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**Factors influencing the distribution and abundance of the coral reef fish  
*Chromis cyanea***

by

Mitchell R. Smith

A Thesis  
Submitted to the  
Faculty of Graduate Studies and Research  
Through Biological Sciences  
in Partial Fulfillment of the Requirements for the Degree  
of Master of Science at the  
University of Windsor.

Windsor, Ontario, Canada

2006

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## ABSTRACT

The relative importance of factors influencing the distribution and abundance of coral reef fishes remains a central issue in coral reef fish ecology. Information pertaining to the complete life cycle of reef fishes is necessary in understanding recruitment and the subsequent processes influencing fishes in the reef environment. In this thesis, I report a study of the factors influencing the distribution and abundance of the coral reef fish *Chromis cyanea* (Pomacentridae). Here, I evaluate the influence of 1) larval growth and duration 2) small-scale microhabitat characteristics and 3) large-scale microhabitat characteristics, on recruitment. Although larval growth rate and the duration of larval life were significantly correlated, where individuals experiencing faster growth during the middle stage of larval life were settling significantly younger, neither larval growth nor duration could explain spatial or temporal variability in the recruitment of *C.cyanea*. Microhabitat characteristics at small spatial scales were found to significantly influence the recruitment of *C.cyanea*, in addition to the presence of resident conspecifics. However, microhabitat characteristics measured at sites separated by distances of up to tens of kilometers could not explain the observed variability in recruitment. These results suggest that, at large spatial and temporal scales, factors unrelated directly to larval traits and microhabitat characteristics determine spatio-temporal patterns in *C.cyanea* recruitment.

## **ACKNOWLEDGEMENTS**

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## **STATEMENT OF ORIGINALITY**

I hereby certify that the work embodied  
in this thesis is the result of original  
research and has not been submitted  
for a higher degree to any other  
University or Institution

## Table of Contents

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
STATEMENT OF ORIGINALITY.....	v
LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
<b>Chapter I</b>	
GENERAL INTRODUCTION.....	1
Study location and sampling.....	5
Study Species.....	6
LITERATURE CITED.....	11
<b>Chapter II – An analysis of pelagic larval duration and larval growth rate, and their influence on the recruitment of <i>Chromis cyanea</i>.....</b>	
ABSTRACT.....	14
INTRODUCTION.....	15
METHODS.....	17
RESULTS.....	21
FIGURES.....	24
TABLES.....	36
DISCUSSION.....	40
LITERATURE CITED.....	48

### **Chapter III - Factors influencing the small-scale recruitment of *Chromis cyanea***

ABSTRACT.....	52
INTRODUCTION.....	53
METHODS.....	56
RESULTS.....	60
FIGURES.....	62
TABLES.....	67
DISCUSSION.....	69
LITERATURE CITED.....	74

### **Chapter IV - The influence of habitat on the recruitment of *Chromis cyanea* across a large spatial scale**

ABSTRACT.....	80
INTRODUCTION.....	81
METHODS.....	83
RESULTS.....	85
FIGURES.....	87
TABLES.....	93
DISCUSSION.....	96
LITERATURE CITED.....	98

### **Chapter V**

GENERAL DISCUSSION.....	102
LITERATURE CITED.....	108



**VITA AUCTORIS.....111**

## LIST OF TABLES

<b>Table I-1.</b> GPS coordinates of ECONAR sampling sites and depths established along the Mesoamerican Barrier Reef System.....	9
<b>Table I-2.</b> Dates and lunar phases of recruitment censuses and collections at Banco Chinchorro, Mexico and Turneffe Atoll, Belize. ....	10
<b>Table II-1.</b> Sampling design for PLD, growth rate and recruitment analysis of <i>C.cyanea</i> recruits. Sites listed in bold were analyzed for spatial and temporal variability in recruitment and PLD/growth rates using separate two-way ANOVA's. Banco Chinchorro sites 5 and 6 during census period 1 were analyzed using PLD/growth ANOVA's, but recruitment data was not collected. Sites not bolded for Turneffe Atoll represent those where PLD/growth rates were determined for recruits, but were not included in ANOVA's due to design balancing.....	37
<b>Table II-2.</b> Results of two-factor ANOVA for dependent variable recruitment. Significant p-values are bolded. ....	37
<b>Table II-3.</b> Results of two-factor ANOVA's for dependent variable pelagic larval duration. Significant p-values are bolded.....	38
<b>Table II-4.</b> Results from two-factor ANOVA's for dependent variable growth rate. Separate ANOVA's were run for each location and growth stage. Significant p-values are bolded. ....	39
<b>Table III-1.</b> Microhabitat categories quantified for coral patches at study sites.....	68
<b>Table III-2.</b> Results of repeated measures ANCOVA of effects of conspecific presence on recruitment. Significant p-values are bolded.....	68
<b>Table IV-1.</b> Microhabitat types quantified within Turneffe Atoll, Belize.....	94
<b>Table IV-2.</b> Results of two-factor ANOVA of recruitment. Significant p-values are bolded.....	94
<b>Table IV-3.</b> Results of two-factor ANOVA site x position interactions for microhabitat characteristics measured across Turneffe Atoll (Df=13).....	95
<b>Table IV-4.</b> Component loadings from principal components analysis of microhabitat characteristics for position/site measurements.....	95

## LIST OF FIGURES

<b>Figure I-1.</b> ECONAR study locations along the Mesoamerican Barrier Reef System.....	7
<b>Figure I-2.</b> Locations and sites of recruitment censuses and collections of <i>C.cyanea</i> used in Chapters II and IV.....	8
<b>Figure II-1.</b> Mean recruitment per site/census period ( $\pm$ S.D.) measured for recruits in Banco Chinchorro 2002 (n=47) (top), Turneffe Atoll 2002 (n=347) (middle) and Turneffe Atoll 2003 (n=141) (bottom).....	25
<b>Figure II-2.</b> Distribution of PLD for <i>C.cyanea</i> measured across Banco Chinchorro, Mexico, and Turneffe Atoll, Belize (n=535).....	26
<b>Figure II-3.</b> Mean PLD per site/census period ( $\pm$ S.D.) measured for recruits in Banco Chinchorro 2002 (n=47) (top), Turneffe Atoll 2002 (n=347) (middle) and Turneffe Atoll 2003 (n=141) (bottom).....	27
<b>Figure II-4.</b> Mean larval growth rates ( $\pm$ S.D.) for whole, early, mid and late larval stages for all measured fish (n=535).....	28
<b>Figure II-5.</b> Mean daily increment width for census period and sites, Banco Chinchorro 2002 ( $\pm$ S.E.). Averages are across census periods 1,3 and 5 (n=535).....	28
<b>Figure II-6.</b> Mean daily increment width for census period and site averages, Turneffe Atoll 2002 ( $\pm$ S.E.). Whole duration, early stage (days 1-10), mid stage (days 11-20), and late stage (days 21+) growth rates are shown. Averages are across census periods 1, 2, 3 and 6 (n=347). Note the pattern of increasing growth rate throughout the larval life.....	29
<b>Figure II-7.</b> Mean daily increment width for site averages in Turneffe Atoll, 2003 ( $\pm$ S.E.). Site averages for whole, early, mid and late larval stages are across census periods 1,2,and 5 (n=141). Note the pattern of increasing growth rate throughout the larval life.....	29
<b>Figure II-8.</b> Mean otolith increment width ( $\pm$ S.D.) per site/census period for whole (top) and early (bottom) larval stages in Turneffe Atoll, 2002. (n=347).....	30
<b>Figure II-9.</b> Mean otolith increment width ( $\pm$ S.D.) per site/census period for mid (top) and late (bottom) larval stages in Turneffe Atoll, 2002. (n=347).....	31
<b>Figure II-10.</b> Mean otolith increment width ( $\pm$ S.D.) per site/census period for a) whole b) early c) mid and d) late larval stages in Turneffe Atoll, 2003. (n=141).....	32

<b>Figure II-11.</b> Mean otolith increment width ( $\pm$ S.D.) per site/census period for a) whole b) early c) mid and d) late larval stages in Banco Chinchorro, 2002. (n=47).....	33
<b>Figure II-12.</b> Mean daily growth versus mean PLD for site averages within single census periods (n=46). The above plots display whole, early, mid, and late larval stage growth.....	34
<b>Figure II-13.</b> Log(x+1) transformed total recruitment per site/census period versus PLD (n=46).....	35
<b>Figure II-14.</b> Log(x+1) recruitment per site/census period versus mean larval growth rate for a) whole, b) early, c) mid and d) late larval stages (n=46). Data points where recruitment is zero exist because recruits were not always collected at the exact locality where recruitment transects were performed within a site.....	35
<b>Figure III-1.</b> Location of North (N), Calabash (C), and South (S) sites within Calabash Caye, Turneffe Atoll, Belize.....	63
<b>Figure III-2.</b> Mean percent microhabitat cover for all coral patches within the three study sites ( $\pm$ S.E. n=21).....	64
<b>Figure III-3.</b> Mean percent microhabitat cover for removal and control patches ( $\pm$ S.E. n=21).....	64
<b>Figure III-4.</b> Number of recruits plus juveniles prior to removals of June 2005, post 10 weeks recolonization (August 2005), and 9 months post recolonization (April 2006) (n=15). Ca represents Calabash site, No North site and So South site. C1 and C2 represent control patches. Note that second removals were performed August 2005, 8 months prior to the April 2006 census.....	65
<b>Figure III-5.</b> Mean number of conspecifics vs. recruits ( $\pm$ S.E. ) on a) control (n=6) and b) removal (n=15) coral patches for bi-weekly census periods 1 through 4. Census period 1 represents two weeks post removals (for removal patches) of June, 2005. Note the magnitude of difference in mean recruitment between control and removal patches. All patches were analyzed for a conspecific effect through a single repeated-measures ANCOVA. The presence of conspecifics significantly influenced recruitment.....	66
<b>Figure IV-1.</b> Total number of <i>C.cyanea</i> recruits settling to deep and shallow positions within the 7 sites of Turneffe Atoll, Belize for all of 2002 and 2003.....	88
<b>Figure IV-2.</b> Average arcsine transformed microhabitat cover proportions per site for algae, encrusting coral, sponge and massive coral ( $\pm$ S.E.).....	89

**Figure IV-3.** Average arcsine transformed microhabitat cover per site for inert substrata, rubble, branching coral and gorgonian ( $\pm$ S.E.).....89

**Figure IV-4.** Average arcsine transformed microhabitat cover for all microhabitat types quantified at deep and shallow positions ( $\pm$ S.E.).....90

**Figure IV-5.** Mean position/site rugosity ( $\pm$ S.E.) for Turneffe Atoll.....90

**Figure IV-6.** PCA analysis of habitat features quantified at each depth for all 7 sites within Turneffe Atoll.....91

**Figure IV-7.** Rugosity and massive coral cover versus total recruitment of *C.cyanea* for deep and shallow positions within each of the seven sites in Turneffe Atoll for 2002 and 2003.....92

## **Chapter I: GENERAL INTRODUCTION**

It is the goal of ecologists to recognize and understand the factors that ultimately determine the distribution and abundance of organisms. Ecology is a science involving often complex study systems of biotic and abiotic interactions, and since the days of Clements (1905) ecologists have attempted to classify and understand ecological communities.

Coral reefs have provided ecologists with one of the most diverse ecological systems in the world to study (e.g. Connell 1978, Odum and Odum 1955). In addition to an abundance of other organisms, coral reefs house hundreds to thousands of fish species, representing an estimated one third of all marine fishes (McAllister 1991). Coral reef fishes serve as an important worldwide food source (approximately 10% of all consumed fish; Smith 1978), and are an important part of the coral reef ecosystems that drive an exploding tourism industry. With growing anthropogenic stresses, the need to understand coral reefs and the organisms that inhabit them has become apparent.

Since SCUBA was adopted as a means of studying coral reefs in the early 1960's, the field of coral reef fish ecology continues to evolve. From observational studies of the 1970's to genetic studies of the present day, researchers continue to work towards a better understanding of the factors involved in influencing the distribution and abundance of reef fishes. Part of the difficulty in understanding the ecology of reef fishes is the high diversity of species. Between-species variability exists in modes of reproduction (e.g. benthic vs. demersal spawners), size (centimeters to meters in length), feeding behavior (e.g. carnivore vs. planktivore),

and habitat use and movement (transient vs. territorial) among other differences (Sale 1991). However, despite this, the life of most reef fishes is a bipartite one, consisting of both pelagic and benthic stages. Subsequently, studies on the distribution and abundance of reef fishes are often focused on either pre-settlement factors, those factors influencing fishes during their pelagic larval life, or post-settlement factors, those factors influencing fishes at the time of settlement to a reef as juveniles on through to the adult life stage.

Studies focusing on post-settlement processes were historically prominent in reef fish ecology, and still make up a large part of the research body to date. Due largely to the abundance of fishes among the reef environment, mechanisms such as density-dependent competition (e.g. Hixon and Carr 1997, Anderson et al. 1981) and predation (Holbrook and Schmitt 2002, Forrester 1995) are commonly thought to be important factors determining the distribution and abundance of reef fishes. The basis for this belief is derived from the theory that resources are limited in the coral reef environment (Jones 1987). As a result, fish are believed to compete for food and refuge from predators (Webster 1984).

There is a relatively long history of studies evaluating habitat effects on reef fishes from the time of settlement to a reef on to the adult life stage (Helfman 1978, Sale 1977). Although studies on habitat effects are commonly carried out in the context of density-dependent resource availability as mentioned above, they can also be considered in relation to spatial variability in recruitment (e.g. Caselle and Warner 1996, Levin 1993), defined here as a measure of the replenishment of a population through time. Patterns in recruitment have been shown to correspond to

variability in reef habitat (Tolimieri 1998, Sale et al. 2005), and it has been suggested that habitat plays an essential role in determining subsequent reef fish assemblages (e.g. Munday 2002).

Although post-settlement processes have been shown to influence the distribution and abundances of fishes, a growing body of research pertaining to the larval life stage (Leis 1991) and recruitment (Doherty 1983) have created debate among reef fish ecologists as to the relative importance of pre- versus post-settlement factors (Levin 1994). Generally, the larval life stage is considered in context with the distribution and abundance of fishes through the study of recruitment. Recruitment has proven to be a stochastic process (Caley et al. 1996, Fowler et al. 1992, Doherty and Williams 1988), and presently we know little about the pelagic larval life stage and the pressures that lead to rates of pre-settlement mortality as high as 99% (Levin 1994). Measures of recruitment will reflect the mortality of pelagic larvae, in addition to the spawning behavior of adults, the duration of pelagic life, and hydrodynamics (Leis 1991). Knowledge of these four factors is essential in allowing us to better understand and predict the recruitment and population connectivity of reef fishes, which has implications in the designing of marine protected areas (see Armsworth 2002).

To date, the number of studies evaluating spatial and temporal variability in recruitment with the incorporation of ocean circulation patterns is sparse, and models of larval dispersal are generally quite simplified due to the absence of numerous influencing factors (e.g. Roberts 1997, Schultz and Cowen 1994). In addition, the duration of pelagic life may have important implications as to the



distribution and abundance of reef fishes (Shulman et al. 1983, Williams 1980), however the within-species variability in larval traits has not been studied thoroughly to date in relation to recruitment at large scales in the tropics. In addition, studies often focus on single factors affecting single species, despite the fact that a combination of multiple factors determines where fish are found and in what abundance.

Here, I studied multiple factors potentially influencing the distribution and abundance of the coral reef damselfish *Chromis cyanea* (Pomacentridae). Specifically, I have studied the larval life stage of *C.cyanea* collected at Turneffe Atoll, Belize, Central American, and Banco Chinorro, Mexico, evaluating the relationship between larval durations and growth rates, and recruitment. I also evaluated the recruitment-microhabitat relationship of *C.cyanea* at two spatial scales. First, I tested for small-scale recruitment-microhabitat effects, and measured the potential of recruitment to replenish areas depleted of *C.cyanea* through time by the use of a removal experiment. I then tested for recruitment-microhabitat effects at the spatial scale of Turneffe Atoll, spanning 50 km by 16 km.

