory recruits (Fig. 4.4A; two-way ANOVA: interaction $P = 0.028$). In the presence of prior residents, high habitat complexity reduced recruit mortality ($\pm 95\%CI$) by $63\% \pm 25\%$ (linear contrast, $P = 0.0003$). In the absence of prior residents, high habitat complexity reduced recruit mortality by $22\% \pm 25\%$ (linear contrast, $P = 0.077$). The presence of prior residents increased recruit mortality by $14\% \pm 25\%$ on high complexity reefs (linear contrast, $P = 0.224$), and by $55\% \pm 25\%$ on low complexity reefs (linear contrast, $P = 0.0007$). However, when mortality estimates were re-calculated based on the assumption that approximately 70 new settlers recruited to each treatment, there was no interactive effect of habitat complexity and prior residents on recruit mortality (Fig. 4.4B; parallel lines indicate no interaction).

Adult Abundance – Abundance of adults did not differ significantly among the four treatments at the beginning of the experiment and after selective removals (Fig. 4.2; two-way ANOVA: $P = 0.825$). After 60 days, abundance was strongly affected by habitat complexity, independent of prior residents (Fig. 4.2; two-way ANOVA: complexity $P = 0.0009$, prior residents $P = 0.183$), and there was no evidence for an interactive effect of the two factors (two-way ANOVA: interaction $P = 0.464$). Abundance was greater on high complexity reefs by an average ($\pm 95\%CI$) of 30.6 ± 14.6 fishes per reef. Changes in abundance on high and low

complexity reefs were significantly different for three families: squirrelfishes (Holocentridae; t-test: $P = 0.011$; mean [SE]: low complexity = 0.1 [1.2], 6% decrease; high complexity = 6.6 [1.9], 280% increase), parrotfishes (t-test: $P =$

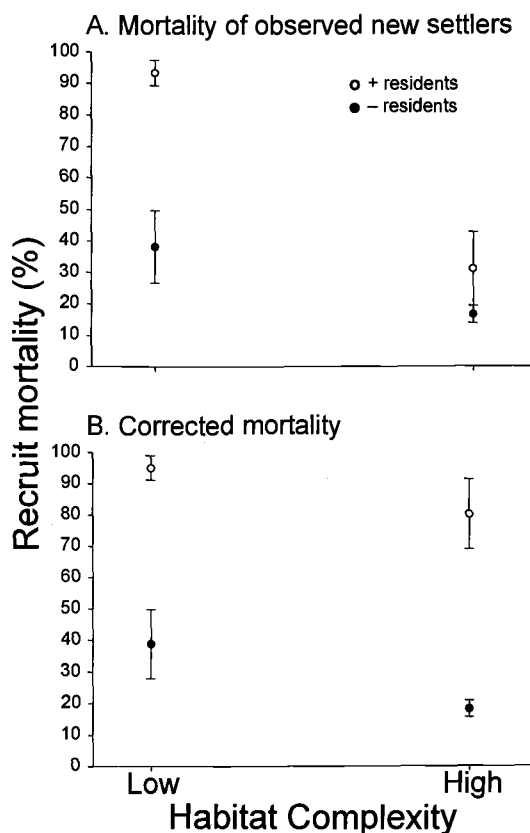


Figure 4.4: Effects of habitat complexity and prior residency by piscivores and adult damselfishes on mortality of beaugregory damselfish (*Stegastes leucostictus*) recruits. Treatments consisted of two levels of habitat complexity (low and high) cross-factored with the presence (+) or absence (–) of resident piscivores and adult territorial damselfish. (A) Average mortality of observed new settlers, calculated as (# of disappearances) / (# of observed new settlers). (B) Corrected recruit mortality, where mortality estimates were adjusted by assuming that the average number of settlers observed where prior residents had been removed (≈ 70 fish) also settled to the two treatments where they were present, and that the difference between settler counts in the presence and absence of prior residents was caused by early postsettlement mortality. Error bars are ± 1 SE. Note that Y-axis scale varies between plots.

0.044; mean [SE]: low complexity = 5.3 [1.0], 220% increase; high complexity = 13.4 [3.2], 430% increase), and goatfishes (Mullidae; t-test: $P = 0.013$; mean [SE]: low complexity = 0.6 [0.7], 71% increase; high complexity = 4.9 [1.2], 975% increase). Body depth distributions of all adult squirrelfish, parrotfish, and goatfish indicated that individuals tended to be larger on low complexity reefs, and that the body depth distribution of these fishes more closely matched hole diameter distribution on high complexity reefs than on low complexity reefs (Fig. 4.5A, B).

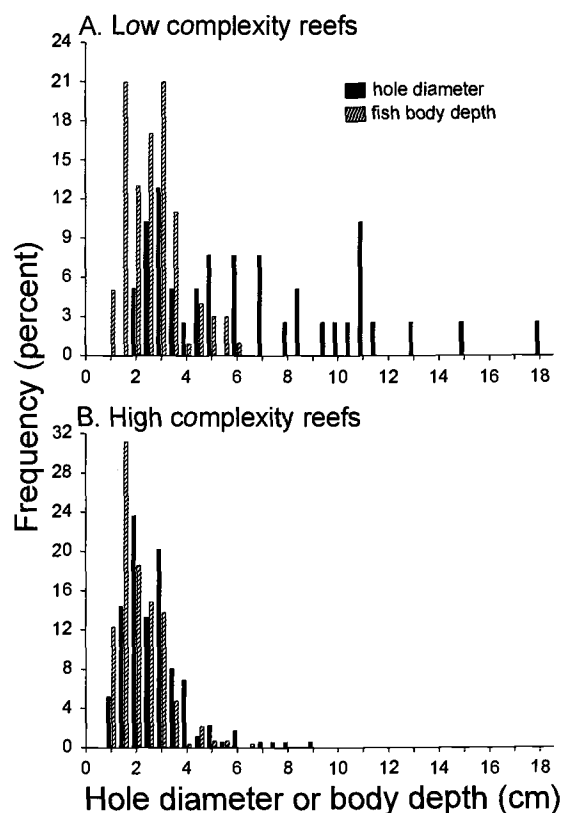


Figure 4.5: Comparison of frequency distributions of hole diameter and body depths of all adult squirrelfishes, parrotfishes, and goatfishes on low and high complexity reefs. These three families were significantly more abundant on high complexity reefs at the end of experiment 2. (A) Low complexity reefs: frequency distribution of hole diameter ($n = 39$ holes) and body depths of all adult squirrelfishes, parrotfishes, and goatfishes ($n = 100$). (B) High complexity reefs: frequency distribution of hole diameter ($n = 173$ holes) and body depths of all adult squirrelfishes, parrotfishes, and goatfishes ($n = 269$). Note that Y-axis scale varies between plots.