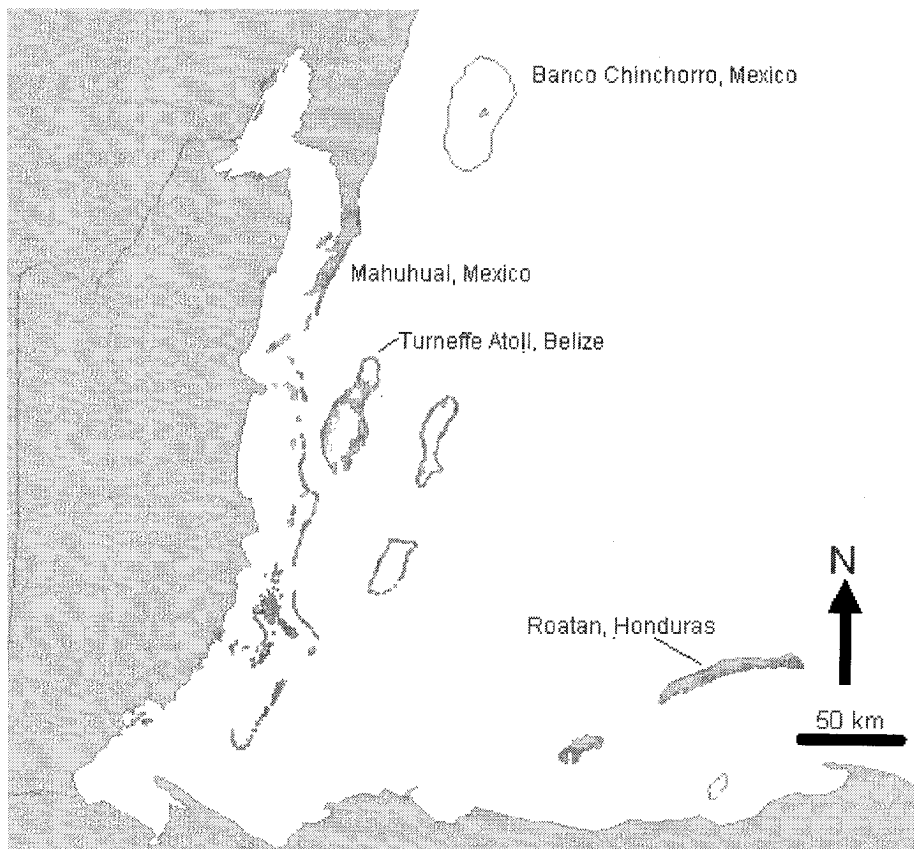
## Study location and sampling

This study was conducted along the Mesoamerican Barrier Reef System, which extends 1000 km from the northern tip of the Yucatan peninsula of Mexico south to the Bay Islands of Honduras (Figures I-1, I-2). Recruitment data for *C.cyanea* used in chapters II and IV was collected at two sites within Banco Chinchorro, Mexico, and seven sites within Turneffe Atoll, Belize. Banco Chinchorro is located 30 km east of the Yucatan peninsula and 100 km north of Turneffe Atoll, and measures 47 km long and 18 km wide. Turneffe Atoll is located 51 km east off the coast of Belize and is approximately 50 km long and 16 km wide (Figures I-1, I-2). This sampling design represented a sub-sample of data collected for the Ecological Connections Among Reefs (ECONAR) project, which was carried out at 5 sites in Banco Chinchorro, Mexico (N18° 33.208', W87° 17.877'), 3 sites in Mahuhual, Mexico (N87° 42.477', W18° 42.110'), 7 sites in Turneffe Atoll, Belize (N17° 17.205', W87° 48.718'), and 3 sites in Roatan, Honduras (N16° 16.204', W86° 36.159') (Table I-I). Recruitment surveys were conducted every two weeks during the seven days immediately following each new and full moon from May to August of 2002 and 2003 (Table II-2). During each bi-weekly recruitment survey, referred to herein as a census period, sites within all locations were visited. Each site consisted of a deep (10-14 m) and shallow position (3-5 m) where recruitment surveys of my study species *C.cyanea* along with 16 other fish species were conducted. Deep and shallow positions at each site were originally marked using a handheld GPS to ensure recruitment surveys were being performed at the same site and position during each census period. At each position, two divers would each perform four, 30

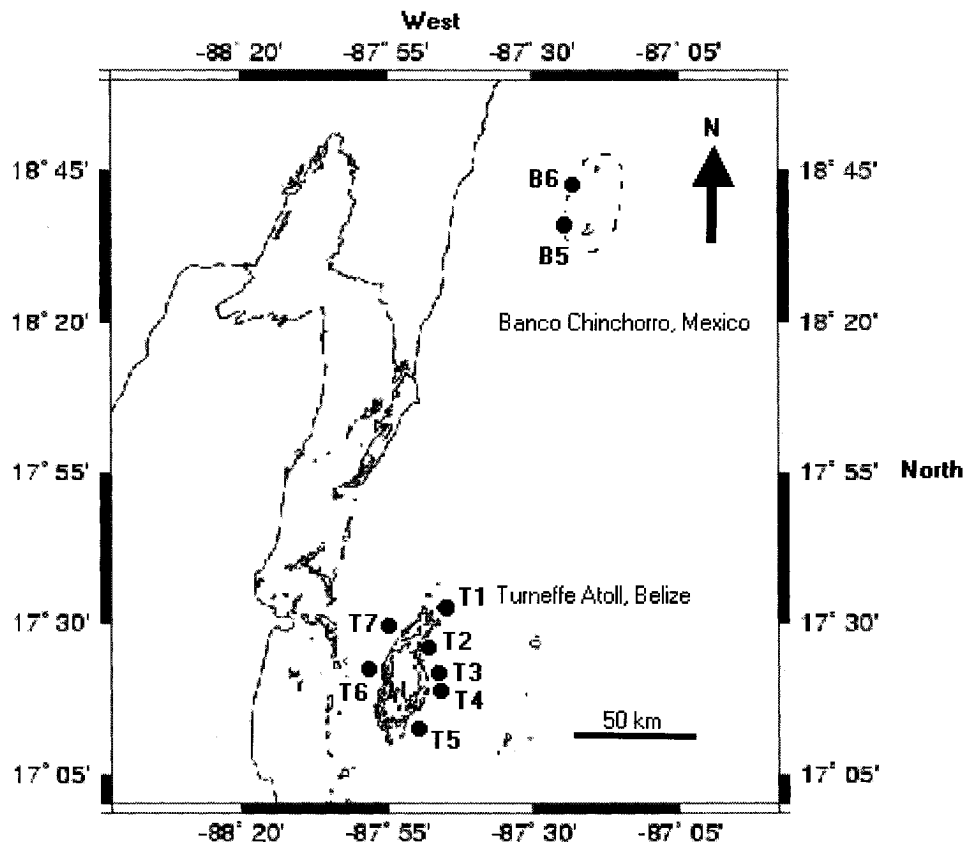
x 1 m belt transects using SCUBA. Each 30 m transect tape was reeled out as the diver swam the transect parallel to the reef, using a 1 m wide PVC t-bar as a reference for transect width. Divers swam parallel to each other, remaining approximately 5 m apart, while recording the number of recruits of the 17 species. Recruits were classified as individuals less than 2.0 cm total length within the transect. Because fish were counted every two weeks, individuals recorded as recruits would have settled sometime within the two weeks prior. In addition, at sites where recruitment data were collected, *C.cyanea* recruits among other selected species were collected. *C.cyanea* samples were used for PLD/growth rate analysis in Chapter II. Due to logistical constraints, recruitment censuses and/or collections were not performed at certain sites and census periods through out both years. Recruitment data and samples used in this thesis were collected during the summer seasons of 2002 and 2003, during which time I had not yet joined on as a member of the ECONAR research team.

### **Study species**

All work was carried out on the coral reef damselfish *Chromis cyanea*. *C.cyanea* are plantivores of the family Pomacentridae. Individuals are found primarily in aggregations consisting of numerous juveniles with fewer adult members. Recruits are generally observed joining aggregations at the time of settlement. Younger members in aggregations display high site fidelity, while adults show greater mobility within their home territories (approximately 3 m<sup>2</sup>). Adults may reach 15 cm in total body length. Males guard eggs and display high territoriality.



**Figure I-1.** ECONAR study locations along the Mesoamerican Barrier Reef System.



**Figure I-2.** Locations and sites of recruitment censuses and collections of *C. cyanea* used in Chapters II and IV.

**Table I-1.** GPS coordinates of ECONAR sampling sites and depths established along the Mesoamerican Barrier Reef System.

Location	Site	Depth	Latitude	Longitude
Banco Chinchorro	1	Deep	18°45.485	87°16.769
Banco Chinchorro	1	Shallow	18°45.136	87°17.349
Banco Chinchorro	2	Deep	18°39.454	87°13.692
Banco Chinchorro	2	Shallow	18°39.468	87°13.792
Banco Chinchorro	3	Deep	18°33.208	87°17.877
Banco Chinchorro	3	Shallow	18°33.228	87°17.944
Banco Chinchorro	4	Deep	18°23.721	87°24.156
Banco Chinchorro	4	Shallow	18°23.756	87°24.193
Banco Chinchorro	5	Deep	18°31.357	87°26.072
Banco Chinchorro	5	Shallow	18°31.390	87°26.133
Banco Chinchorro	6	Deep	18°39.080	87°24.295
Banco Chinchorro	6	Shallow	18°39.016	87°23.909
Mahahual	1	Deep	18°43.422	87°41.810
Mahahual	2	Deep	18°42.099	87°42.438
Mahahual	2	Shallow	18°42.110	87°42.477
Mahahual	3	Deep	18°38.618	87°43.135
Mahahual	3	Shallow	18°38.615	87°43.269
Turnefe atoll	1	Deep	17°35.295	87°44.631
Turnefe atoll	1	Shallow	17°35.290	87°44.715
Turnefe atoll	2	Deep	17°25.320	87°48.430
Turnefe atoll	2	Shallow	17°25.295	87°48.485
Turnefe atoll	3	Deep	17°19.076	87°47.549
Turnefe atoll	3	Shallow	17°19.087	87°47.594
Turnefe atoll	4	Deep	17°16.414	87°48.674
Turnefe atoll	4	Shallow	17°16.420	87°48.716
Turnefe atoll	5	Deep	17°10.390	87°53.246
Turnefe atoll	5	Shallow	17°10.442	87°53.293
Turnefe atoll	6	Deep	17°20.622	87°57.292
Turnefe atoll	6	Shallow	17°20.580	87°57.287
Turnefe atoll	7	Deep	17°26.212	87°54.805
Turnefe atoll	7	Shallow	17°26.206	87°54.725
Roatan island	1	Deep	16°22.730	86°28.810
Roatan island	1	Shallow	16°22.667	86°28.775
Roatan island	2	Deep	16°20.259	86°34.061
Roatan island	2	Shallow	16°20.235	86°34.028
Roatan island	3	Deep	16°16.204	86°36.159
Roatan island	3	Shallow	16°16.185	86°36.144

**Table I-2.** Dates and lunar phases of recruitment censuses and collections at Banco Chinchorro, Mexico and Turneffe Atoll, Belize.

	Census period	Date	Lunar phase
2002	1	June 1-3	Full
	2	June 14-17	New
	3	June 25-July3	Full
	4	July 10-16	New
	5	July 22-28	Full
	6	August 10-19	New
	7	August 23-25	Full
2003	1	June 1-7	New
	2	June 15-21	Full
	3	June 30-July 6	New
	4	July 14-20	Full
	5	July 30-August 5	New
	6	August 13-19	Full
	7	August 27-31	New

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## Chapter II

### **An analysis of pelagic larval duration and larval growth rate, and their influence on the recruitment of *Chromis cyanea***

#### **ABSTRACT**

A majority of reef fishes have a bipartite life cycle whereby they spend a period of time in the open ocean prior to settling to a reef, where the remainder of their life is spent. Although relatively little is known about the larval stage, the interaction of larval life history traits and processes affecting fishes in the pelagic environment are believed to have important influences on their ultimate distribution and abundance on the reef. Here, I evaluated the larval duration and growth rate of *C.cyanea* across Turneffe Atoll in 2002 and 2003, and in Banco Chinchorro in 2002. Spatial and temporal variability was found for both pelagic larval duration and larval growth rates. Larval growth rate consistently increased through out the larval life, and those larvae growing quickly during the middle stage of larval life were found to settle at a significantly younger age than slower growing larvae. However, neither pelagic larval duration nor larval growth rates had significant effects on the recruitment of *C.cyanea*, which was found to show some consistency in spatial differences, but showed less temporal variability.

## INTRODUCTION

A majority of reef fishes spend the beginning of their lives as pelagic larvae away from the reef environment, where they are exposed to ocean currents that potentially disperse them some distance from their natal reef, and whereby rates of mortality are high (Jones 1991; Doherty 1983, Armsworth 2002). The adaptive significance of the larval life stage of reef fishes remains unclear (Doherty et al. 1985), and studies evaluating the movement and behavior of larvae in their natural setting away from the reef environment are sparse, due to the difficulty of conducting such studies. However, reef fish specimens, both larvae and settled individuals, can provide us with useful information pertaining to the pelagic larval life stage. Specifically, the use of otoliths has proven to be an effective means of studying the larval life.

The length of time fish spend as pelagic larvae away from the reef environment (referred to as pelagic larval duration; PLD) is considered an important although not independent determinant of dispersal capability (Shanks et al. 2003). Those larvae exposed to ocean currents for longer periods of time have greater potential for long distance transport away from their natal reef. However, longer exposure to the open ocean may increase the probability of death because of patchy food availability (Thresher et al. 1989), in addition to other possible pressures including predation (Leis 1991).

Knowledge of larval duration and subsequent dispersal potential allows us to form hypotheses as to the source of recruits settling to an area. For example, given that the distance of propagule dispersal is in part a function of PLD, we may infer

that individuals settling to an area with a similar PLD have originated from sites of similar distances, and possibly from the same source.

Interspecifically, the duration of the pelagic stage of fishes is variable, ranging from 10 to 100 days (Victor 1986). Generally, species-specific variation in PLD is assumed to be small, as supported by studies evaluating an abundance of species (e.g. Wellington and Victor 1989, Victor 1986). However, to date the number of studies that thoroughly evaluate variability in PLD for a given species on large spatial and temporal scales is insufficient, given its potential importance in evaluating the connectivity of populations. Although a range in PLD of only a few days may be considered relatively narrow, this represents a significant potential for differential dispersal, even in areas of relatively slow current speeds.

Information pertaining to PLD also allows us to gain insight into the spatial and temporal variability of recruitment, a measure of the replenishment of a population, which is known to vary at both scales (Tolimieri et al. 1998, Doherty 1987, Williams and Sale 1981). Within the PLD range for a given species, the relationship between larval duration and survivorship should theoretically be a negative one. That is, the longer larval fish spend in the open ocean, the higher the chance of mortality (Victor 1991, Sponagule et al. 2006). Due to the fact that many reef fishes face selective pressures in reaching a minimum and relatively invariable species-specific size before settling to a reef (Victor 1986), individuals experiencing faster growth will have grown to a particular settlement size more quickly than slower growing individuals, and will consequently have settled at a younger age (Wellington and Victor 1992, Searcy and Sponaugle 2000, Wilson and Meekan 2002). Few

studies have evaluated this relationship in the tropics to date relative to temperate studies (Sponaugle and Cowen 1997).

The pelagic larval duration for individual *Chromis cyanea* (Pomacentridae) in the Caribbean has previously been determined (Wellington and Victor 1989). However, I looked to quantify the larval durations and growth rates with much finer resolution. I used a significantly greater number of newly settled *C.cyanea* recruits collected across broad spatial and temporal scales in Belize, Central America, and Banco Chinchorro, Mexico, and applied otolith increment counts and width measurements. In addition, I evaluated the potential for PLD and growth rate to explain spatial and temporal variability in recruitment.

## **METHODS**

I first evaluated spatial and temporal variability in the recruitment of *C.cyanea* using a subset of the recruitment data for Banco Chinchorro, Mexico and Turneffe Atoll, Belize (see Study Location and sampling section, page 5). Specifically, I used ANOVA to evaluate recruitment for Turneffe Atoll in 2002 at sites 1 through 7 for census periods 1,2,3 and 6, and in 2003 at sites 2,4 and 7 for census periods 1,2 and 5. For Banco Chinchorro in 2002 recruitment data was analyzed for sites 5 and 6 in census periods 3 and 6 (Table II-1). Separate two-way ANOVA's were run for Turneffe Atoll 2002 and 2003, and Banco Chinchorro 2002 to account for the unbalanced design. Site and census period were categorical predictor variables, and the dependent variable 'recruitment' was compared among sites at the transect level, with 8 transects being run at the deep position at each site where all recruits

were also collected and analyzed for PLD and growth (see below). The number of recruits/transect data was reciprocally transformed ( $1/(x+1)$ ) prior to analysis to normalize data and remove zeros in the dataset.

Pelagic larval duration and growth rate were determined using otolith increment counts from otoliths of *C. cyanea* recruits collected at the same sites measured for recruitment in Turneffe Atoll in 2002 (347 fish) and 2003 (141 fish), and within Banco Chinchorro, Mexico for 2002 (47 fish). Recruits were also collected at additional sites where recruitment was not measured (see Table II-1).

I chose this sampling design for recruitment and PLD/growth analysis due to the fact that throughout Banco Chinchorro and Turneffe Atoll, collections and/or recruitment measures of *C. cyanea* were not performed at certain sites and census periods because of logistical constraints. The sampling design represented the closest to a balanced design that was possible given the recruitment data and fish samples collected.

PLD and growth rate were determined for 15 individuals per site when samples were available, and all individuals were measured for PLD and growth rate in sites with less than 15 specimens. Sagittal otoliths were analyzed, as they provided the highest resolution for accurate and precise daily increment readings. Otolith preparation followed standard protocol from Stevenson and Campana (1993). Briefly, otoliths were embedded in Crystal Bond® glue on a microscope slide and polished along the sagittal plane using 9 and 30 micron lapping film to produce a thin sagittal otolith section. Otoliths were viewed with immersion oil under a light

microscope at 200X power. To determine PLD, otolith increments were counted along the longest axis from the first daily increment to the settlement mark, representing the transition from the pelagic to benthic environment. A total of three counts were taken blindly for each sample to eliminate observer bias. For each otolith, the total variation among the 3 counts was determined, and those otoliths with a variation higher than 5% in PLD were discarded. All otoliths were analyzed using Sigma Scan Pro image analysis software on a computer connected to a light microscope.

Larval growth rates were determined through the measurement of daily otolith increment widths, where faster growth corresponds to wider daily increments. Mean larval growth rates were determined for the whole larval duration and the first 10 days of larval life, days 11 to 20, and 21 days to the end of the larval life, representing early, mid and late larval stages. Growth rates were determined by dividing total length measurements for each stage by the number of daily increments in that stage to produce a mean growth/day ( $\mu\text{m}/\text{day}$ ) value.

Spatial and temporal variability in PLD was evaluated using two-factor ANOVA's, with site and census period as categorical predictor factors for PLD. This analysis allowed me to evaluate differences that may exist in windward vs. leeward and north vs. south sites for example, in addition to temporal comparisons. Due to the unbalanced design between locations and years, Banco Chinchorro 2002, and Turneffe Atoll 2002 and 2003 were analyzed using separate ANOVA's. For Turneffe Atoll 2003, a subsample of the sites where collections were performed was used for



the ANOVA, again due to the unbalanced design within this location and year. Specifically, sites 2, 4 and 7 were analyzed across 3 census periods (Table II-1).

To evaluate spatial and temporal variability in growth rates, I ran separate two-way ANOVA's for whole, early, mid and late larval stages due to a lack of independence. Again, ANOVA's were run separately for locations and years, with the same 3 sites (2,4,7) for Turneffe Atoll 2003 included in the analysis as for PLD. Site and census period were categorical predictor factors for the dependent variable 'growth rate'.

The relationship of PLD and growth rate was evaluated using linear regression analyses. Mean PLD and growth rates were compared at the site level within each census period (n=46), representing 535 individuals. Because I was averaging at the site level within census periods, prior to this analysis I confirmed that no significant site x census period effects for site averaged growth rate existed for any of the larval stages ( $p>0.05$ ). Separate linear regressions were used to test mean site PLD against mean site growth rate for the whole larval duration, days 0-10, 11-20, and 21+, again because mean growth rate measurements at each stage were not independent.

The influence of PLD and growth rates on recruitment was also tested using linear regression analysis. I ran separate linear regressions to evaluate the PLD/recruitment and growth rate/recruitment relationships because of the correlation found between independent variables PLD and growth rate at the mid larval stage (see results). Mean recruitment for each site was  $\log(x+1)$  transformed prior to

analysis to normalize data. Each of the whole, early, mid and late larval stages was tested independently against recruitment.

## RESULTS

Within Turneffe Atoll in 2002 recruitment did not vary significantly among census periods, however a significant site effect was found. A Tukey HSD post-hoc test revealed that recruitment was significantly higher at site 2 than sites 3, 5, 6 and 7. No site x census period interaction was found. In 2003, recruitment again varied significantly in Turneffe Atoll among sites, with site 2 recruitment higher than site 4 (Tukey HSD,  $p < 0.05$ ). A significant census period effects was also found, with census period 5 recruitment significantly higher than census period 1 recruitment (Tukey HSD,  $p < 0.05$ ). Again, no site x census period interaction was found. In 2002 at Banco Chinchorro, I found that recruitment did not vary significantly between sites or census periods, and no significant site x census period interaction was found. (Figure II-1, Table II-2).

The average pelagic larval duration of *C. cyanea* was 30 days, with a range of 24 to 35 days (Figure II-2). In evaluating the spatial and temporal variability in PLD, within Banco Chinchorro, the two-factor ANOVA showed no significant census period effect, although a site difference was found, with site 5 PLD significantly lower than site 6 in census period 3 (Tukey HSD,  $p < 0.05$ ). No significant site x census period interaction was found (Figure II-3, Table II-3). For Turneffe Atoll in 2002, PLD varied significantly among sites and census periods. However, neither site nor census period could explain PLD independently, as a significant site x census period

interaction was also found (Figure II-2, Table II-3). From the Tukey HSD post-hoc test it was found that within sites, significant temporal differences only occurred at sites 1 and 7. Among sites, aside from site 6, all sites varied significantly in PLD between other sites either within or among census periods. However, within these site x census period differences, a detectable pattern could not be found, as no sites differed in PLD from others in a consistent manner throughout the summer. (Figure II-3, Table II-3)

In contrast to 2002, PLD did not vary significantly among sites or census periods within Turneffe Atoll in 2003, although a significant site x census period effect was also found (Figure II-3, Table II-3). Again, no consistently significant site x census period differences were found from the Tukey HSD post-hoc test.

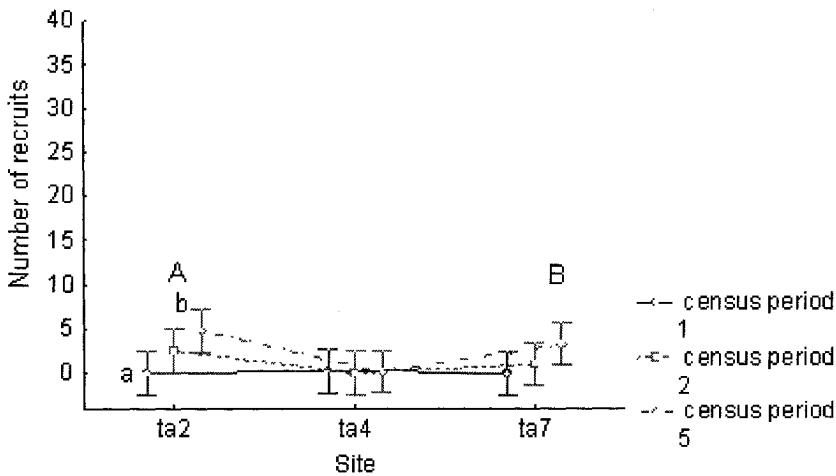
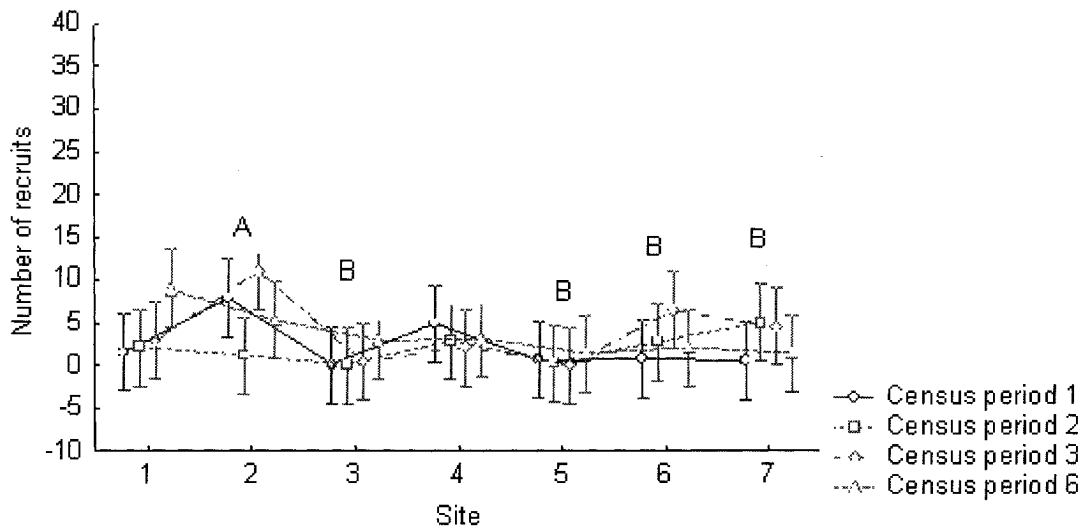
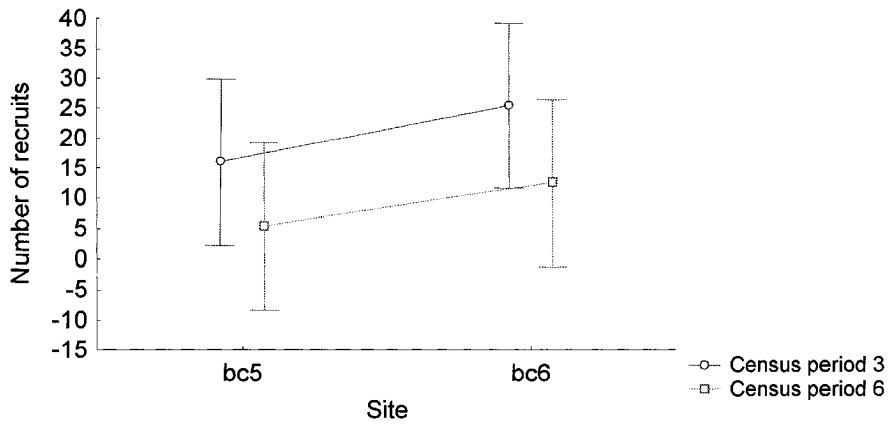
Larval growth rate increased through out the larval life, with the fastest growth occurring at 21+ days when averaged for all individuals measured (Figure II-4). This pattern was common across most sites within Banco Chinchorro 2002 and Turneffe Atoll 2002 and 2003 (Figures II-5 to II-7). Site and census period differences in larval growth rates were found for Turneffe Atoll only (Figures II-8 to II-11, Table II-4). Specifically, growth rates at all larval stages were significantly variable between census periods in 2002. Recruits settling in the mid/late summer grew consistently faster than recruits settling during early summer census periods. Recruits settling during census periods 3 and 6 consistently grew faster than recruits settling during early summer census periods 1 and 2 for whole and late larval stages. For the mid larval stage, recruits grew significantly faster during census periods 6 and 3 than 2, and during census period 6 than 1.

In Turneffe Atoll in 2003, a significant site x census period effect was found in growth rates at the mid larval stage, where recruits settling to site 2 during census period 2 had significantly slower growth rates than fish settling to sites 4 and 7 during census periods 2 and 5 respectively (Figure II-10).

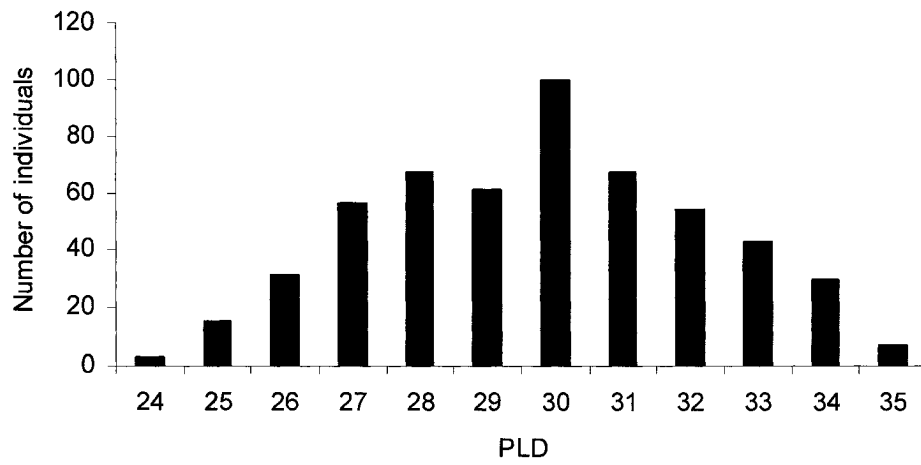
From the linear regression analyses of PLD versus larval growth rate, PLD was found to be significantly correlated with mid stage (11-20 days) growth ( $r^2=0.34$ ,  $p<0.001$ ), where faster growth corresponded to a shorter PLD. No correlation was found between PLD and any of whole ( $r^2=0.01$ ,  $p=0.45$ ), early ( $r^2<0.001$ ,  $p=0.85$ ), or late ( $r^2=0.002$ ,  $p=0.80$ ) larval stages (Figure II-12).

Linear regression analyses also showed that no significant correlation existed between recruitment and PLD ( $r^2=0.01$ ,  $p=0.43$ ; Figure II-13) or recruitment and growth rate at any of the whole ( $r^2<0.01$ ,  $p=0.75$ ), early ( $r^2=0.01$ ,  $p=0.49$ ), mid ( $r^2<0.001$ ,  $p=0.92$ ), or late ( $r^2<0.001$ ,  $p=0.75$ ) larval stage (Figure II-14), suggesting that recruitment was not influenced by these larval traits.

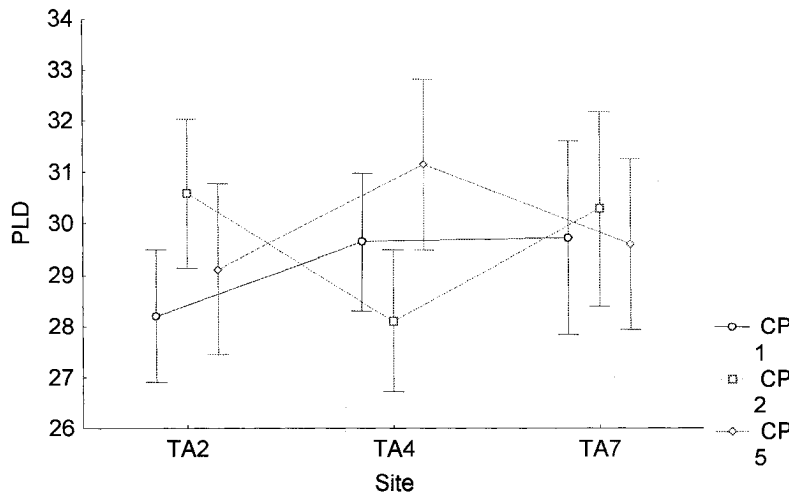
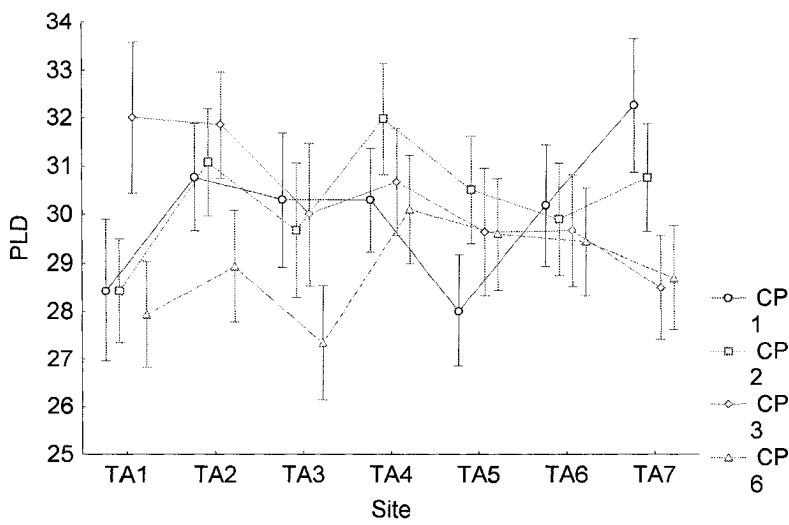
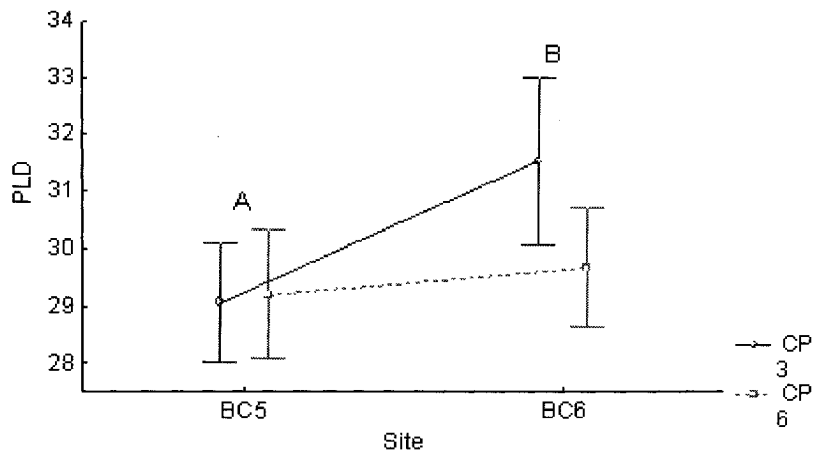
## FIGURES



**Figure II-1.** Mean recruitment per site/census period ( $\pm$ S.D.) measured for recruits in Banco Chinchorro 2002 (n=47) (top), Turneffe Atoll 2002 (n=347) (middle) and Turneffe Atoll 2003 (n=141) (bottom). Contrasting uppercase letters represent significant site differences, lowercase letters represent significant census period differences.

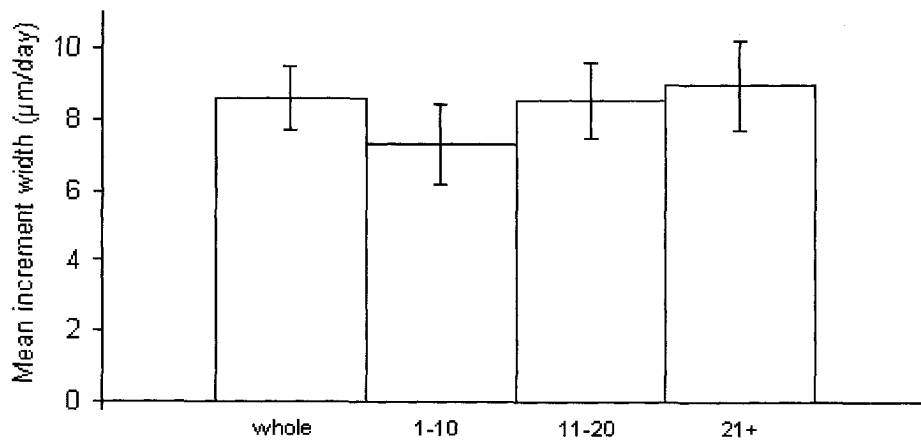


**Figure II-2.** Distribution of PLD for *C. cyanea* measured across Banco Chinchorro, Mexico, and Turneffe Atoll, Belize (n=535).

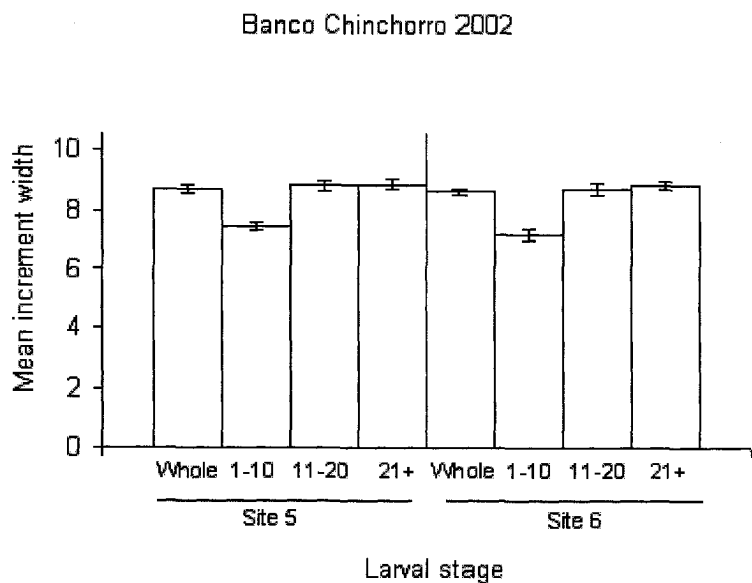


**Figure II-3.** Mean PLD per site/census period ( $\pm$ S.D.) measured for recruits in Banco Chinchorro 2002 (n=47) (top), Turneffe Atoll 2002 (n=347) (middle) and Turneffe Atoll 2003 (n=141) (bottom). Uppercase letters represent significant Tukey post hoc site differences.