Habitat complexity and fish body depth

There was no evidence that reef volume differed between low and high complexity reefs (t-test: $P = 0.370$; mean [SE]: low complexity = 2.6m^3 [0.1], high complexity = 2.8m^3 [0.1]). In contrast, each of the four measures of habitat

complexity differed significantly between habitat complexity treatments. On average (SE), topographic complexity was greater on high complexity reefs (t-test: $P < 0.0001$; low complexity = 1.50 [0.02], high complexity = 1.95 [0.05]), potential shelter holes were more abundant on high complexity reefs (t-test: $P < 0.0001$; low complexity = 4.9 [1.0], high complexity = 21.6 [1.3]), deeper on low complexity reefs (t-test: $P < 0.012$; low complexity = 12.2 cm [0.8], high complexity = 9.3 cm [0.6]), and had larger diameters on low complexity reefs (Fig. 4.6A; t-test: $P < 0.0006$; low complexity = 6.5 cm [0.8], high complexity = 2.8 cm [0.1]). Body depth distributions of small resident piscivores (*Cephalopholis cruentata*, *C. fulva*, *Serranus tigrinus*, and *Rypticus subbifrenatus*) and damselfishes indicate that these fishes had access to most holes on both low and high complexity reefs (Fig. 4.6B, D), while larger Nassau grouper were excluded from most holes on both low and high complexity reefs (Fig. 4.6C).

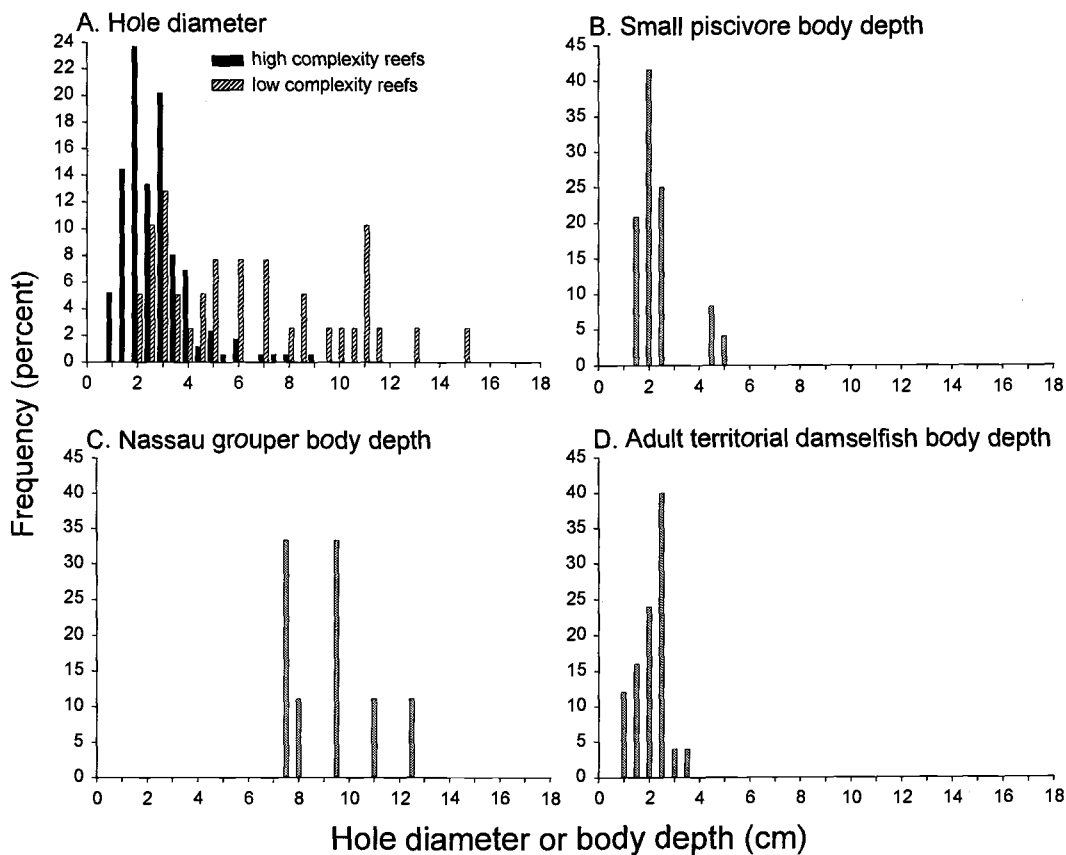


Figure 4.6: Frequency distributions of hole diameter and body depths of resident piscivores and adult territorial damselfishes. (A) Hole diameter distribution on high complexity reefs ($n = 173$ holes) and low complexity reefs ($n = 39$ holes) (t-test: $P < 0.0006$). (B) Body depth distribution of all small resident piscivores (four *Cephalopholis cruentata* [graysby], four *C. fulva* [coney], two *Serranus tigrinus* [harlequin bass], and 14 *Rypticus subbifrenatus* [spotted soapfish]). (C) Body depth distribution of all large resident piscivores (nine *Epinephelus striatus* [Nassau grouper]). (D) Body depth distribution of all resident adult territorial damselfishes (21 *Stegastes leucostictus* [beaugregory] and four *S. partitus* [bicolor]).

DISCUSSION

These experiments revealed a fundamental difference between recruits and adults in their response to differences in habitat complexity and prior residency by predators and interference competitors. Cross-factoring habitat complexity treatments with the presence and absence of resident piscivores and territorial damselfishes demonstrated that these residents reduced recruit abundance independent of habitat complexity, but did not influence adult abundance. In contrast, the abundance of adult fishes was consistently greater on high complexity reefs in both experiments. Additionally, high habitat complexity appeared to significantly reduce the mortality of beaugregory damselfish recruits in the presence of prior residents. These results suggest that both habitat complexity and prior residents influence the abundance of reef fishes, and that the influence of each factor on fish abundance depends on fish size.

Effects of habitat complexity and prior residents on recruits

In the first experiment, recruit abundance was significantly greater on high complexity reefs after one month. In the second experiment, recruit abundance was positively influenced by high habitat complexity, negatively influenced by the presence of predators and competitors, and prior-resident effects did not differ between habitat complexity treatments. Why were the negative effects of resident predators and competitors similar on both low and high complexity reefs? Based on comparisons of their body depths with hole diameter distributions, small resident piscivores and adult territorial damselfishes were not excluded from most holes on either high or low complexity reefs, suggesting that recruits were not able to use most holes as refugia from either predation or interference competition by residents. If true, why did high habitat complexity have a weak positive effect on

recruit abundance? Newly recruited fishes are not only subject to predation from resident predators, but also larger transient predators, such as widely ranging jacks. If increased habitat complexity decreases predation on recruits by one or both groups of predators, recruit abundance would be greater on high complexity reefs. Since small resident predators were not excluded from most potential shelter holes, it is unlikely that increased habitat complexity inhibited their foraging. However, larger transient predators were probably excluded from many potential shelter holes, thereby allowing recruits to use holes as refugia from predation by transient predators. If transient piscivores were less efficient foragers on high complexity reefs, this could explain the greater recruit abundance on high complexity reefs. Consistent with the hypothesis that mortality from transient predators was lower on high complexity reefs, beaugregory damselfish recruit mortality was 40% on low complexity reefs and 17% on high complexity reefs where resident predators and competitors had been removed. These results suggest that predation on recruits by transient predators was lower on high complexity reefs.

The presence of resident predators and competitors had a strong negative effect on the abundance of beaugregory damselfish recruits, and there was a weak, positive effect of high habitat complexity. Mortality of beaugregory recruits appeared to be influenced by an interaction between habitat complexity and prior residents – high habitat complexity significantly reduced recruit mortality in the presence of resident predators and competitors, but not in their absence, while the presence of predators and competitors significantly increased recruit mortality on low complexity reefs, but not high complexity reefs. These results suggest that increased habitat complexity mediated the negative effect of prior residents on recruit mortality. This conclusion is not supported by the pattern of similarly low recruit abundance on both high and low complexity reefs with predators and competitors at the end of the experiment, and the conclusion that resident effects are lessened by increased habitat complexity should be viewed with skepticism for several additional reasons. First, newly settled beaugregories were nearly three

times more abundant on reefs where prior residents had been removed relative to where they were present. This disparity could arise because (1) settling larvae avoided reefs where prior residents were present, or (2) mortality rates of new settlers differed substantially among treatments prior to censusing. The first mechanism is unlikely because a previous study in this system demonstrated that beaugregory settlers do not select or reject settlement sites based on the presence or absence of either resident piscivores or territorial damselfishes (Almany *in review-b*). It is therefore more likely that settlement was relatively even among treatments at the spatial scale of this experiment, and that differences in new settler counts were caused by high, differential postsettlement mortality among treatments before censuses. Several recent studies support the conclusion that early postsettlement mortality can quickly obscure patterns of settlement (Hixon and Carr 1997, Planes and Lecaillon 2001, Webster 2002, Almany *in review-b*). If settlement was even among treatments and high differential mortality among treatments generated the observed differences in new settler counts, then the estimated effect of prior residents on recruit mortality for high complexity reefs with prior residents was underestimated by approximately 50%, and the interactive effect between prior residents and habitat complexity becomes non-significant. Therefore, based on corrected mortality estimates, increased habitat complexity did not mediate the negative effect of prior residents on beaugregory recruit mortality.

In a recent study, I demonstrated that prior residency by adult territorial damselfishes reduced the abundance of damselfish recruits, both in the presence and absence of resident piscivores (Almany *in review-b*). How do adult territorial damselfishes affect damselfish recruits? In the presence of resident piscivores, aggression by adult damselfishes may make recruits more susceptible to predation by residents by excluding recruits from shelter (see also Carr et al. *in press*). In the presence or absence of resident piscivores, damselfish aggression may force recruits off or to the edge of reefs, thereby exposing recruits to transient predators (Sweatman and St. John 1990). Additionally, large omnivorous damselfishes, such

as the adult *Stegastes leucostictus* manipulated in this study, may directly affect recruit abundance by occasionally consuming newly settled recruits (Randall 1967, Almany *in review-b*).

Effects of habitat complexity and prior residents on adults

In the first experiment, the overall abundance of adult fishes was greater on high complexity reefs after one month. Specifically, the abundance of adults of three families – grunts, surgeonfishes, and parrotfishes – declined on low complexity reefs and increased on high complexity reefs. Caribbean species from these families feed in the sand on infaunal invertebrates (grunts) or graze on algae and seagrass (parrotfishes and surgeonfishes) surrounding reefs (Randall 1965, 1967, Parrish and Zimmerman 1977, Baelde 1990, Tilghman et al. 2001). Thus, these fishes are not strongly reef-associated, and primarily utilize reefs for shelter from predation (Parrish and Zimmerman 1977). Because parrotfishes, grunts, and surgeonfishes have relatively large home ranges and frequently move between reef shelter sites and feeding areas (Randall 1965, Baelde 1990, McAfee and Morgan 1996), it is likely that changes in their abundance were, in part, due to emigration from low complexity reefs and immigration to high complexity reefs. Additionally, differential mortality of adults between low and high complexity reefs, perhaps due to differences in shelter availability and therefore predation risk, may have influenced patterns of adult abundance.

In the second experiment, habitat complexity treatments were cross-factored with the presence and absence of resident predators and competitors. Overall abundance of adult fishes was again greater on high complexity reefs, and there was no evidence for an effect of resident predators and competitors on adult abundance. Specifically, adults from three families – squirrelfishes, parrotfishes, and goatfishes – were significantly more abundant on high complexity reefs.