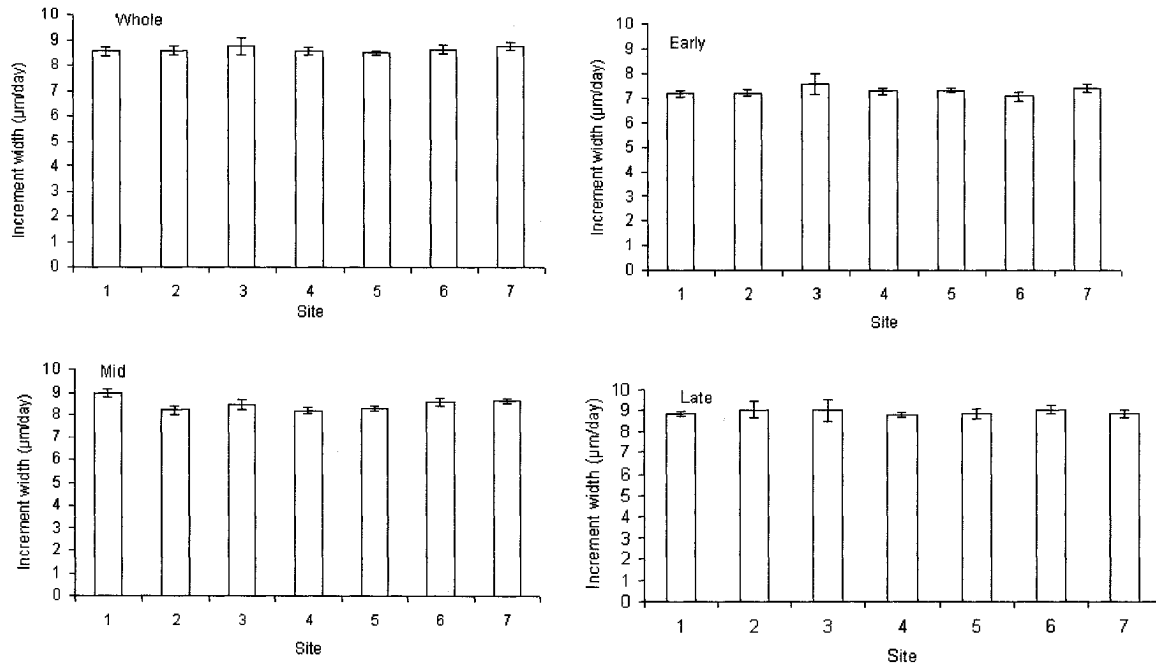




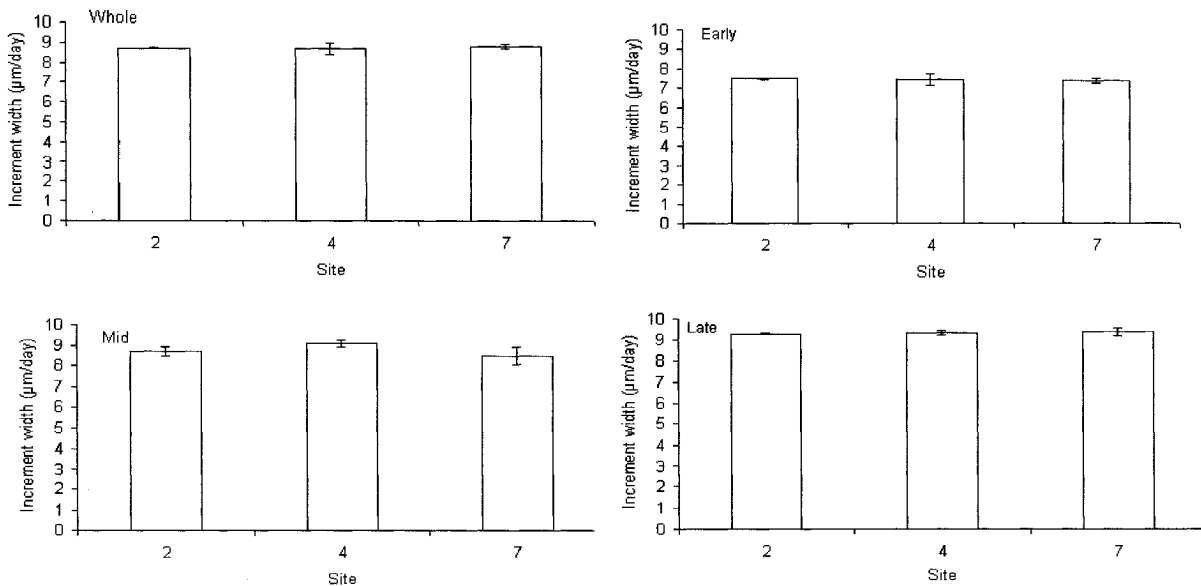
**Figure II-4.** Mean larval growth rates ( $\pm$ S.D.) for whole, early, mid and late larval stages for all fish measured (n=535).



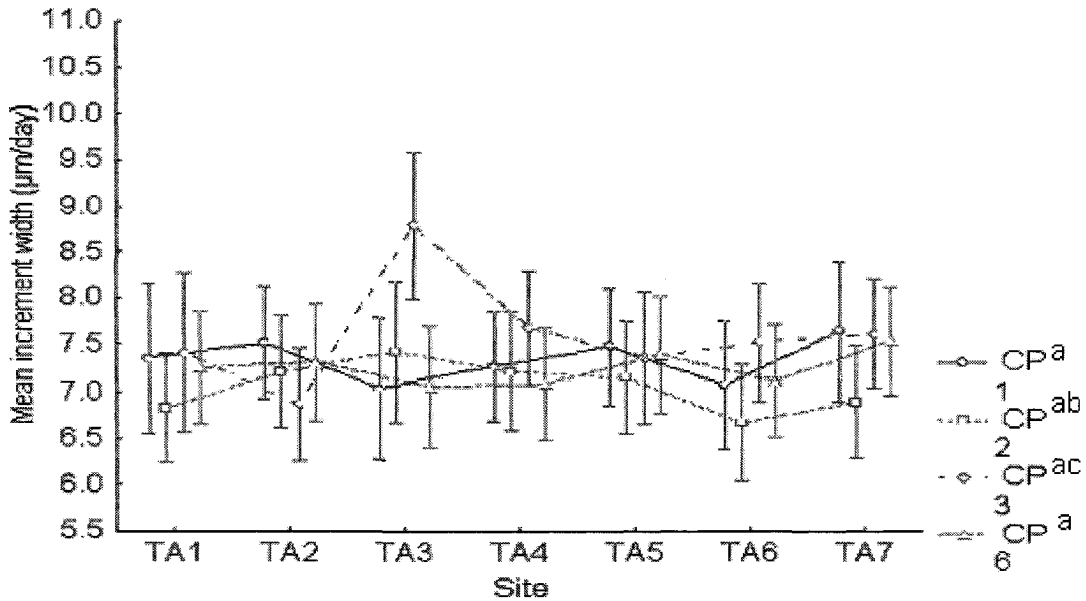
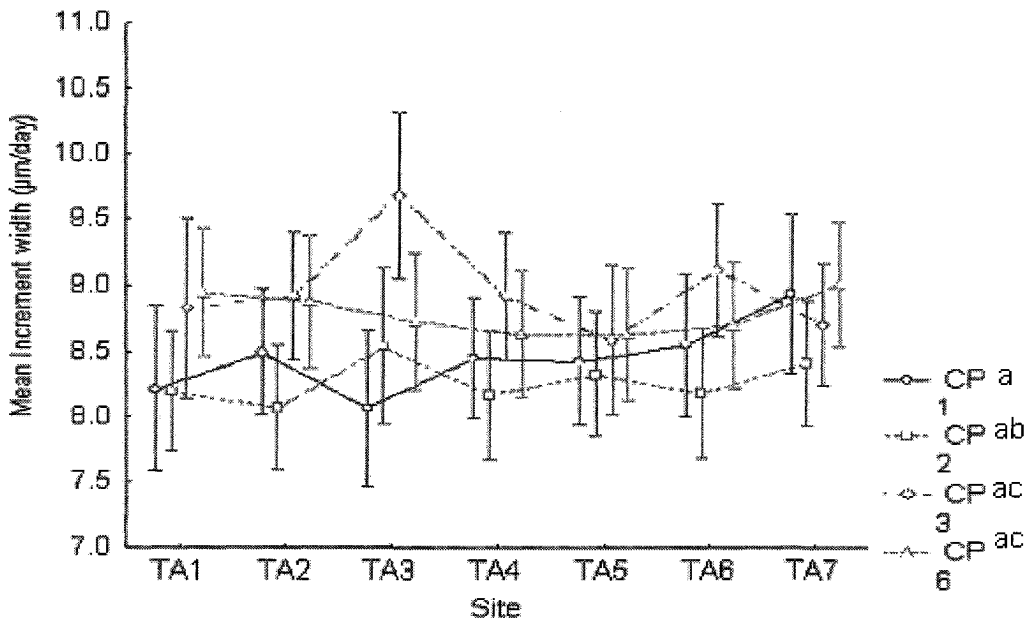
**Figure II-5.** Mean daily increment width for census period and sites, Banco Chinchorro 2002 ( $\pm$ S.E.). Averages are across census periods 1,3 and 5 (n=47).



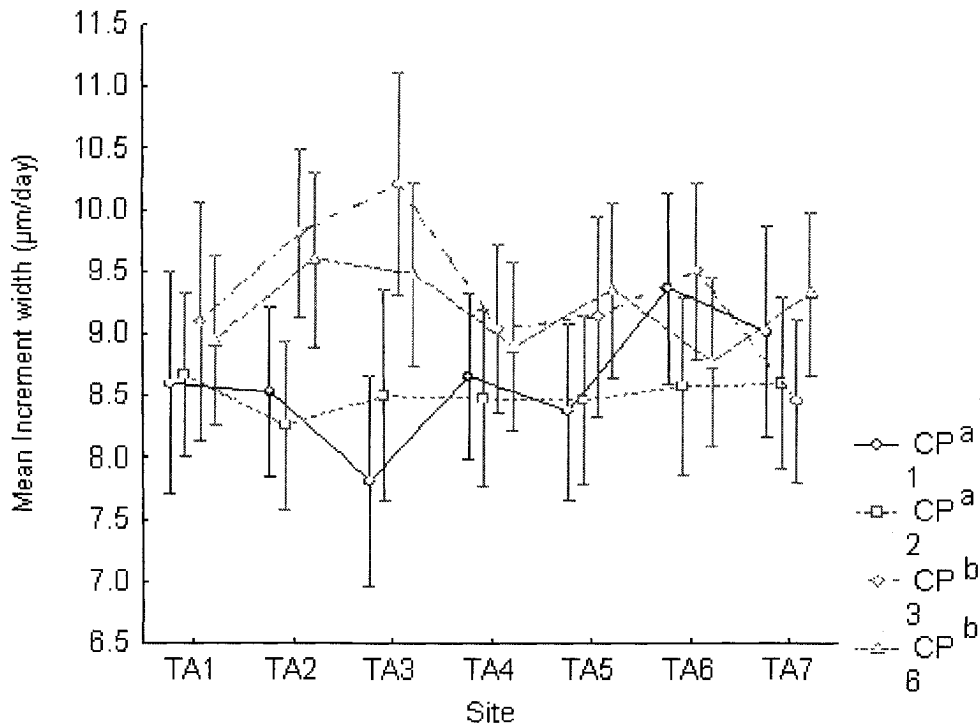
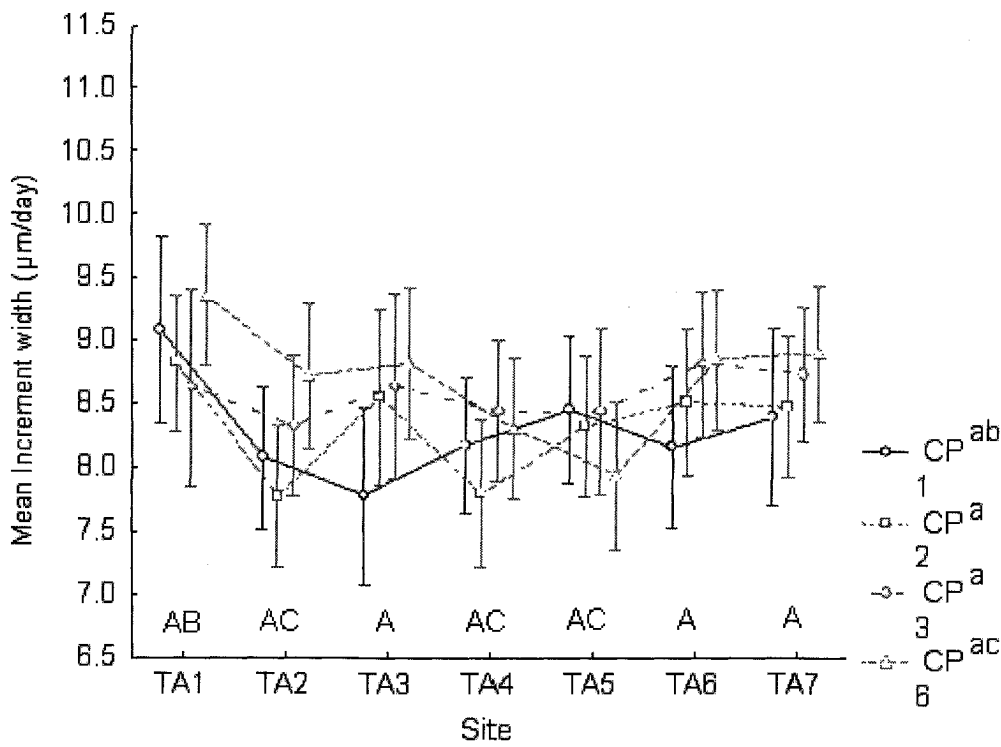
**Figure II-6.** Mean daily increment width site averages in Turneffe Atoll 2002 ( $\pm$ S.E.). Whole duration, early stage (days 1-10), mid stage (days 11-20), and late stage (days 21+) growth rates are shown. Averages are across census periods 1, 2, 3 and 6 (n=347). Note the pattern of increasing growth rate through out the larval life.



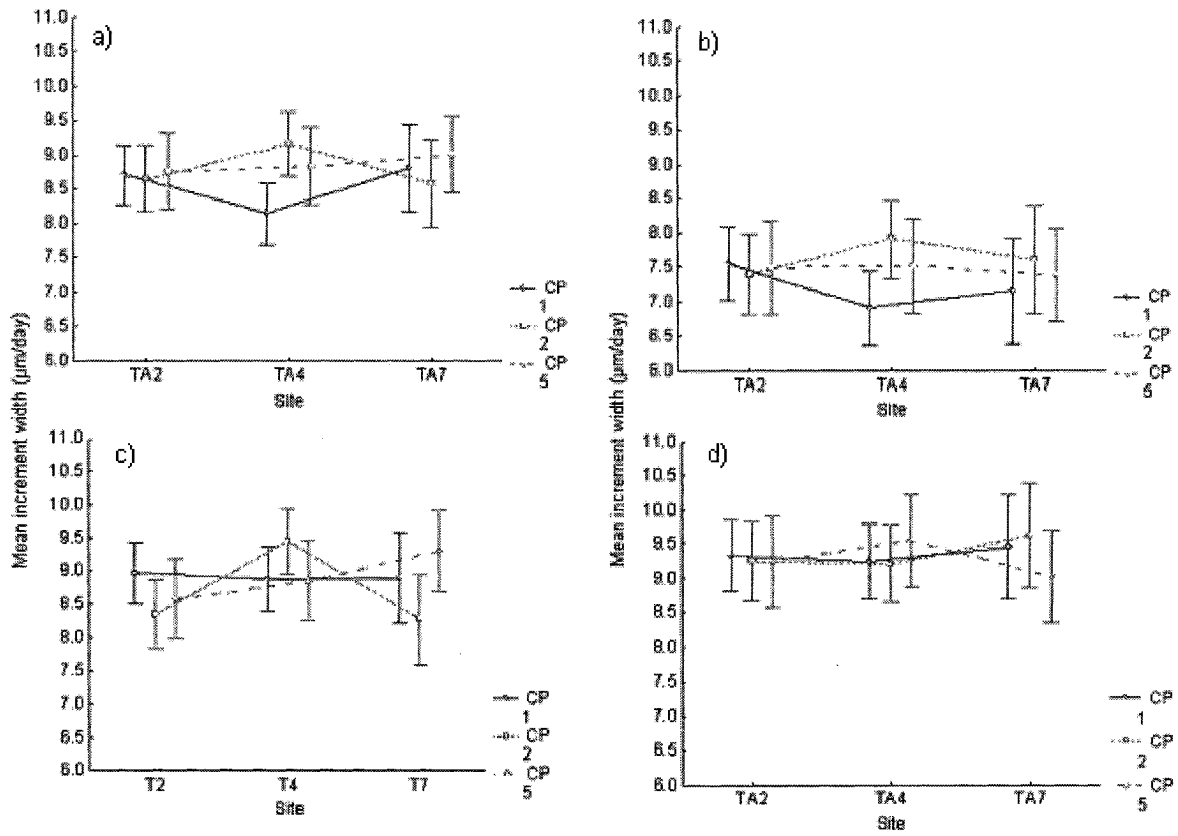
**Figure II-7.** Mean daily increment width for site averages in Turneffe Atoll, 2003 ( $\pm$ S.E.). Site averages for whole, early, mid and late larval stages are across census periods 1,2,and 5 (n=141). Note the pattern of increasing growth rate through out the larval life.



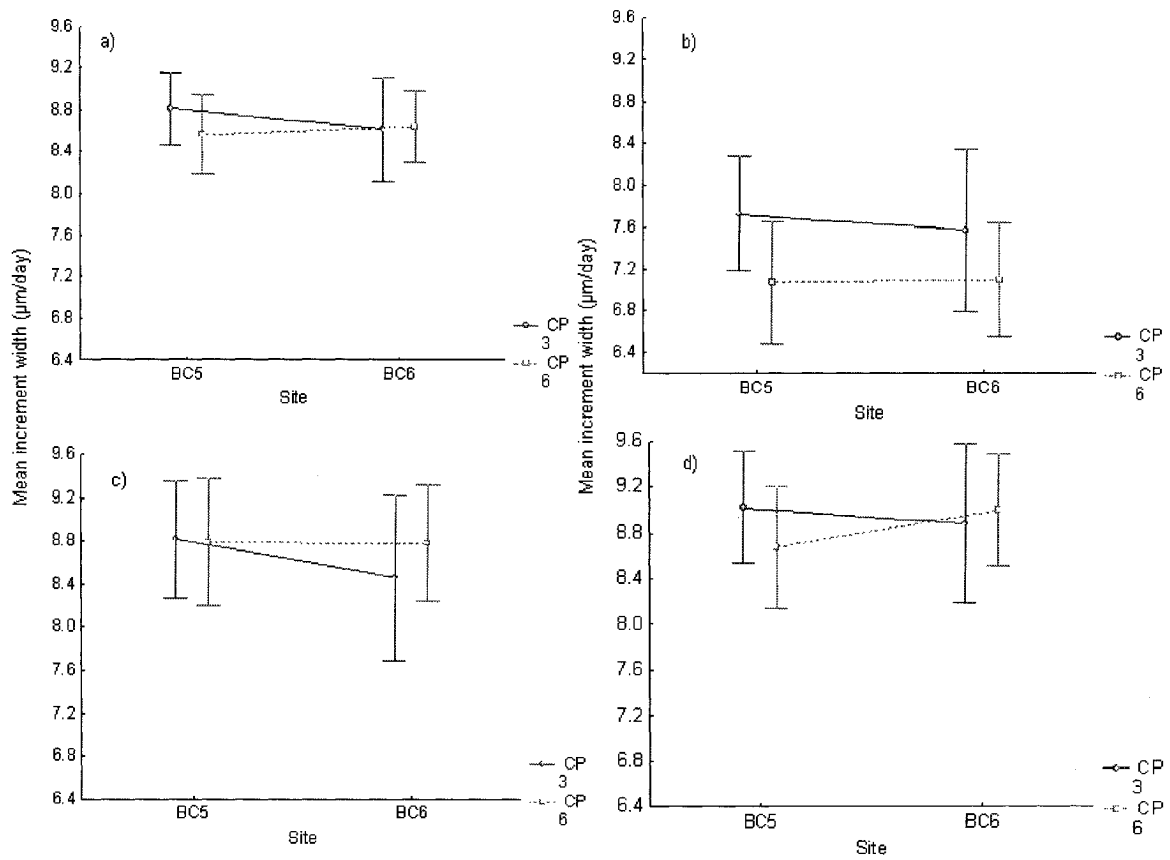
**Figure II-8.** Mean otolith increment width ( $\pm$ S.D.) per site/census period for whole (top) and early (bottom) larval stages in Turneffe Atoll, 2002 (n=347). Significant differences in growth between census periods are indicated by contrasting first and/or second lowercase letters.



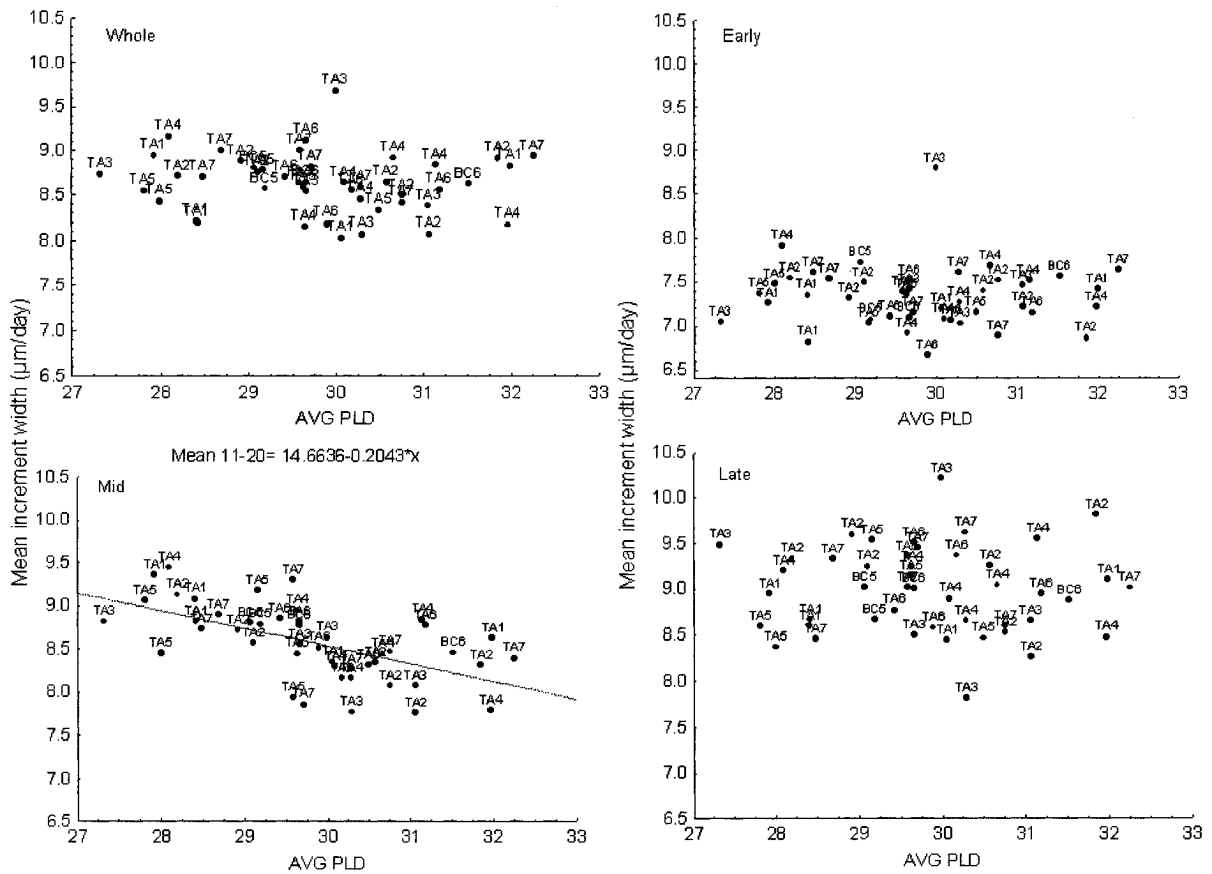
**Figure II-9.** Mean otolith increment width ( $\pm$ S.D.) per site/census period for mid (top) and late (bottom) larval stages in Turneffe Atoll, 2002 (n=347). Significant differences in growth between census periods are indicated by contrasting first and/or second lowercase letters. Significant site differences are indicated by contrasting uppercase letters.



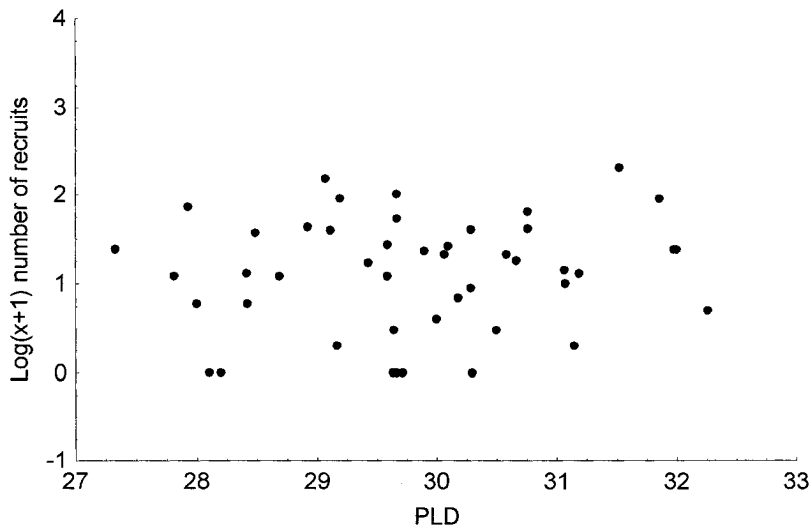
**Figure II-10.** Mean otolith increment width ( $\pm$ S.D.) per site/census period for a) whole b) early c) mid and d) late larval stages in Turneffe Atoll, 2003. (n=141)



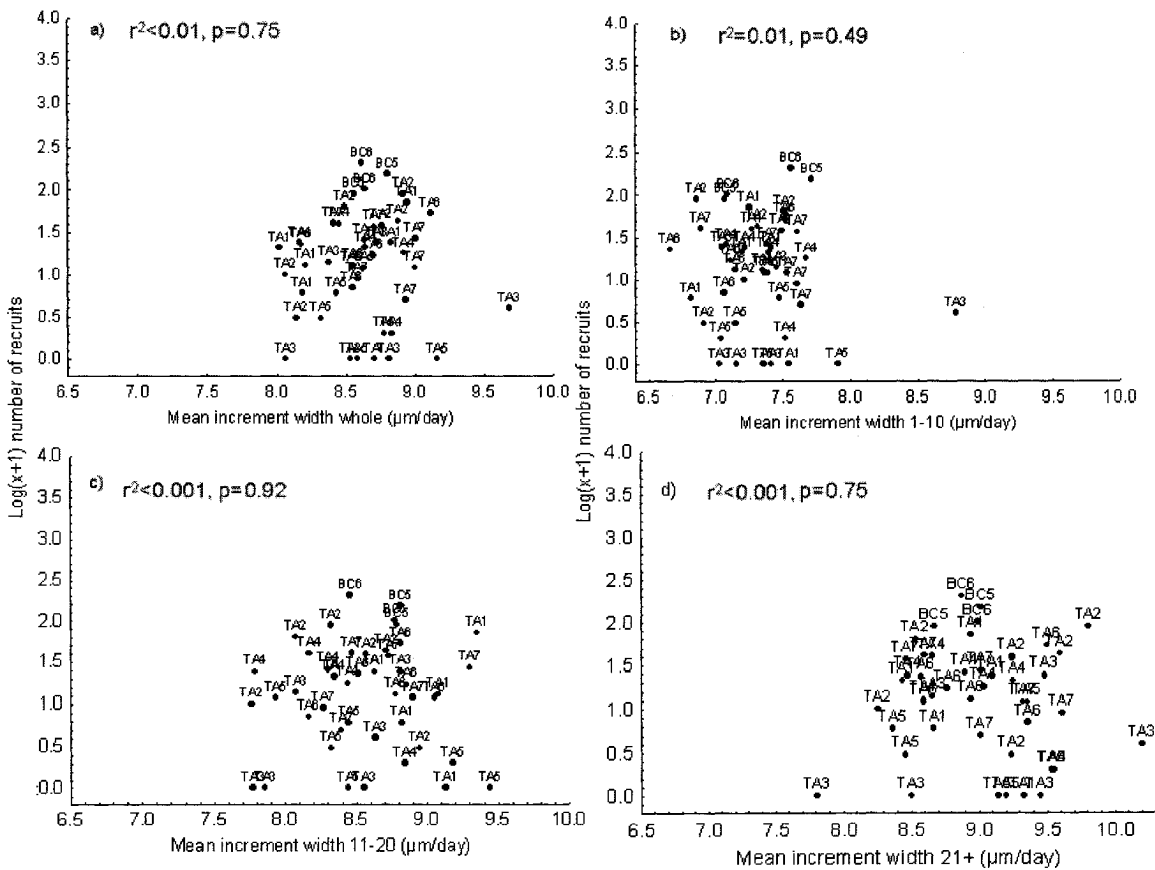
**Figure II-11.** Mean otolith increment width ( $\pm$ S.D.) per site within census periods for a) whole b) early c) mid and d) late larval stages in Banco Chinchorro, 2002 (n=47). No significant spatial or temporal differences were found.



**Figure II-12.** Mean daily growth versus mean PLD for site averages within single census periods (n=46). The above plots display whole, early, mid, and late larval stage growth.



**Figure II-13.** Log(x+1) transformed total recruitment versus site averaged PLD within single census periods where samples were collected (n=46).



**Figure II-14.** Log(x+1) recruitment per site within single census periods versus mean larval growth rate for a) whole, b) early, c) mid and d) late larval stages (n=46). Data points where recruitment is zero exist because recruits were not always collected at the exact locality where recruitment transects were performed within a site.



## TABLES

**Table II-1.** Sampling design for PLD, growth rate and recruitment analysis of *C.cyanea* recruits. Sites listed in bold were analyzed for spatial and temporal variability in recruitment and PLD/growth rates using separate two-way ANOVA's. Banco Chinchorro sites 5 and 6 during census period 1 were analyzed using PLD/growth ANOVA's, but recruitment data was not collected. Sites not bolded for Turneffe Atoll represent those where PLD/growth rates were determined for recruits, but were not included in ANOVA's due to design balancing.

Turneffe Atoll 2002	
Census period	Site
1	<b>1,2,3,4,5,6,7</b>
2	<b>1,2,3,4,5,6,7</b>
3	<b>1,2,3,4,5,6,7</b>
6	<b>1,2,3,4,5,6,7</b>

Turneffe Atoll 2003	
Census period	Site
1	<b>2,4,7</b>
2	<b>2,4,5,7</b>
5	<b>1,2,3,4,5,6,7</b>

Banco Chinchorro 2002	
Census period	Site
1	5,6
3	<b>5,6</b>
6	<b>5,6</b>

**Table II-2.** Results of two-factor ANOVA for dependent variable recruitment. Significant p-values are bolded.

Source	df	MS	F	p
Turneffe Atoll 2002				
Census period	3	0.08	0.57	0.62
Site	6	0.5	4.14	<b>&lt;0.001</b>
Site x census period	18	0.17	1.26	0.22
Turneffe Atoll 2003				
Census period	2	0.51	6.25	<b>&lt;0.01</b>
Site	2	0.28	3.4	<b>0.04</b>
Site x census period	4	0.18	2.21	0.08
Banco Chinchorro 2002				
Census period	1	0.17	0.58	0.45
Site	1	0.16	2.3	0.14
Site x census period	1	0.13	3.63	0.44

**Table II-3.** Results of two-factor ANOVA's for dependent variable pelagic larval duration. Where significant site x census periods interactions were found, main effects are not reported. Significant p-values are bolded.

Source	df	MS	F	p
Banco Chinchorro 2002				
Census period	1	8.15	2.2	0.15
Site	1	23.18	6.86	<b>0.02</b>
Site x census period	1	10.62	2.87	0.1
Turneffe Atoll 2002				
Census period	-	-	-	-
Site	-	-	-	-
Site x census period	18	15.6	3.49	<b>&lt;0.001</b>
Turneffe Atoll 2003				
Census period	-	-	-	-
Site	-	-	-	-
Site x census period	4	19.85	3.15	<b>0.02</b>

**Table II-4.** Results from two-factor ANOVA's for dependent variable growth rate. Separate ANOVA's were run for each location and growth stage. Significant p-values are bolded. Where significant site x census period interactions were found, main effects are not reported.

Source		Df	MS	F	p
<b>Banco Chinchorro 2002</b>					
Census period	Whole	1	0.03	0.08	0.58
	0-10	1	3.43	3.36	0.07
	11-20	1	0.23	0.23	0.63
	21+	1	0.14	0.17	0.68
Site	Whole	1	0.13	0.31	0.79
	0-10	1	0.05	0.05	0.83
	11-20	1	0.36	0.36	0.55
	21+	1	0.09	0.11	0.74
Site x Census period	Whole	1	0.19	0.45	0.5
	0-10	1	0.09	0.08	0.77
	11-20	1	0.32	0.31	0.58
	21+	1	0.6	0.73	0.4
<b>Turneffe Atoll 2002</b>					
Census period	Whole	3	8.34	9.98	<b>&lt;0.001</b>
	0-10	3	4.27	3.26	<b>0.02</b>
	11-20	3	3.28	2.93	<b>0.03</b>
	21+	3	13.85	8.24	<b>&lt;0.001</b>
Site	Whole	6	0.52	0.62	0.71
	0-10	6	1.07	0.82	0.56
	11-20	6	3.61	3.22	<b>&lt;0.001</b>
	21+	6	0.72	0.43	0.86
Site x Census period	Whole	18	0.71	0.85	0.63
	0-10	18	1.41	1.08	0.37
	11-20	18	0.32	0.31	0.58
	21+	18	2.38	1.41	0.12
<b>Turneffe Atoll 2003</b>					
Census period	Whole	2	0.81	1.1	0.34
	0-10	2	1.49	1.42	0.25
	11-20	2	-	-	-
	21+	2	0.06	0.06	0.95
Site	Whole	2	0.07	0.1	0.9
	0-10	2	0.06	0.06	0.94
	11-20	2	-	-	-
	21+	2	0.05	0.05	0.95
Site x Census period	Whole	4	1.39	1.89	0.12
	0-10	4	1.11	1.07	0.38
	11-20	4	2.3	2.79	<b>0.03</b>
	21+	4	0.57	0.55	0.7

## DISCUSSION

Historically, ecologists did not consider settlement an important process contributing to the replenishment of fish populations (Ehrlich 1975). However, its potential importance in determining population distribution and abundance is more widely recognized, although not always agreed upon (see Caley et al. 1996).

In analyzing the recruitment of *C.cyanea*, I found both spatial and temporal variability in Turneffe Atoll. This was not the case for Banco Chinchorro, possibly due to the relatively small spatial scale evaluated, where adjacent sites BC5 and BC6 were measured for recruitment once during the mid and late summer of 2002. In finding spatial variability in recruitment at Turneffe Atoll in 2002 and spatial and temporal variability in 2003, I attempted to reveal potential recruitment patterns. The windward side of Turneffe Atoll is exposed to ocean currents directed from the east and south, and from the ocean circulation model of Tang et al. (2006), it is predicted to have relatively low water retention and to receive its source of recruits from as far away as the Bay Islands of Honduras to the south. Leeward sites 6 and 7 are conversely predicted to display relatively higher larval retention. Within Turneffe Atoll in 2002, where recruitment was measured across the whole atoll during the mid, early and late summer, site 2, located on the northwest windward side of the atoll, consistently received more recruits than sites to its direct south and to the two sites on the eastern leeward side of the atoll. However, no other windward sites differed in recruitment from leeward sites in Turneffe Atoll in 2002, and no windward/leeward differences were found in Turneffe Atoll in 2003. In addition, no consistent north/south atoll differences in recruitment were found in either 2002 or

2003. Temporally, recruitment varied significantly only between census periods 5 and 1 at Turneffe Atoll in 2003, suggesting that the number of recruits settling to sites was relatively consistent on a bi-weekly basis.

These results support a wide body of evidence suggesting that the recruitment of pelagic larvae into the benthic environment varies spatially, often unpredictably (Williams 1983, Doherty and Williams 1988, Sale 2004). Coral reef fish larvae are exposed to a suite of factors that can potentially result in differential mortality (Leis 1991). In addition, variability in spawning activities (Danilowicz 1997) and ocean circulation (Nishimoto and Washburn 2002) among other interacting factors results in a high degree of uncertainty as to where larvae will settle and in what abundance (Gust et al. 2001). Studies have also shown that reef fish commonly recruit to areas in lunar pulses (Robertson 1992, Spoaugle and Cowen 1996). However, here I detected no lunar patterns in recruitment.

The mean pelagic larval duration of approximately 30 days for *C.cyanea* recruits found here agrees with that found previously by Wellington and Victor (1989). The 12 day range of 24-35 days represents a slightly larger one than they had previously recorded (27-34 days). Within Banco Chinchorro in 2002, although results again must be interpreted with caution due to the low sample size, recruits were settling at a significantly younger age to BC5 than to BC6, its southern adjacent site approximately 10 km away. Site x census period differences were found for Turneffe Atoll in 2002 and 2003, indicating that neither site nor census period were useful predictors of PLD independently. Although, no consistent between-site patterns could be detected in either year from site x census period

interactions, it is interesting to note that in 2002, 5 of the 7 Turneffe sites showed no within-site differences in PLD across census periods, suggesting that the PLD of settling *C.cyanea* displayed some level of within-site predictability. Sites 1 and 7 were the only two sites displaying significant within-site temporal variability in PLD ( $\bar{x}$ =28.83  $\pm$  0.15 S.E. and 29.79 days  $\pm$  0.14 S.E. respectively). Sites 2 (30.68 days), 3 (29.15 days), 4 (30.73 days), 5 (29.44 days), and 6 (29.77 days) showed no within-site temporal variability. This pattern cannot be explained by Tang et al.'s retention time index predictions, as sites 1 and 7, in contrast to each other, are expected to display low and high water retention respectively. However, sites 1 and 7 do represent the two most northern sites in Turneffe Atoll, possibly contributing to the observed site differences in PLD. Aside from site 6, all sites showed significant among-site variability in PLD, although among-site differences were not consistent through time. PLD was thus most consistent within sites.