Species from these families are again only loosely associated with reefs: squirrelfishes shelter on reefs by day, and leave reefs at night to feed on benthic crustaceans in sand and seagrass beds (Gladfelter and Johnson 1983), parrotfishes graze on algae and seagrass surrounding reefs, and goatfishes forage widely for infaunal invertebrates in sand and seagrass beds (Itzkowitz 1977, Parrish and Zimmerman 1977). Thus, the greater abundance of parrotfishes, squirrelfishes, and goatfishes on high complexity reefs could be due to immigration to these reefs, and differences in abundance between low and high complexity reefs may also have been influenced by differential adult mortality among treatments. A census one year later revealed that the overall abundance of adult fishes remained greater on high complexity reefs.

Why was there no effect of resident predators and competitors on the abundance of adult fishes, and why was adult abundance consistently greater on high complexity reefs? It seems likely that the loosely reef-associated adult parrotfishes, surgeonfishes, squirrelfishes, goatfishes, and grunts are relatively immune to predation from small ambush predators, such as most of the resident piscivores manipulated in this study, due to their comparatively large size (Munday and Jones 1998). The largest resident piscivore in this study, the Nassau grouper, was large enough to consume adult fishes, but comparisons of Nassau grouper body depth and hole diameter distributions on both habitat complexity treatments suggest that the majority of potential shelter holes provided effective refuges from predation by Nassau grouper. The primary source of mortality for less reef-associated fishes is likely to be larger transient piscivores, such as barracudas (Sphyraenidae), which frequently move among reefs in the experimental matrix (Hixon and Carr 1997). High habitat complexity may decrease predation by larger transient piscivores by providing more prey refuges and interfering with a predator's ability to chase prey. Consistent with the hypothesis that high complexity reefs provided a greater abundance of suitable shelter for adult fishes, the body depth distribution of all adult squirrelfish, parrotfish, and goatfish, which

were significantly more abundant on high complexity reefs, closely matched hole diameter distribution on high complexity reefs. In addition, adults from these three families were larger on low complexity reefs where potential shelter holes were significantly larger. The number and size of potential shelter holes present on a reef may influence both the abundance and size distribution of reef fishes, presumably because fishes select shelter sites that closely match their size, thereby minimizing predation risk (Shulman 1984, Hixon and Beets 1989, 1993). Additionally, because transient piscivores actively chase their prey, rather than ambush, increased habitat complexity may have interfered with their ability to chase and capture prey. Taken together, these results suggest that increased habitat complexity reduced predation on adults by transient predators, resulting in a greater abundance of adult fishes on high complexity reefs.

Conclusions: ontogenetic shifts in predation risk

These experiments highlight the differential responses of recruits and adults to habitat complexity and prior residency by piscivores and territorial damselfishes. Results indicate that the abundance of recruits was primarily determined by predation and/or competition from reef-associated residents, and that the negative effect of residents was equally strong on both low and high complexity reefs. In contrast, the abundance of adult fishes was primarily determined by habitat complexity and was independent of the presence and absence of resident predators and competitors. I hypothesize that the small reef-associated piscivores manipulated in this study, which are primarily ambush predators, are the most important source of mortality for recruits that are strongly reef-associated, although less reef-associated recruits are often most influenced by transient predators (see Hixon and Carr 1997, Webster 2002). Resident predators and competitors appear to have been unaffected by high habitat complexity, resulting in lower recruit

abundance where they were present. In contrast, the most important predators of larger and more mobile adult fishes are likely to be transient piscivores, which actively chase their prey and are typically larger than resident piscivores. High habitat complexity appears to have decreased predation on adults by transient predators, resulting in a higher abundance of adult fish on high complexity reefs.

The demonstration that habitat complexity can strongly influence the abundance of fish on coral reefs raises concerns given that many of the current threats to coral reefs strongly affect high complexity corals. High complexity coral species are more susceptible to damage caused by coral bleaching, siltation, pollution, and storm damage (review by Brown 1997). By causing a decline in overall reef complexity through the disproportionate destruction of complex corals, these disturbances are likely to have important consequences for coral reef fish communities and the human populations that depend on them (Jones and Syms 1998).

CHAPTER 5: GENERAL CONCLUSIONS

The combined results of these experiments clearly demonstrate that early postsettlement interactions between recruits and resident fishes play an important role in structuring coral reef fish communities. The primary conclusions derived from my research are: (1) interactions between newly settled recruits and resident predators and competitors strongly influenced recruit abundance, mortality, and species richness, (2) effects of prior residents on recruits were similar on both Bahamian and Australian patch reefs, suggesting that such effects are widespread, (3) there was no evidence that settling larvae choose settlement sites based on the presence or absence of resident predators and competitors, (4) effects of prior residents on recruits were not modified by changes in habitat complexity, (5) abundance of adult fishes was strongly influenced by habitat complexity, but not by the presence or absence of resident predators and competitors, and (6) the effects of resident predators and competitors on recruits was strongest within 48 hours after settlement, resulting in the rapid establishment of recruitment patterns.

In the experiments reported in Chapter 2, I found that prior residency by piscivores and adult territorial damselfishes strongly influenced recruit abundance, and did so in a species-specific manner. Piscivores inhibited recruitment of a damselfish and a surgeonfish, and enhanced recruitment of a wrasse, while prior residency by damselfishes inhibited recruitment of the damselfish and wrasse, and enhanced recruitment of the surgeonfish. The negative effect of piscivores on recruitment was almost certainly due to piscivores consuming newly settled recruits, which appear to be most vulnerable to predation shortly after settlement. The positive effect of piscivores on recruitment of the wrasse *Thallasoma bifasciatum* could be due to the fact that juveniles of this species are facultative cleaners, which might have experienced increased survival in the presence of predators due to a greater access to ectoparasites. Territorial damselfishes may