Generally, the pelagic larval duration of fishes is thought to display low within-species variability, and single mean PLD values are commonly used when predicting larval dispersal (see Leis 2002) and the genetic differentiation of populations for example (Doherty et al. 1995). However, studies showing significant intraspecific variability in PLD suggest that a single mean PLD value for a given species may produce over-generalized predictive models. Bay et al. (2006) recently completed a study evaluating the PLD of 12 tropical reef fishes, finding that the majority of fishes studied displayed significant variability in PLD between sampling times, among sampling regions, and among sites within sampling times, as I found here.

In this study, differences in PLD of up to 5 days between sites within single census periods were found in Turneffe Atoll. From Tang et al.'s ocean circulation model, even with a relatively low surface current speed of 15 cm/s within the Mesoamerican Barrier Reef System, a 5 day difference in PLD represents a maximum differential dispersal distance of approximately 65 km, assuming passive and unidirectional dispersal of larvae. Although this represents an overestimated dispersal distance, it nonetheless signifies the potential importance of variability in PLD when considering population connectivity. That is, individuals settling to a site with PLD's varying only by a few days, for example, could have potentially come from sources separated by distances of 10's of kilometers.

To gain a better understanding of PLD and its significance to the study of dispersal, it is important to recognize the factors that ultimately affect PLD. Although numerous factors including temperature, salinity and prey availability have been shown to be important and may have contributed to the spatial and temporal variability in PLD found here, little is known about any of their direct effects in the pelagic environment (Bradbury and Snelgrove 2001), and further research in this area is required.

In evaluating larval growth I found that daily otolith increment widths became increasingly wider throughout the larval life, reflecting a continually increasing growth rate of larvae from early to late larval life. Although these results agree with other studies in that the early part of larval life is the slowest, they differ in that previously, larvae have displayed slower growth towards the end of their pelagic life (e.g. Bergenius et al. 2002, Wilson and Meekan 2002, Denit and Sponaugle 2004).



Larval growth is known to vary among individuals in space and time as a result of both maternal (Kerrigan 1997) and environmental factors (Searcy and Sponaugle 2000, Sponaugle et al 2006). However, early stage larvae are relatively weak swimmers with underdeveloped sensory systems and given that larval sensory and swimming capabilities develop throughout the larval life (Myrberg and Fuiman 2002), larvae should theoretically have an increasingly greater ability to obtain food during the later stage in the pelagic environment. This may explain the pattern of increasing growth found here, where greater access to food resources results in faster growth (Talbot 1985, McCormick and Molony 1992).

Although the pattern of increasing growth rate was common throughout both study locations and years, where significant differences in growth rate among sites or census periods were found, no consistent pattern could be established. There was however, a temporal difference in growth rates found for Turneffe Atoll in 2002 for all larval stages, where fish grew significantly faster during middle and late (late June/August) summer census periods than early (late may/early June) summer census periods. As for PLD, given that larval growth rates are influenced by temperature (Moosegard et al. 1988), food availability (Molony and Sheaves 1998) and salinity (Sponaugle and Pinkard 2004), and given the relatively large temporal scale at which this study was carried out, census period differences found for larval growth rates here may represent equivalent temporal differences in any or all of the environmental factors larvae were exposed to during their larval life. Considering water temperature specifically, Belize and the surrounding area along the Mesoamerican Barrier Reef experienced the typical seasonal increases in mean

monthly surface water temperature from May to August of 2002, possibly contributing to the observed faster growth of recruits settling during the mid/late summer versus those settling during the early/mid summer.

In comparing PLD and growth rates, I found that growth during the mid larval stage was correlated with larval duration, supporting the hypothesis that faster growing larvae will reach a minimum settlement size earlier, resulting in a shorter PLD (Wellington and Victor 1992, Bertram et al. 1993). Because the relationship was not found for the whole, early or late larval stages, this suggests that the mid stage of larval life is particularly important for *C.cyanea* in determining when larvae will settle to the reef. Due to the difficulty of studying the larval stage, little is known about reef fish larvae in their natural environment, and it is thus difficult to hypothesize the significance of the mid stage of larval life in determining the age at which larvae will settle to the reef.

However, assuming some level of dispersal, larval fish presumably spend the entirety of their mid larval life feeding in the pelagic environment. This contrasts to the early stage of larval life where larvae spend some period of time dispersing out from the reef as individuals with poorly developed sensory systems and swimming abilities, capable of limited feeding as mentioned above. This also contrasts the late larval stage, where larvae spend some time in proximity to the reef, probably searching for a suitable habitat (Light and Jones 1996) while avoiding the many predators in the reef environment (Johannes 1978, Hixon 1991). Although my results suggest that if feeding does indeed play a major role in growth, the late stage of larval life represents the greatest feeding period, studies have shown that

plankton may be more abundant and less patchy within the reef environment (Sale et al. 1976, Powell and Okubo 1994, Mutlu 1999) where late stage larvae do not spend all of their time, as compared to the open ocean where mid stage larvae presumably spend all of their time. We may therefore expect the mid larval stage to be a critical feeding period, whereby plankton as a patchy food resource is limited, and those individuals exposed to plankton patches will experience faster growth, subsequently settling to a reef at an earlier age. However, testing such a hypothesis is very difficult, as information pertaining to the location of larvae through out the larval duration would be required.

Finally, I was not able to produce data supporting the growth-mortality hypothesis, which predicts that faster growing larvae will experience greater survivorship (Wilson and Meekan 2002), a pattern that will be revealed in measures of recruitment. In addition, recruitment was not correlated with PLD. These findings suggest that factors unrelated to these life history traits determine patterns of *C.cyanea* recruitment.

Cohorts of larvae often settle to the reef at certain times of the month, commonly during particular lunar phases (Thorrold et al. 1994, Sponaugle and Pinkard 2004). Because cohorts may consist of individuals spawned on different days, the PLD of individuals within a settling cohort will vary. As a result, Robertson et al. (1999) suggested that if larvae settling with a longer PLD experience higher mortality due to prolonged life in the pelagic environment, this effect may not be observable due to the relative advantage gained by these fishes in settling during a particular 'optimal' time of the month. This also applies to larval growth rate, where

the disadvantage of slower growth would be balanced by the advantage of settling during a particular time. In this study, although no reliable census period (ie. lunar) differences in recruitment were found, the possibility exists that larvae were settling during particular times within the two weeks prior to when visual censuses were performed, a trend that would not be revealed from the bi-weekly censuses.

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## Chapter III

### Factors influencing the small-scale recruitment of *Chromis cyanea*

#### ABSTRACT

An understanding of the small-scale processes contributing to larger-scale patterns of distribution and abundance is essential to the study of ecology. In coral reef fish ecology the role of recruitment in determining population abundance remains one of the central issues of debate. Here, through the use of a small-scale removal and recolonization experiment I measured the recruitment of the coral reef fish *Chromis cyanea* (Pomacentridae) over two months during the summer of 2005 and again after 8 months of recruitment during April of 2006, at Calabash Caye of Turneffe Atoll, Belize. In addition to monitoring the replenishment of coral patches, I tested for microhabitat and conspecific effects on recruitment. Recruitment of *C.cyanea* was positively correlated with rugosity and massive coral cover. A significantly greater number of recruits were found on control patches throughout the experiment, where resident fishes were not removed, suggesting that a strong conspecific effect also existed. After both 2 and 8 months of recolonization, coral patches where individuals had been initially removed remained largely unreplenished, suggesting that recruitment may have been limiting the abundance of *C.cyanea* on the reef.

## INTRODUCTION

The relationship between organisms and their environment is a fundamental concern in ecology (Jones and Syms 1998), and the relative importance of factors determining the distribution and abundance of species is often debated among ecologists (Nee and Stone 2003). Among such factors are habitat effects. Habitat provides food and shelter essential for survival, and has been shown to influence assemblages of many organisms including plants (Watt 1947, Whittaker 1956, Collins 1990), vertebrates (Jones et al. 1985, Sisk et al. 1997, McCoy and Mushinsky 1999) and invertebrates (Walsh 1995, Gjerlov et al. 2003). Knowledge of habitat use becomes important as species can be greatly affected by changes or stresses to the habitats in which they live, whether the changes are natural or anthropogenic. In addition, if habitat influences the distribution and abundance of individuals, it will provide predictive power in determining their spatial distribution.

Processes influencing fishes in the pelagic environment play an important role in determining their distribution and abundance on a reef (Leis 1991, Caley et al. 1997), and some have suggested recruitment to be the limiting factor of reef fish populations (Victor 1983, Doherty and Fowler 1994, Armsworth 2002). However, studies evaluating potentially important factors from the time of settlement to a reef on into adulthood must also be considered, as reef fishes, particularly during their early stages of demersal life, often experience high rates of mortality (Victor 1991, Levin 1994).

The significant role of habitat in determining the distribution and abundance of reef fishes has been widely supported (e.g. Shulman 1984, Tolimieri 1995, Schmitt

and Holbrook 2000, 2003), and both habitat selection of settling larvae (Gutierrez 1998, Montgomery et al. 2001, Leis and McCormick 2002) and resource limitation (Doherty 1991) have been considered as mechanisms contributing to these effects. Coral reefs provide a diversity of habitats for larvae to settle to, and we can predict that larvae settling to particular habitat types will be spatially distributed across a reef accordingly (Hixon and Beets 1989, Booth and Wellington 1998, Ohman et al. 1998). In addition, the resource limitation theory states that resources are limited in the coral reef environment. Under this assumption, the number of individuals of a given species within an area will therefore depend on the habitat and consequent abundance of resources (Roberts and Ormond 1987, Shima 2001). In this case, sufficient recruitment is assumed, resulting in a competitive environment with a limited carrying capacity (see Doherty 1983).

An effective method of testing for both habitat effects and resource limitation is to use a recolonization experiment, where all individuals of a given species are removed within an area. After a recolonization period, pre-removal and post-removal abundances can be compared, and two possible hypotheses may subsequently be formed. The first involves the resource limitation theory. If habitat and resource availability do limit the abundance of a species, post-removal abundances should reach a capacity equal to pre-removal abundances, as recruitment will have been sufficient to replenish areas from which fish were removed. However, if post-removal abundances have not returned to pre-removal abundances, recruitment may be a limiting factor of abundance, and habitat and resource availability may be less important in limiting population sizes. Both “natural

experiments”, where fishes are removed from an area by a natural occurrence and experimental removals can be useful tools in evaluating species distributions and abundances. Empirical evidence from such experiments has been inconclusive to date.

In support of the resource limitation theory, Walsh (1983) observed resident fish population assemblages in a Hawaiian shallow reef flat before and after a major storm event, finding resilience to any changes in assemblages and abundances through time for a number of juvenile fishes subjected to complete initial removals in several areas. This suggested that recruitment was not a limiting factor and that some level of assemblage predictability existed. Similarly, Planes et al. (2005) were able to utilize a nuclear test site to monitor the response of reef fish populations at a relatively large spatial scale, finding stability in assemblages after a period of recolonization, suggesting recruitment was sufficient to replenish populations. However, recovery of assemblages was also due to migration in this case.

Sale (1974) presented an argument for the importance of unpredictability in community structure and recently provided evidence from past studies suggesting that the abundance of fishes on a reef will fluctuate through time, and that recruitment may help explain this variability (Sale 2004). Mixed results in experimentation suggest the relative importance of habitat and resources versus recruitment limitation and the scale at which these effects are important in influencing the abundance of fishes need to be further explored.

To evaluate recruitment of the coral reef damselfish *Chromis cyanea*, I removed all conspecifics from selected coral patch habitats and monitored the

recolonization to patches over a two month period during the summer of 2005 and once after an 8 month period of recolonization in April of 2006. I set out to answer the following questions: 1. Do microhabitat characteristics influence the recruitment of *Chromis cyanea*? 2. Is recruitment sufficiently high to replenish areas denuded of all individuals? 3. Does the presence of resident conspecific fish influence recruitment?

## **METHODS**

Microhabitat quantification was carried out at Calabash Caye of Turneffe Atoll, Belize in June 2005. In each of three sites spaced 500 m apart north to south, seven separate haphazardly selected coral patches inhabited by *C.cyanea* were quantified for microhabitat. Selected patches were isolated at a minimum distance of approximately 8 m from other patches containing *C.cyanea* to ensure migration between neighboring patches would not occur (*personal observations*). The northern site is referred to herein as North site, the central site as Calabash site, and the southern site as South site (Figure III-1). In order to characterize the habitat available, three microhabitat characteristics were measured for each coral patch: percent microhabitat cover, rugosity (spatial complexity), and volume. To measure microhabitat cover for each patch, 6 measuring tapes were placed from the center of the coral patch outwards to the edge of the patch at 60-degree angles. Measuring tapes were laid along the exact contours of the coral patch. Along each tape the point-intersect method was used (Loya 1972), with microhabitat type recorded every 5 cm as one of 15 categories (Table III-1). The percent microhabitat cover of each patch was then determined by dividing the total number of transect points

categorized for each microhabitat type by the total number of transect points categorized. Structural complexity, or rugosity, was measured for each coral patch by placing four thin brass linked chains along the exact contours of the substratum of the patch at 90 degree angles from the center of the patch. Four measuring tapes were then stretched tight above the substratum out from the center of the coral patch along the same four angles as the chains. Rugosity could subsequently be determined by finding the ratio of total chain length to total linear length for the four directions. A rugose coral patch will therefore have a higher chain to linear ratio than a less rugose coral patch. Volume of each coral patch was determined by measuring the height and determining the closest shape resembling each patch (e.g. circle, rectangle) or sections of a patch where possible. The appropriate shape dimensions (e.g. length, radius) for each patch were then used to calculate the subsequent volume. Volumes were summed when sections of patches were measured separately.

Five coral patches within each site were randomly chosen as removal patches, and 2 as control patches. I first determined whether the microhabitat characteristics varied significantly between coral patches, both at the site level and between removal and control patches. Comparisons of microhabitat characteristics were made using MANOVA. Habitat proportions were arcsine transformed prior to analysis. This analysis was performed to ensure that potential differences in recruitment among coral patches to be tested were not simply a result of site or treatment effects.

To determine whether the measured microhabitat characteristics played a deterministic role in the recruitment of *C.cyanea* among coral patches and sites, I removed and size classed all *C.cyanea* on 5 of the 7 coral patches at each site (total length (TL); 5 removal patches, 2 unmanipulated control patches). Recruits were classified as individuals <2.0cm (TL), defined as the distance from the tip of the snout to the tip of the caudal fin. Visual censuses were performed to classify *C.cyanea* to size classes on control patches, as removals were not performed on these patches. All collections and measurements/censuses were completed during the third week of June 2005. These initial recruit counts were then entered into a forward stepwise multiple regression against the measured microhabitat characteristics for each coral patch to test for a microhabitat effect on recruitment. A correlation matrix showed that microhabitat characteristics were uncorrelated, allowing me to treat each one as an independent variable in the multiple regression. I entered 6 selected arcsine transformed microhabitat variables including algae, hole, rock, rubble, sponge and massive coral, along with rugosity and volume into the regression versus the number of recruits for each coral patch. The 6 microhabitat types accounted for 88% of the total cover across the 3 sites, while all excluded microhabitat types each accounted for less than 4% of total cover, and produced mostly zeros in the dataset.

Two weeks after removals were completed on June 22, 2005, bi-weekly visual counts were performed from July 6, 2005 to August 17, 2005 to determine the number of *C.cyanea* recruits settling to the 21 coral patches. August 17, 2005 represented two months of recolonization, and at this date removals were performed

for a second time to obtain exact TL body measurements, allowing for pre versus post recolonization abundance comparisons (June 22, 2005 vs. August 17, 2005). Due to the isolation of coral patches, all *C.cyanea* settling throughout the experiment were newly settled recruits. In some instances older migrant individuals were found on cleared coral patches, but were removed immediately. I performed a paired samples t-test to determine if coral patches where all *C.cyanea* had been removed were replenished by recruitment to their original pre-removal abundances after 8 weeks of recolonization. The t-test included recruits and juveniles (<4.0cm) in the analysis, as recruits settling at the beginning of the experiment would have grown into juveniles by the end of the 8 week recolonization period.

I then tested whether variability in recruitment to coral patches throughout the 8 week recolonization period could be explained by the presence of conspecifics. Recruitment to coral patches at each census period was not an independent measure when considering conspecific effects, as settlement during earlier recruitment events may influence those during later dates. I therefore ran a two-way repeated-measures ANCOVA, with the number of recruits per coral patch as the dependent variable, the number of conspecifics per patch as the covariate, and census period and site as predictor factors. The number of conspecifics for a given census period represented the total number of *C.cyanea* on patches at the beginning of the two week period prior to each census period. For example, the number of conspecifics for census period 2 represented the number of *C.cyanea* found on patches two weeks earlier during census period 1. Both recruitment and conspecific data were reciprocally transformed ( $1/(x+1)$ ) prior to analysis, as this



transformation was strongest for data normalization, while removing zeros in the recruitment dataset.

On April 22, 2006, 8 months after the 4<sup>th</sup> census period/second removals (August 17, 2005), I returned to the study location to again evaluate the replenishment of coral patches. I size classed all *C.cyanea* that had settled to coral patches after the 8 month recolonization period. Because I was interested in how the post recolonization abundance of *C.cyanea* compared to natural abundances prior to any removals, I performed a paired-samples t-test comparing June 2005 abundances on removal patches to April 2006 abundances.