have had indirect negative effects on recruitment of other damselfishes and wrasse by chasing juveniles away from shelter and thereby exposing them to predation from resident piscivores, and/or by forcing them to the edge of the reef where they were susceptible to passing transient piscivores. Additionally, territorial damselfishes may directly influence recruitment by opportunistically consuming newly settled recruits. The positive effect of territorial damselfishes on surgeonfish recruitment could have been caused by damselfish aggression towards transient predators if such aggression inhibited predation by transient predators on surgeonfish recruits. In a second experiment, I found no evidence that settling larvae selected among settlement sites, either within or between reefs, based on the presence or absence of predators and competitors. This finding suggests that the effects of prior residents were the result of direct interactions between recruits and residents. The ability of larvae to detect residents prior to settling, perhaps through chemical or visual cues, would most likely evolve in species that live in dense social groups and derive benefits from settling to aggregations. High-density groups are a likely prerequisite because only under such conditions would chemical or visual cues be sufficiently strong to allow detection. For species that do not live in dense aggregations, such as the piscivores and territorial damselfishes in this study, chemical and visual cues are probably relatively weak or diffuse, thereby preventing the development of a reliable means to detect their presence. This is despite the fact that this ability would seem to be beneficial to recruits given that the effects of residents on recruits are often strongly negative. It appears that most larvae simply settle on any suitable reef.

In the study reported in Chapter 3, I found that prior residency by piscivores and damselfishes on Australian reefs resulted in negative effects on the recruitment of other fishes that were similar to the effects of prior residency by resident piscivores and damselfishes on Bahamian reefs. However, Australian piscivores had strong negative effects on recruitment of all species except the damselfish *Neopomacentrus cyanomos*, while adult Australian damselfishes only had negative

effects on recruitment of other damselfishes, except for *Neopomacentrus cyanomos*. The negative effect of Australian damselfishes was weaker than the negative effects of Bahamian damselfishes. Bahamian damselfishes likely had greater negative effects than their Australian counterparts, despite the fact that adult damselfishes were approximately 10 times more abundant on Australian reefs, because Bahamian damselfishes are more aggressive and territorial. Once again, the negative effects of adult damselfishes could have been due to adults chasing juveniles away from shelter or to the edge of reefs, thereby exposing them to predation by either resident or transient piscivores, and adults may have occasionally consumed newly settled recruits. Piscivores and damselfishes did not affect recruitment of the damselfish *Neopomacentrus cyanomos*, perhaps because this species settles and remains above the reef where it is not likely to be strongly affected by reef-associated resident predators and competitors, but rather more influenced by transient predators.

In the experiments reported in Chapter 4, I cross-factored the presence and absence of resident predators and competitors with two levels of reef habitat complexity, low and high. I found that recruit abundance was negatively affected by the presence of predators and competitors, and that resident effects did not differ between low and high complexity reefs. In contrast, high habitat complexity had a strong positive effect on the abundance of adult fishes, and resident predators and competitors did not influence adult fish abundance. I hypothesize that the different responses of recruit and adult fishes to differences in habitat complexity and prior residency by predators and competitors is due to the differential effects of habitat complexity on reef-associated predators and non reef-associated transient predators. Recruits are relatively small and highly sedentary, and thus their primary predators are probably small, reef-associated piscivores, such as most of the resident predators manipulated in this study. Because the resident predators in this study are primarily ambush predators, they are not likely to be negatively affected by increased habitat complexity, which would explain why resident effects did not

differ between low and high complexity reefs. In contrast, larger and more mobile adult fishes are unlikely to be strongly affected by smaller resident predators due to their relatively large size, but are most likely influenced by larger transient predators such as barracudas. Because transient predators actively pursue rather than ambush their prey, they are often less effective predators in high complexity environments, which would explain why adults were consistently more abundant on high complexity reefs, and why adult abundance was unaffected by resident predators and competitors.

In each of these studies, recruitment patterns were established rapidly after larval settlement: in Chapter 2 within 24 hours, in Chapter 3 within 48 hours, and in Chapter 4 within 72 hours. In each case, this represents the earliest census taken. In other words, it did not matter whether I censused reefs every 1, 2, or 3 days, settlement always appeared to be heavily modified by the time I arrived. Therefore, in each experiment, the effects of resident predators and competitors on newly settled recruits were strongest shortly after recruits had made the transition from the planktonic to benthic habitat. Based on the results of Chapter 1, these negative effects occur sometime between nocturnal settlement and the following morning. Newly settled fishes may be especially vulnerable to predation and interference competition immediately after settlement due to an unfamiliarity with their new surroundings and consequent difficulty in finding adequate shelter. Moreover, predation on new settlers is likely highest during dawn following settlement, when low, changing light levels favor piscivorous fishes that hunt by sight (Hobson 1991, McFarland 1991).

One criticism of studies on patch reefs is that results are difficult to extrapolate to larger continuous reefs. However, coral reefs are inherently patchy environments due to spatial variability in habitat structure, small-scale water movement, and coral distribution. In addition, individual patches are likely to be colonized by different species simply due to variations in larval supply and species-specific habitat preferences. The order in which species arrive to each patch will

influence the future dynamics of that patch because, as these studies show, residents and recruits interact with one another in a variety of ways that can influence recruit survival. For example, well-defined damselfish territories can occupy more than 50% of the total area of shallow-water continuous reefs (Sammarco and Williams 1982, Klumpp et al. 1987). Thus, the reef consists of patches of relatively favorable and unfavorable recruit habitat depending on how each species interacts with damselfishes. Similarly, many resident piscivores occupy spatially explicit home ranges, such as adult and subadult graysby, which forage in home ranges of 20 to 30 m² on continuous reefs (Sullivan and Sluka 1996). As a result, the reef is a patchwork of high and low predation risk areas based on the location of piscivore home ranges. Because many other fish species occupy home ranges, coral reefs are essentially a conglomeration of patches, each with its own occupants, and recruits are forced to interact with residents wherever they settle. Even in spatially continuous environments, this can lead to the development of dynamic patchiness (Levin 1974). Therefore, inasmuch as continuous reefs represent a mosaic of different patches, studies conducted on patch reefs may be useful in understanding the dynamics of fish communities on continuous reefs.

The combined results of these studies illustrate the importance of early postsettlement interactions in coral reef fish communities. Because resident-recruit interactions were often taxon-specific, these studies provide a qualitative means of predicting the future structure of coral reef fish communities based on their current composition. The results of my research do not support many views that are prevalent in studies of coral reef fishes, such as (1) coral reef fish communities are entirely stochastic and unpredictable assemblages (e.g., Sale 1980, Sale and Douglas 1984, Sale et al. 1994), (2) larval supply is generally insufficient to allow populations to achieve sizes at which postsettlement interactions are important (e.g., Doherty 1981, Victor 1983), (3) there is little postsettlement modification of larval settlement patterns (e.g., Doherty 1981, Victor 1983), and (4) recruitment

surveys can be used as indicators of larval supply and settlement (e.g., Williams et al. 1994). Rather, the results of my research suggest that (1) interactions between newly settled recruits and residents can introduce a level of determinism to the dynamics of coral reef fish communities, (2) larval supply is often sufficient to allow for postsettlement interactions to be important, (3) postsettlement interactions can strongly modify initial patterns of settlement, and (4) rapid modification of settlement patterns via strong resident-recruit interactions often prevents using recruitment surveys to estimate larval supply and settlement. Furthermore, demonstrating that habitat complexity plays an important role in determining the abundance and distribution of reef fishes should sound a warning given that many of the current threats to coral reefs disproportionately damage high complexity coral species. It is my sincere hope that my research has contributed to a greater understanding of coral reef fish communities, and that we can use our growing knowledge to save these fragile systems before they disappear.

BIBLIOGRAPHY

- Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. *Ecology* **66**:1097-1105.
- Allen, G. R. 1991. *Damselfishes of the World*. Mergus Publishers, Melle, Germany.
- Almany, G. R. *in review-a*. Differential responses of juvenile and adult coral reef fishes to habitat complexity and prior residency by predators and competitors. *Oecologia*.
- Almany, G. R. *in review-b*. Priority effects in coral reef fish communities. *Ecology*.
- Anderson, T. W., and M. H. Carr. 1998. BINCKE: A highly efficient net for collecting reef fishes. *Environmental Biology of Fishes* **51**:111-115.
- Arnal, C., I. M. Cote, P. Sasal, and S. Morand. 2000. Cleaner-client interactions on a Caribbean reef: influence of correlates of parasitism. *Behavioral Ecology & Sociobiology* **47**:353-358.
- Ault, T. R., and C. R. Johnson. 1998a. Relationships between habitat and recruitment of three species of damselfish (Pomacentridae) at Heron Reef, Great Barrier Reef. *Journal of Experimental Marine Biology & Ecology* **223**:145-166.
- Ault, T. R., and C. R. Johnson. 1998b. Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs* **68**:25-50.
- Babbitt, K. J., and G. W. Tanner. 1998. Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia* **114**:258-262.

- Baelde, P. 1990. Differences in the structures of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. *Marine Biology* **105**:163-173.
- Bartels, P. J. 1984. Extra-territorial movements of a perennially territorial damselfish, *Eupomacentrus dorsopunicans* Poey. *Behaviour* **91**:312-322.
- Beets, J. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. *Marine Ecology Progress Series* **148**:11-21.
- Bell, S. S., E. D. McCoy, and H. R. Mushinsky. 1991. *Habitat Structure: The physical arrangement of objects in space*. Chapman and Hall, London.
- Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* **142**:718-724.
- Beukers, J. S., and G. P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**:50-59.
- Blaber, S. J. M., D. A. Milton, N. J. F. Rawlinson, G. Tiroba, and P. V. Nichols. 1990. Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. *Fisheries Research* **8**:263-286.
- Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* **65**:77-84.
- Bohlke, J. E., and C. C. G. Chaplin. 1993. *Fishes of the Bahamas and adjacent territorial waters*, 2nd edition. University of Texas Press, Austin.

- Booth, D. J. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. *Journal of Experimental Marine Biology and Ecology* **155**:85-104.
- Booth, D. J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and demography. *Ecology* **76**:91-106.
- Booth, D. J., and G. A. Beretta. 1994. Seasonal recruitment, habitat associations, and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* **13**:81-89.
- Booth, D. J., and G. Wellington. 1998. Settlement preferences in coral-reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology* **23**:274-279.
- Brown, B. E. 1997. Disturbances to reefs in recent times. Pages 354-379 in C. Birkeland, editor. *Life and Death of Coral Reefs*. Chapman and Hall, New York.
- Buchheim, J. R., and M. A. Hixon. 1992. Competition for shelter holes in the coral-reef fish *Acanthemblemaria spinosa* Metzelaar. *Journal of Experimental Marine Biology and Ecology* **164**:45-54.
- Burrows, C. J. 1990. *Processes of vegetation change*. Unwin Hyman, Winchester, Massachusetts.
- Caley, M. J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. *Marine Biology* **117**:33-43.
- Caley, M. J., and J. St. John. 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology* **65**:414-428.
- Candolin, U., and H. R. Voigt. 1998. Predator-induced nest site preference: safe nests allow courtship in sticklebacks. *Animal Behaviour* **56**:1205-1211.

- Carr, M. H., T. W. Anderson, and M. A. Hixon. *in press*. Biodiversity, population regulation, and the stability of coral-reef fish communities. Proceedings of the National Academy of Science.
- Carr, M. H., and M. A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Marine Ecology Progress Series* **124**:31-42.
- Caselle, J. E., and R. R. Warner. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* **77**:2488-2504.
- Chapman, M. R., and D. L. Kramer. 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* **57**:11-24.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Cthamalus stellatus*. *Ecology* **42**:710-723.
- Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecological Monographs* **69**:277-296.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81**:2227-2240.
- Danilowicz, B. S. 1996. Choice of coral species by naive and field-caught damselfish. *Copeia* **1996**:735-739.
- Dickman, C. R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* **73**:313-322.