## RESULTS

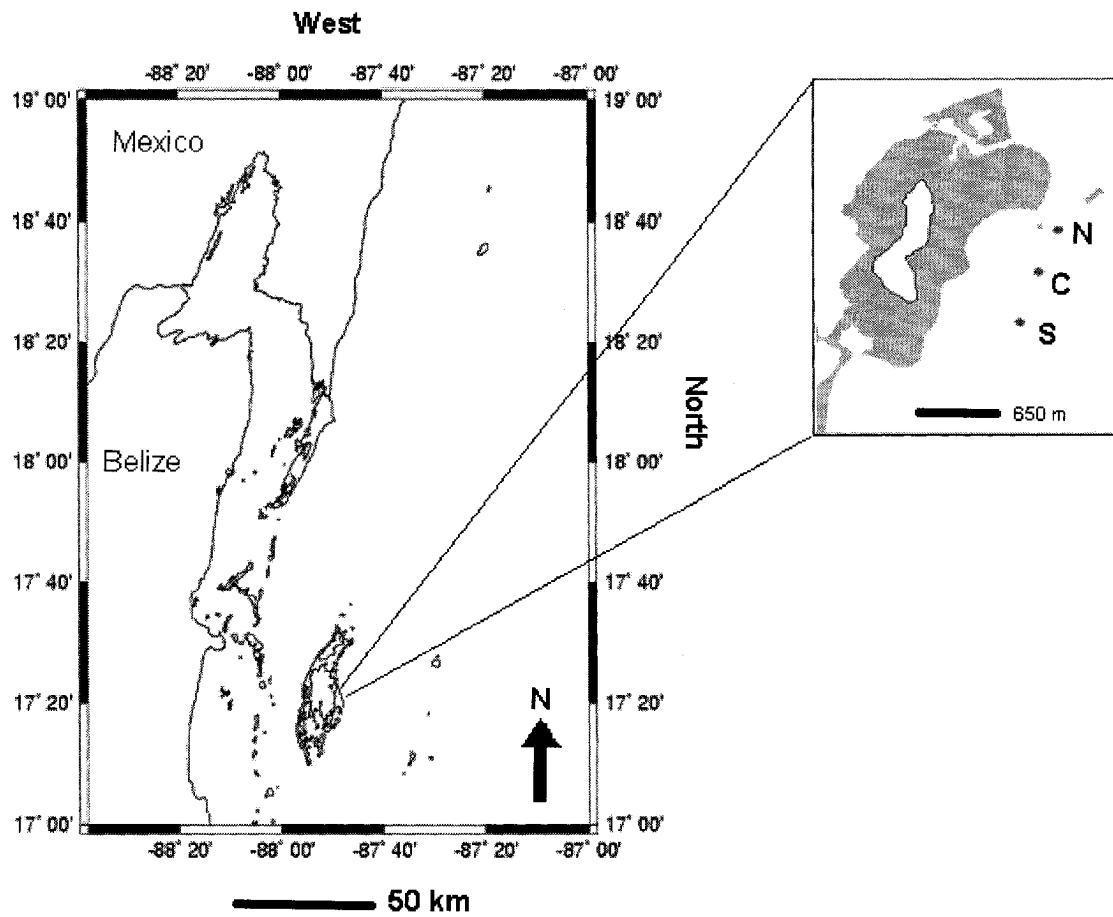
Overall, no significant differences among sites (Wilks Lamda <0.001, F=2.42, p=0.33), or treatments (Wilks Lamda=0.001, F=0.68, p=0.77) were found for microhabitat characteristics (Figure III-2, III-3). However, particularly for soft and branching coral, and inert substrata including dead branched and dead massive coral and sand, where sites cannot be reliably discriminated from zero, differences in mean % coral cover were evident.

In testing for a microhabitat effect on recruitment, the forward stepwise multiple regression model produced massive coral and rugosity as output factors I and II respectively, which together significantly influenced the number of recruits on patches ( $r^2=0.29$ ,  $F_{(2,18)} = 3.68$ ,  $p=0.04$ ). Independently, neither massive coral nor rugosity was significant in the model, although both approached significance (massive coral:  $r^2=0.17$ ,  $p=0.07$ ; rugosity:  $r^2=0.29$ ,  $p=0.09$ ).

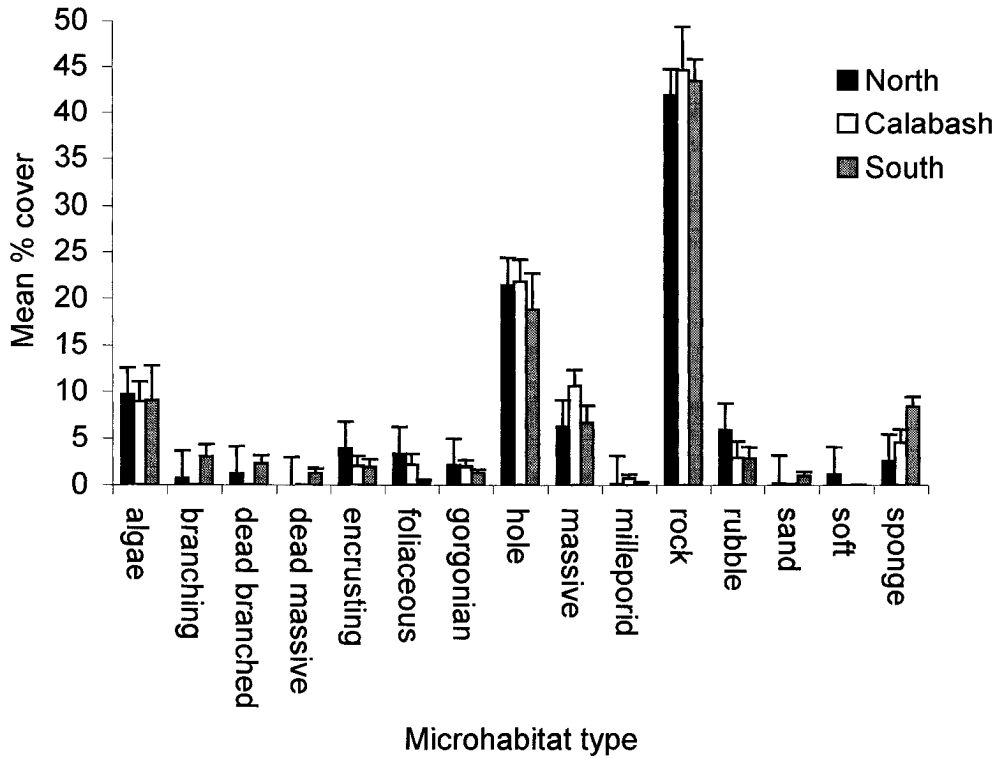
In comparing pre and post recolonization abundances of *C.cyanea* on removal patches, it was found that the number of individuals present on removal patches after 8 weeks of recolonization was significantly lower than pre-removal ( $t=6.32$ ,  $df=14$ ,  $p<0.001$ ). Before the initial removals began during the third week of June, 2005, removal coral patches averaged a total of 14 recruits and juveniles ( $\pm 2.0$  S.E.) per patch. Following 8 weeks of recolonization the same patches averaged only a total of 3 recruits and juveniles ( $\pm 1.16$  S.E.) per patch (Figure III-4). Upon returning to the study location 9 months after the initial removals of June 2005, I found that post-recolonization removal patches remained significantly depleted relative to their natural abundances prior to any removals at the beginning of the experiment ( $t=6.59$ ,  $df=14$ ,  $p<0.001$ ) (Figure III-4).

The presence of conspecifics alone was found to significantly influence recruitment to the 21 coral patches through out the 8 week recolonization period. Neither site x conspecific, census period x conspecific, nor site x census period x conspecific interactions significantly influenced recruitment to coral patches (Figure III-5, Table III-2).

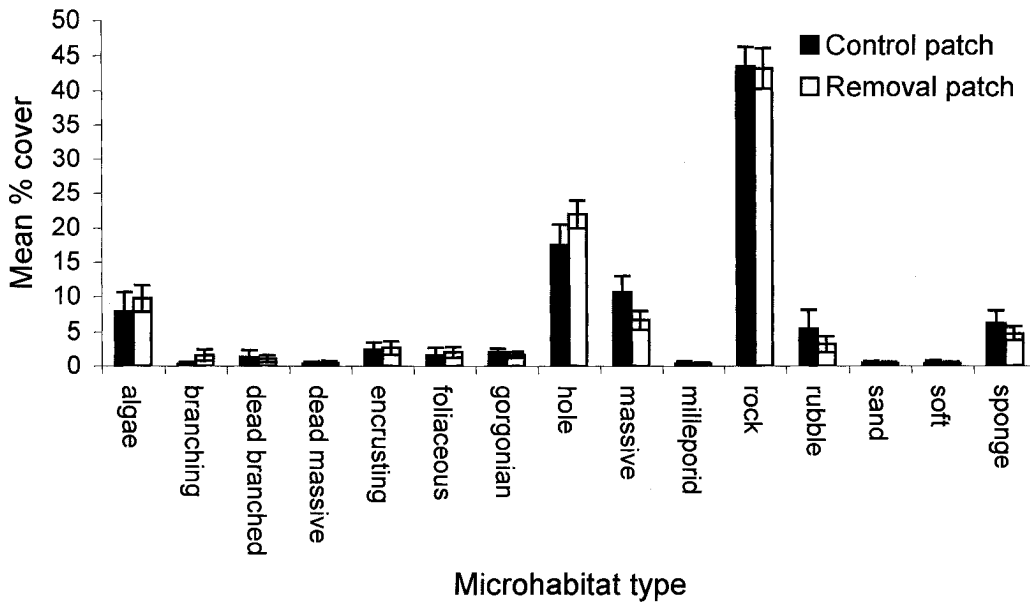
## FIGURES



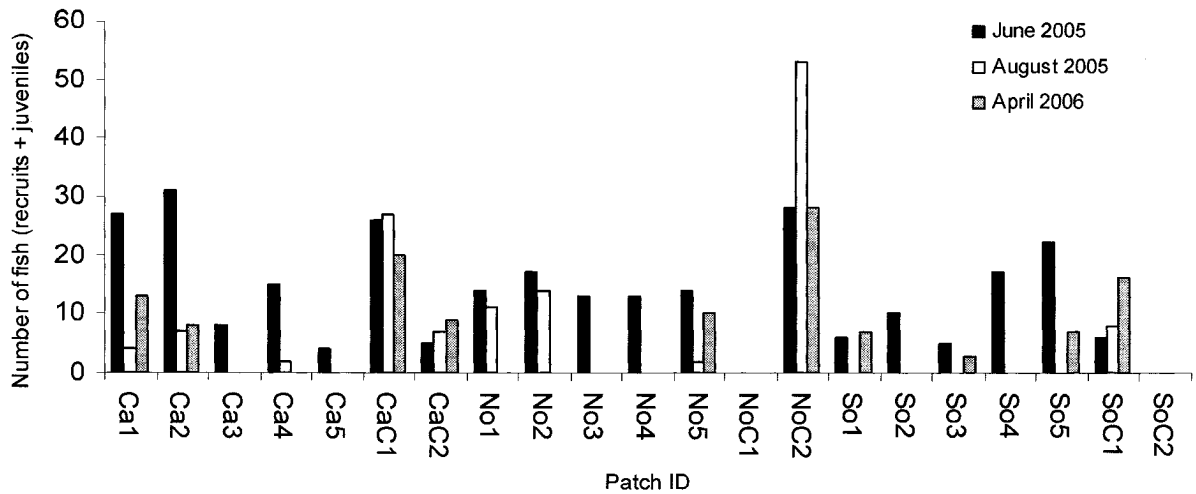
**Figure III-1.** Location of North (N), Calabash (C), and South (S) sites within Calabash Caye, Turneffe Atoll, Belize.



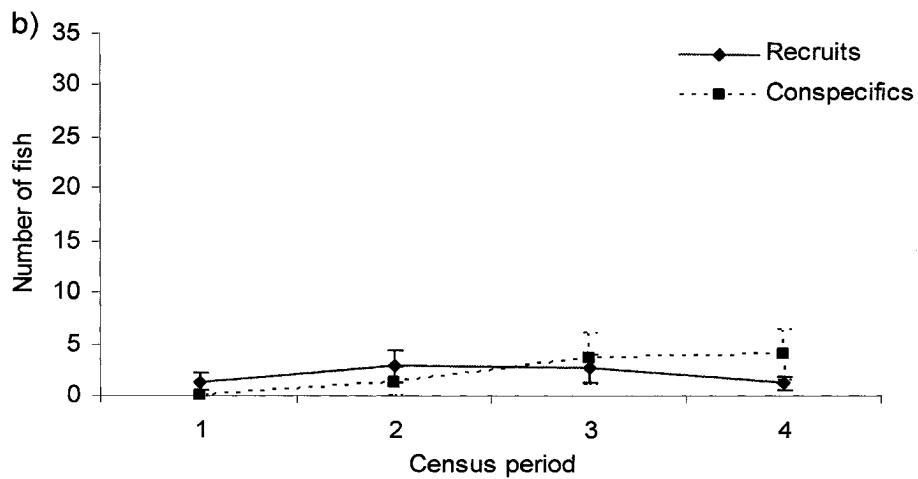
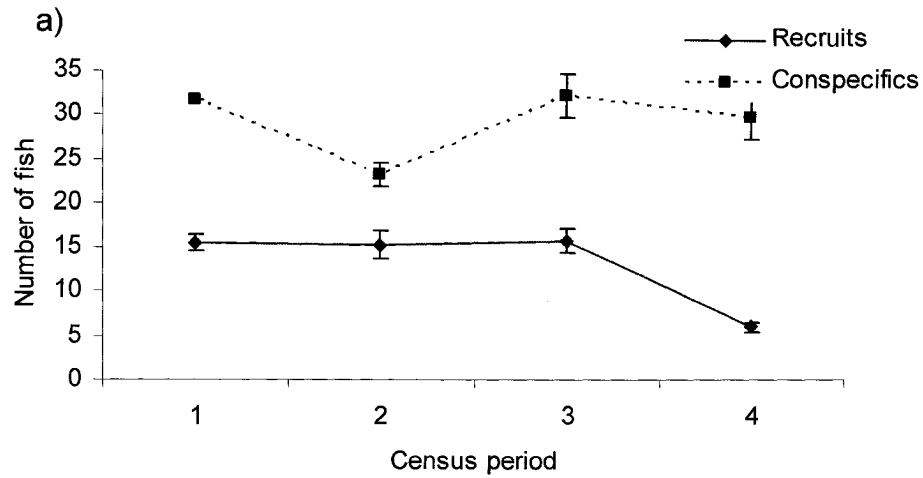
**Figure III-2.** Mean percent microhabitat cover for all coral patches within the three study sites ( $\pm$ S.E. n=21).



**Figure III-3.** Mean percent microhabitat cover for removal and control patches ( $\pm$ S.E. n=21).



**Figure III-4.** Number of recruits plus juveniles prior to removals of June 2005, post 8 weeks recolonization (August 2005), and 8 months post recolonization (April 2006) (n=15). Ca represents Calabash site, No North site and So South site. C1 and C2 represent control patches. Note that second removals were performed August 2005, 8 months prior to the April 2006 census. Significantly fewer fish ( $p < 0.05$ ) were present on coral patches after 8 weeks and 8 months of recolonization relative to pre-removal abundances.



**Figure III-5.** Mean number of conspecifics vs. recruits ( $\pm$ S.E. ) on a) control ( $n=6$ ) and b) removal ( $n=15$ ) coral patches for bi-weekly census periods 1 through 4. Census period 1 represents two weeks post removals (for removal patches) of June, 2005. Note the magnitude of difference in mean recruitment between control and removal patches. All patches were analyzed for a conspecific effect through a single repeated-measures ANCOVA. The presence of conspecifics significantly influenced recruitment.

## TABLES



**Table III-1.** Microhabitat categories quantified for coral patches at study sites.

Microhabitat type
Algae
Branching Coral
Dead Massive
Dead Branched
Encrusting Coral
Foliaceous Coral
Gorgonian
Hole
Massive Coral
Milleporid
Rock
Rubble
Sand
Soft coral
Sponge

**Table III-2.** Results of repeated measures ANCOVA of effects of conspecific presence on recruitment. Significant p-values are bolded.

Source	Df	MS	F	p
Conspecific	1	5.944	51.69321	<b>&lt;0.001</b>
Site x Conspecific	2	0.065	0.557	0.57
Census period x Conspecific	3	0.108	0.943	0.42
Site x Census period x Conspecific	6	0.057	0.493	0.81
Error	71	0.114979		

## DISCUSSION

Research in reef fish ecology is filled with a history of studies evaluating recruitment and potential influencing factors including microhabitat and conspecific effects, many through similar experimental means. However, intraspecific (Jones 1988, Russ 2003) and interspecific variability (Syms and Jones 2000, Searcy and Sponaugle 2001, Webster 2002), and spatial (Warner 1995) and temporal (Planes et al. 1993) effects have been widely reported. This work contributes to an important body of research in evaluating ecological questions for which no general consensus has yet been met.

### *Microhabitat*

The importance of habitat in influencing the recruitment of coral reef fishes has been widely documented (Williams and Sale 1981, Ault and Johnson 1998, Tolimieri 1998, Bergman et al. 2000). As each species has particular resource requirements including those of food and refuge from predators (Levin 1994), specific microhabitat characteristics at the scale of an individual's home range become essential for survival (Shulman 1985). The process of settlement to a reef from the pelagic environment is therefore essential for fishes in gaining access to a suitable habitat in which resource requirements can be met.

In this experiment I demonstrated the importance of particular microhabitat characteristics to the settlement of *C.cyanea* recruits. Both rugosity, or spatial complexity, and the presence of massive coral, mostly in the form of *Montastrea* and *Siderastrea* species, were found to influence spatial patterns in recruitment to coral

patches. Predation on juvenile fishes within the coral reef environment is commonly high (Levin 1991), and the importance of a highly rugose substrate as a shelter for fish has been widely reported (Werner et al. 1983, Caley and St. John 1997, Beukers and Jones 1998). To gain access to plankton in the water column above coral patches, *C.cyanea* hover above the substrata, making them particularly vulnerable to attacks from transient predators (Hixon and Carr 1997). In response to predation threats, *C.cyanea* will dive to the coral patch directly beneath them, taking refuge within holes or crevices in the substrata. Areas of high rugosity subsequently aid these fish in avoiding attacks from above their inhabited patches. As reported by De Boer (1978), the importance of refuge to *C.cyanea* remains apparent throughout their life in the benthic environment, and it may be particularly important for small, vulnerable recruits.

Rugosity can also be considered in context with the finding that coral patches higher in massive coral cover received a greater number of recruits. As suggested by Tolimieri (1998), larger heads of massive coral often form many crevices, potentially acting as an effective shelter for fish.