- Doherty, P. J. 1981. Coral reef fishes: recruitment-limited assemblages? *Proceedings of the Fourth International Coral Reef Symposium* **2**:465-470.
- Doherty, P. J. 1982. Some effects of density on the juveniles of two species of tropical, territorial damselfishes. *Journal of Experimental Marine Biology and Ecology* **65**:249-261.
- Doherty, P. J., and D. M. Williams. 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology Annual Reviews* **26**:487-551.
- Ehrlich, P. R. 1975. The population biology of coral reef fishes. *Annual Review of Ecology and Systematics* **6**:211-247.
- Elliot, J. K., J. M. Elliot, and R. N. Mariscal. 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Marine Biology* **122**:377-389.
- Emery, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bulletin of Marine Science* **23**:649-770.
- Flynn, A. J., and D. A. Ritz. 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom* **79**:487-494.
- Forrester, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**:1666-1681.
- Frederick, J. L. 1997. Post-settlement movement of coral reef fishes and bias in survival estimates. *Marine Ecology Progress Series* **150**:65-74.

- Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* **224**:1-30.
- Gladfelter, W. B., and W. S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology* **64**:552-563.
- Greenberg, L. A., C. A. Paszkowski, and W. M. Tonn. 1995. Effects of prey species composition and habitat structure on foraging by two functionally distinct piscivores. *Oikos* **74**:522-532.
- Grigg, R. W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* **103**:25-34.
- Hixon, M. A. 1986. Fish predation and local prey diversity. Pages 235-257 *in* G. M. Cailliet, editor. *Contemporary Studies on Fish Feeding*. Junk, Dordrecht.
- Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. Pages 475-508 *in* P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California.
- Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* **44**:666-680.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63**:77-101.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946-949.

- Hixon, M. A., and B. A. Menge. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology* **39**:178-200.
- Hixon, M. A., and M. S. Webster. *in press*. Density dependence in reef fish populations. *in* P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, CA.
- Hobson, E. S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. Pages 69-95 *in* P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California.
- Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* **69**:125-134.
- Holt, R. D. 1987. Prey communities in patchy environments. *Oikos* **50**:276-290.
- Huston, M., and T. Smith. 1987. Plant succession: life history and competition. *American Naturalist* **130**:168-198.
- Itzkowitz, M. 1977. Social dynamics of mixed-species groups of Jamaican reef fishes. *Behavioural Ecology and Sociobiology* **2**:361-384.
- Itzkowitz, M. 1979. The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum* (Pisces: Labridae). *Journal of Zoology* **187**:403-413.
- James, P. L., and K. L. Heck. 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of Experimental Marine Biology & Ecology* **176**:187-200.
- Jones, G. P. 1987. Some interactions between residents and recruits in two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **114**:169-182.

- Jones, G. P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **123**:115-126.
- Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. Pages 294-328 *in* P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Science* **402**:802-804.
- Jones, G. P., and C. Syms. 1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* **23**:287-297.
- Klumpp, D. W., D. McKinnon, and P. Daniel. 1987. Damselfish territories: zones of high productivity on coral reefs. *Marine Ecological Progress Series* **40**:41-51.
- Knowlton, N., and J. B. C. Jackson. 2001. The ecology of coral reefs. Pages 395-422 *in* M. E. Hay, editor. *Marine community ecology*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Kohn, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* in Indo-West Pacific reef platforms. *American Naturalist* **101**:251-259.
- Lawler, S. P., and P. J. Morin. 1993. Temporal overlap, competition, and priority effects in larval anurans. *Ecology* **74**:174-182.
- Leis, J. M. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. Pages 183-230 *in* P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California.

- Levin, S. A. 1974. Dispersion and population interaction. *American Naturalist* **108**:207-228.
- Lewis, A. R. 1997. Recruitment and post-recruit immigration affect the local population size of coral reef fishes. *Coral Reefs* **16**:139-149.
- Lindholm, J. B., P. J. Auster, and L. S. Kaufman. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **180**:247-255.
- Lirman, D. 1994. Ontogenetic shifts in habitat preference in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *Journal of Experimental Marine Biology and Ecology* **180**:71-81.
- Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* **49**:317-323.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceeding of the National Academy of Sciences* **51**:1207-1210.
- Mcafee, S. T., and S. G. Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology* **125**:427-437.
- McCormick, M. I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* **112**:87-96.
- McFarland, W. N. 1991. The visual world of coral reef fishes. Pages 16-38 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California.

- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:730-757.
- Morgan, S. G. 2001. The larval ecology of marine communities. Pages 159-181 in M. E. Hay, editor. *Marine community ecology*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Inc., Malden, Massachusetts.
- Munday, P. L., and G. P. Jones. 1998. The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review* **36**:373-411.
- Munday, P. L., and S. K. Wilson. 1997. Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *Journal of Fish Biology* **51**:931-938.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* **9**:1-132.
- O'Conner, N. A. 1991. The effects of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland stream. *Oecologia* **85**:504-512.
- Ostfeld, R. S., R. H. Manson, and C. D. Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* **78**:1531-1542.
- Parrish, J. D., and R. J. Zimmerman. 1977. Utilization by fishes of space and food resources on an off-shore Puerto Rican coral reef and its surroundings. *Proceedings of the Third International Coral Reef Symposium* **1**:297-303.

- Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. *Ecology* **48**:333-351.
- Pierce, C. L. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia* **77**:81-90.
- Planes, S., and G. Lecaillon. 2001. Caging experiment to examine mortality during metamorphosis of coral reef fish larvae. *Coral Reefs* **20**:211-218.
- Poulin, R., and W. L. Vickery. 1995. Cleaning symbiosis as an evolutionary game: to cheat or not to cheat? *Journal of Theoretical Biology* **175**:63-70.
- Ramsey, F. L., and D. W. Schafer. 1997. *The Statistical Sleuth: A Course in Methods of Data Analysis*. Duxbury Press, Belmont, California.
- Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. *Ecology* **46**:255-260.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**:665-847.
- Rice, J. A., L. B. Crowder, and K. A. Rose. 1993. Interactions between size-structured predator and prey populations: experimental test and model comparison. *Transactions of the American Fisheries Society* **122**:481-491.
- Risk, A. 1998. The effects of interactions with reef residents on the settlement and subsequent persistence of ocean surgeonfish, *Acanthurus Bahianus*. *Environmental Biology of Fishes* **51**:377-389.
- Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* **153**:1-6.

- Roberts, C. M. 1985. Resource sharing in territorial herbivorous reef fishes. *Proceedings of the 5th International Coral Reef Congress* **4**:17-22.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* **41**:1-8.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* **77**:885-899.
- Robertson, D. R., and V. C. Polunin. 1981. Coexistence: symbiotic sharing of feeding territories and algal food by some coral reef fishes from the western Indian Ocean. *Marine Biology* **62**:185-195.
- Robertson, D. R., and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *Journal of Experimental Marine Biology and Ecology* **40**:285-298.
- Sale, P. F. 1974. Mechanisms of co-existence in a guild of territorial fishes at Heron Island. *Proceedings of the Second International Coral Reef Symposium* **1**:193-206.
- Sale, P. F. 1976. The effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. *Journal of Experimental Marine Biology and Ecology* **24**:297-306.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *The American Naturalist* **111**:337-359.
- Sale, P. F. 1978. Coexistence of coral reef fishes - a lottery for living space. *Environmental Biology of Fishes* **3**:85-102.
- Sale, P. F. 1980. Assemblages of fish on patch reefs - predictable or unpredictable? *Environmental Biology of Fishes* **5**:243-249.

- Sale, P. F. 1991. Introduction. Pages 3-15 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, San Diego, California.
- Sale, P. F., and W. A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* **65**:409-422.
- Sale, P. F., J. A. Guy, and W. J. Steel. 1994. Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia* **98**:83-99.
- Sammarco, P. W., and A. H. Williams. 1982. Damselfish territoriality: influences on *Diadema* distribution and implications for coral community structure. *Marine Ecological Progress Series* **8**:53-59.
- Schmitt, R. J., and S. J. Holbrook. 1999. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* **80**:35-50.
- Schneider, K. J. 1984. Dominance, predation and optimal foraging in white-throated sparrow flocks. *Ecology* **65**:1820-1827.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* **74**:85-109.
- Shulman, M. J. 1985a. Coral reef fish assemblages: Intra- and interspecific competition for shelter sites. *Environmental Biology of Fishes* **13**:81-92.
- Shulman, M. J. 1985b. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**:1056-1066.

- Shulman, M. J., J. C. Ogden, J. P. Ebersole, W. N. Mcfarland, S. L. Miller, and N. G. Wolf. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* **64**:1508-1513.
- Sih, A. 1987. Predators and prey lifestyles: An evolutionary and ecological overview. Pages 203-224 *in* A. Sih, editor. *Predation. Direct and indirect impacts on aquatic communities*. University Press of New England, Hanover.
- Sih, A., L. B. Kats, and R. D. Moore. 1992. Effects of a predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology* **73**:1418-1430.
- Smith, C. L., and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Bulletin of the Natural History Museum of Los Angeles County* **14**:125-170.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of a teleost fish: a review. *Bulletin of Marine Science* **60**:1129-1157.
- Sokal, R. R., and F. J. Rohlf, editors. 1995. *Biometry*, 3rd edition. W. H. Freeman and Company, New York.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**:1225-1239.
- Steele, M. A. 1997. The relative importance of processes affecting recruitment of two temperate reef fishes. *Ecology* **78**:129-145.
- Stewart, B. D. 1998. Interactions between piscivorous coral reef fishes and their prey. Ph.D. Thesis. Department of Marine Biology, James Cook University, Townsville, Australia.

- Sullivan, K. M., and R. Sluka. 1996. The ecology of shallow-water groupers (Pisces: Serranidae) in the upper Florida Keys, USA. International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings **48**:74-84.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**:799-802.
- Sweatman, H. P. A. 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Marine Biology* **75**:225-229.
- Sweatman, H. P. A. 1984. A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the lizardfish *Synodus englemani*. *Copeia* **1984**:187-193.
- Sweatman, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecological Monographs* **55**:469-485.
- Sweatman, H. P. A. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *Journal of Experimental Marine Biology and Ecology* **124**:163-174.
- Sweatman, H. P. A., and J. St. John. 1990. Effects of selective settlement and of aggression by residents on distribution of young recruits of two tropical damselfishes. *Marine Biology* **105**:247-252.
- Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? *Ecological Monographs* **48**:425-440.
- Tatrai, I., and A. Herzig. 1995. Effect of habitat structure on the feeding efficiency of young stages of razor fish (*Pelecus cultratus*) - An experimental approach. *Hydrobiologia* **299**:75-81.

- Thresher, R. E. 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. Pages 401-436 in P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, San Diego.
- Tilghman, G. C., R. Klinger-Bowen, and R. Francis-Floyd. 2001. Feeding electivity indices in surgeonfish (Acanthuridae) of the Florida Keys. *Aquarium Sciences and Conservation* 3:215-223.
- Tolimieri, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia* 102:52-63.
- van Rooij, J. M., F. J. Kroon, and J. J. Videler. 1996. The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. *Environmental Biology of Fishes* 47:353-378.
- Van Valen, L. 1974. Predation and species diversity. *Journal of Theoretical Biology* 44:19-21.
- Victor, B. C. 1983. Recruitment and population dynamics of a coral reef fish. *Science* 219:419-420.
- Victor, B. C. 1991. Settlement strategies and biogeography of reef fishes. Pages 231-260 in P. F. Sale, editor. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego.
- Webster, M. S. 2002. Role of predators in the early post-settlement demography of coral-reef fishes. *Oecologia* 131:52-60.
- Webster, M. S., and G. R. Almany. *in review*. Positive indirect effects in a coral reef fish community. *Ecology Letters*.

- Wilbur, H. M., and R. A. Alford. 1985. Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* **66**:1106-1114.
- Williams, D. M. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bulletin of Marine Science* **30**:159-170.
- Williams, D. M. 1991. Patterns and process in the distribution of coral reef fishes. Pages 437-474 in P. F. Sale, editor. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego.
- Williams, D. M., S. English, and M. J. Milicich. 1994. Annual recruitment surveys of coral reef fishes are good indicators of patterns of settlement. *Bulletin of Marine Science* **54**:314-331.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th edition. Simon & Schuster, Upper Saddle River, New Jersey.
- Zeller, D. C. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series* **154**:65-77.