In addition, because live massive corals feed on plankton, their distribution may in part reflect plankton availability, which has been shown to vary non-randomly at small, or micro-scales (Holzman et al. 2005).

The importance of microhabitat in influencing the distribution and abundance of fishes has important implications in predicting the effects of disturbance to coral reefs. Many reef fish species require complex habitat for shelter and across the Caribbean damage to coral colonies has resulted in a change from complex,

heterogeneous communities to homogenous areas dominated by fleshy algae (Hughes 1994, Aronson and Precht 2001). The potential impacts on fishes due to long term anthropogenic disturbances to coral reefs are severe, given that a decline in hard coral cover up to 80% in the next three decades in the Caribbean is expected (Gardener et al. 2003).

### *Recolonization*

Over the 8 week recolonization period from June to August of 2005, recruitment to coral patches where all *C.cyanea* were removed was low, and removal patches remained largely unreplenished relative to their original pre-removal abundances. This discounts the possibility that the abundance of individuals present within aggregations of *C.cyanea* was limited by resources over the duration of the study, as a resource limited environment would result in relatively rapid recolonization of cleared areas. Because recruitment to removal patches was relatively high, removal patches could be assumed suitable as settlement habitats for new recruits. The lack of recruitment can thus not be explained by habitat effects, and I therefore suggest that recruitment may have been limiting the replenishment of *C.cyanea* to removal patches (Jones 1991, Doherty and Fowler 1994). Although the 8 week duration of recolonization may be considered relatively short, it covered a large part of the peak summer recruitment season for many Caribbean reef fishes (Doherty 1983, Booth and Beretta 1994), including that of *C.cyanea* (De Boer 1978). In addition, I was able to show that over a period of 8 months coral patches remained unreplenished of *C.cyanea*. Alternative to

recruitment limitation, it is possible that the presence of conspecifics may have been a cue required for settling larvae (see below).

### *Conspecifics*

The importance of conspecific presence to the recruitment of reef fishes has been shown in numerous studies (Jones 1987, Sweatman 1983, Fowler 1990, Ohman et al. 1998), however in many cases where conspecific effects are found, alternative explanations must often be considered. Some of these include the influence of local water currents directing larvae to particular patches, the physical availability of coral patches to settling larvae, the occurrence of migration after settlement, and microhabitat preferences (Booth 1992). In this study I was able to discount these possibilities. I found that differences in microhabitat characteristics between study sites and coral patch treatments did not significantly differ. As a result, higher recruitment to control patches could not be explained by differences in microhabitat. In addition, recruitment to removal patches prior to manipulations was regular relative to control patches as mentioned above, confirming they were conspicuous to settling larvae. Larvae may have therefore settled to coral patches with conspecifics at the time of settlement, or alternatively, larvae settled to all coral patches in equal numbers and those individuals settling to patches with conspecifics present were experiencing greater survivorship.

The applicability of the 'safety in numbers' hypothesis to newly settled coral reef fishes remains unclear (Connell 2000). While some studies of predation provide evidence that reef fish experience greater mortality when living in large groups

(Forrester 1995, Beukers and Jones 1998, Connell 2000), a positive density-survivorship relationship has commonly been found (Magurran 1990, Pitcher and Parrish 1997). Sandan and Pacala (2005) found that the survivorship of *C.cyanea* was positively related to aggregation density, where predators consistently visited and struck at smaller *C.cyanea* aggregations, possibly explaining the conspecific effect on recruitment found here.

The advantage to fishes living within an area of conspecifics may be dependent on age and/or size class. De Boer (1978) documented the territorial behavior of male adult *C.cyanea*, resulting in an established spatial arrangement of individuals. In the case of territorial adults, the presence of conspecifics thus may not provide individual benefits. However, benefits to recruits living in the presence of conspecifics are likely strong for site-attached territorial species, as older territorial members provide protection from potential predators and indicate the availability of food, shelter, and potential mates (Sweatman 1983, Levin 1993).

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## Chapter IV

### The influence of habitat on the recruitment of *Chromis cyanea* across a large spatial scale

#### ABSTRACT

Given the large spatial scale at which reef fish populations are believed to be connected, variability in habitat across large scales can potentially play an important role in influencing reef fish recruitment. Here, the recruitment of *C.cyanea* was monitored during the summer season of 2002 and 2003 at seven sites around Turneffe Atoll, Belize. Recruitment was found to vary both among sites and between depths, with a significantly greater number of *C.cyanea* recruits settling to deep than shallow positions. At the seven sites where recruitment data was collected, microhabitat cover and spatial complexity at deep and shallow positions was also quantified. In testing for a recruitment-habitat relationship, differences in recruitment across Turneffe Atoll could not be explained by spatial variability in the measured microhabitat characteristics.

## INTRODUCTION

“It is argued that the problem of pattern and scale is the central problem in ecology... There is no single natural scale at which ecological phenomena should be studied; systems generally show characteristic variability on a range of spatial, temporal and organizational scales,” (Levin 1992).

Traditionally, in studying the effects of habitat on the distribution and abundance of reef fishes, ecologists focused on small spatial scales (Sale 1971, Ebersole 1977, Talbot et al. 1978), often at that of an individual's home range. However, ecologists have long since recognized that habitat characteristics on a larger spatial scale beyond that of the individual home range can also influence the distribution and abundance of species (see Wiens 1989, Morris 1987). For organisms with a dispersive life stage this may be especially applicable, as propagules are often exposed to a suite of habitats during their dispersal before arriving to a location where they will spend the remainder of their lives.

Studies of genetic connectivity (Shulman and Bermingham 1995) and models incorporating ocean currents (Roberts 1997, Doherty et al. 1985) have provided evidence that coral reef fish larvae can potentially disperse hundreds of kilometers from their natal reef. It is evident that reef fishes are influenced by the reef habitat (Jones 1991), and larval fish are known to settle to particular microhabitats (Andrews and Anderson 2004). Larval fish have been shown to use environmental cues during settlement (Kingsford 2002, Leis et al. 2002, Tolimieri et al. 2000) at distances of at least 1 kilometer (Leis et al. 1996), and may be capable of maintaining proximity to a suitable reef habitat until the time of settlement

(Armsworth et al. 2001). Large-scale habitat characteristics may thus influence where fish will choose to settle, potentially influencing adult population sizes (Gutierrez 1998).

Empirical evidence has shown that the supply of larvae to the reef system is highly variable through space and time (Booth et al. 2000, Tolimieri et al. 1998, Robertson 1988, Williams 1983). However, if habitat influences the distribution and abundance of reef fishes, differences in habitat between two distant areas should be reflected in patterns of recruitment. Conversely, if the recruitment-habitat relationship is minimal, the immigration and emigration of fishes will determine the assemblages of fishes (Sale 1980), and their subsequent spatial distribution on the reef.

In evaluating the effects of habitat on recruitment, reef fish ecologists have commonly performed studies on small, isolated natural or artificial reefs, often in lagoonal areas (Russell et al. 1977, Shulman 1984, Doherty and Fowler 1994, Shima 2001). However, fewer studies have investigated recruitment at large spatial scales on contiguous reefs outside of lagoonal areas, where recruitment dynamics may significantly differ. It has, nevertheless, been difficult to detect large-scale recruitment-habitat associations to date (Tolimieri 1995, Caselle and Warner 1996, Sale et al. 2005).

In the previous chapter microhabitat characteristics at the spatial scale of an individual's home range were quantified and evaluated for effects on the recruitment of *C.cyanea*, and compared across a distance of one kilometer. In this chapter, I

tested for the recruitment-habitat relationship of *C. cyanea* at Turneffe Atoll, Belize, representing a spatial scale of approximately 50 km by 16 km.

## **METHODS**

The recruitment-habitat relationship was evaluated at Turneffe Atoll, Belize in 2002 and 2003. Specifically, I evaluated the total recruitment to all seven sites for census periods 1 and 3 to 7 for both years (see Study location and sampling, page 5). Briefly, at deep (10-14 m) and shallow (3-5 m) positions within each of the seven established sites, eight, 30 x 1 m transects were run, where the number of *C. cyanea* recruits (<2.0 cm TL) was counted within each transect.

At deep and shallow positions within each of the sites where recruitment data was collected, microhabitat cover and spatial complexity (rugosity) were quantified in the summer of 2002. At each depth, six haphazardly placed replicate 30 m transects were laid out directly over the substrata. The point-intercept method was used to quantify microhabitat cover (Loya 1972), where substratum was recorded every 25 cm directly under the 30 m measuring tape as one of 8 categories (Table IV-1). The proportions of measured microhabitat types along each transect were then determined by dividing the total number of transect points categorized for each microhabitat type by the total number of transect points categorized. Rugosity was measured by placing a 5 m long brass chain (1.1 cm links) along the transect tape. Chains were placed so that they followed the exact contours of the substratum, whereas transect tapes were stretched tightly across the substratum. Rugosity was subsequently determined by calculating the ratio of chain length to linear length from



the transect tape. Rugosity measurements were averaged for each transect (6 chains/transect) and then for the position within the site.

### *Statistical analysis*

Spatial variability in recruitment was analyzed using a two-factor analysis of variance, with site and position as categorical predictor variables of recruitment across 2002 and 2003. Recruitment was analyzed at the transect level, with 8 transects run at each position within each site.

To test for spatial differences in microhabitat across Turneffe Atoll, I again ran a two-factor analysis of variance. Proportions of the 8 microhabitat types and rugosity were dependent variables, and site and position categorical predictor variables. Microhabitat proportions were arcsine transformed prior to analysis to normalize data. Microhabitat differences were compared at the transect level, with 6 transects run at each position within each site.

Mean proportions of the eight microhabitat types and rugosity quantified at deep and shallow positions within each site were then analyzed using principal components analysis (PCA). Mean microhabitat cover proportions were arcsine transformed prior to analysis to normalize data. From the PCA I obtained principal components that were subsequently used as predictor microhabitat variables in analyzing the recruitment-habitat relationship (see below).

Because I was interested in the spatial relationship between microhabitat and recruitment, I pooled recruitment data for each of deep and shallow positions within the seven sites across 2002 and 2003 (n=14). The recruitment-habitat relationship

was tested using a forward stepwise multiple regression, with total recruitment per position within each site as the dependent variable, representing 14 measurements. Microhabitat principal components 1 to 3 from the PCA and the categorical predictor 'depth' (0=deep, 1=shallow) were independent variables. The first three principal components were used for the analysis as they together explained a large proportion of the variability in microhabitat between sites. I included depth as a predictor variable due to the fact that a significant depth effect on recruitment was found from the two-way ANOVA (see below). Because in Chapter III I found that both rugosity and massive coral cover influenced the recruitment of *C.cyanea*, I also ran separate linear regressions of rugosity and massive coral cover versus total recruitment for each position within each site.

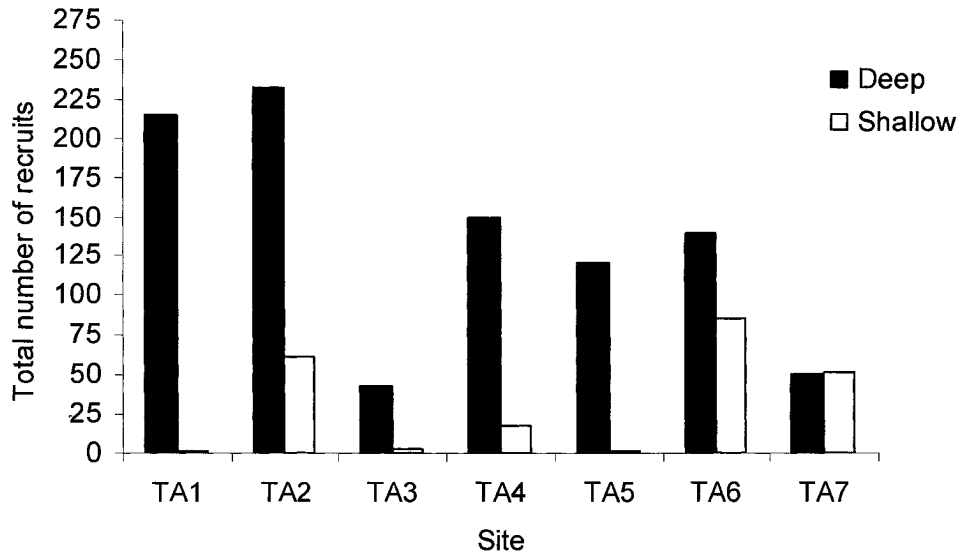
## RESULTS

From the 13 bi-weekly census periods covering the summer seasons of 2002 and 2003, I found recruitment varied significantly both among sites and between positions (Figure IV-1, Table IV-2). Specifically, I found that windward site 2 recruitment was significantly higher than windward site 3 recruitment, while leeward site 6 recruitment was significantly higher than windward sites 3 and 5. Recruitment was also significantly higher at deep than shallow sites. On average, the total number of recruits settling to deep positions in Turneffe Atoll across 2002 and 2003 was 136, while that to shallow positions was 31. No significant site x position interaction was found.

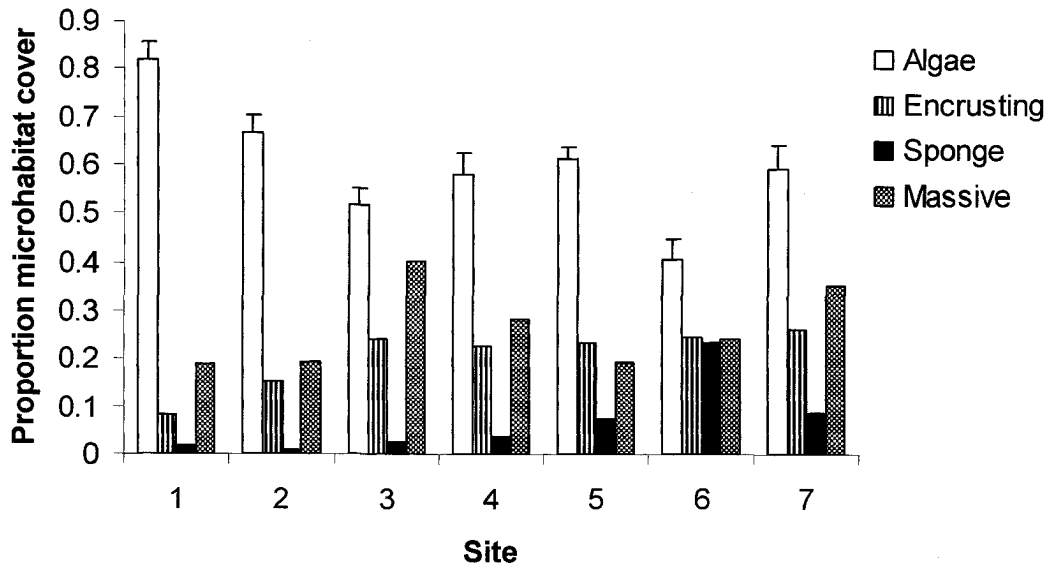
Significant differences in microhabitat were found both among sites and depths (Figures IV2-IV4, Table IV-3), although neither could independently explain spatial variability in microhabitat, as a significant site x position interaction was also found. Specifically, consistent site x position differences in microhabitat (significantly different from average) were found for: site 6 deep, which had low algal and high sponge cover, site 6 shallow also with high sponge cover, site 1 deep with low gorgonian cover and high rugosity, site 1 shallow with low encrusting coral and gorgonian cover, site 7 deep with high sponge cover and rubble, site 7 shallow with high massive coral cover, and site 5 deep with high rubble cover (Figures IV2-IV5).

From the PCA, principal components 1, 2 and 3 were found to explain a total of 72.58% of the variability in microhabitat among sites, representing 33.57%, 24.16% and 14.85% respectively (Figure IV-6, Table IV-4). However, none of the 3 microhabitat variables were included in the forward stepwise multiple regression, which included depth as the only variable significantly affecting the recruitment of *C.cyanea* across Turneffe Atoll ( $r^2 = 0.49$ ,  $p < 0.001$ ). Spatial variability in recruitment of *C.cyanea* also could not be explained by rugosity ( $r^2 = 0.10$ ,  $p = 0.27$ ) or massive coral cover ( $r^2 = 0.05$ ,  $p = 0.43$ ), further suggesting that large-scale differences in microhabitat could not explain large-scale differences in recruitment (Figure IV-7).

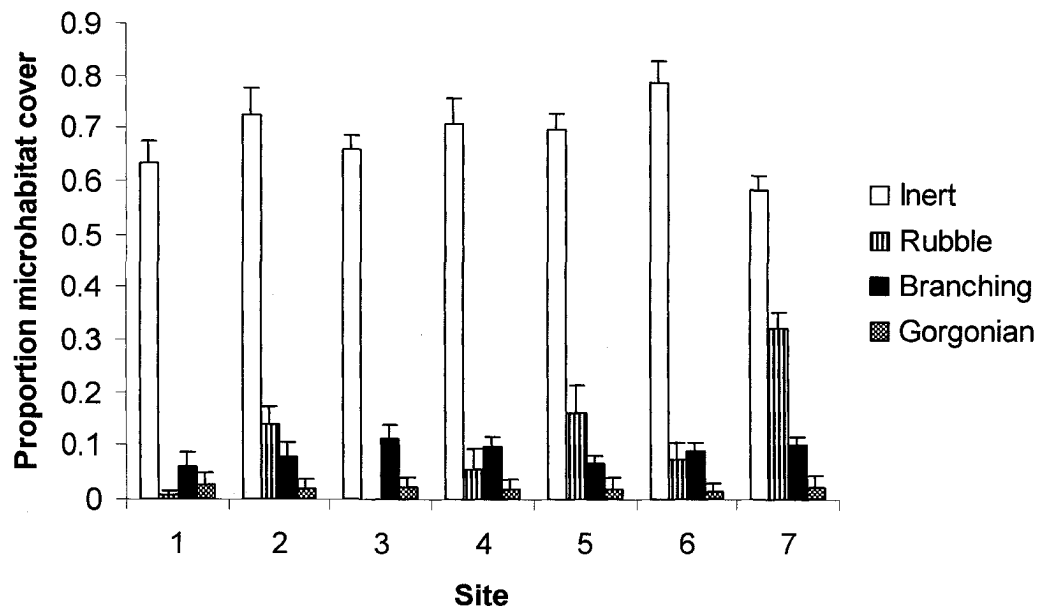
## FIGURES



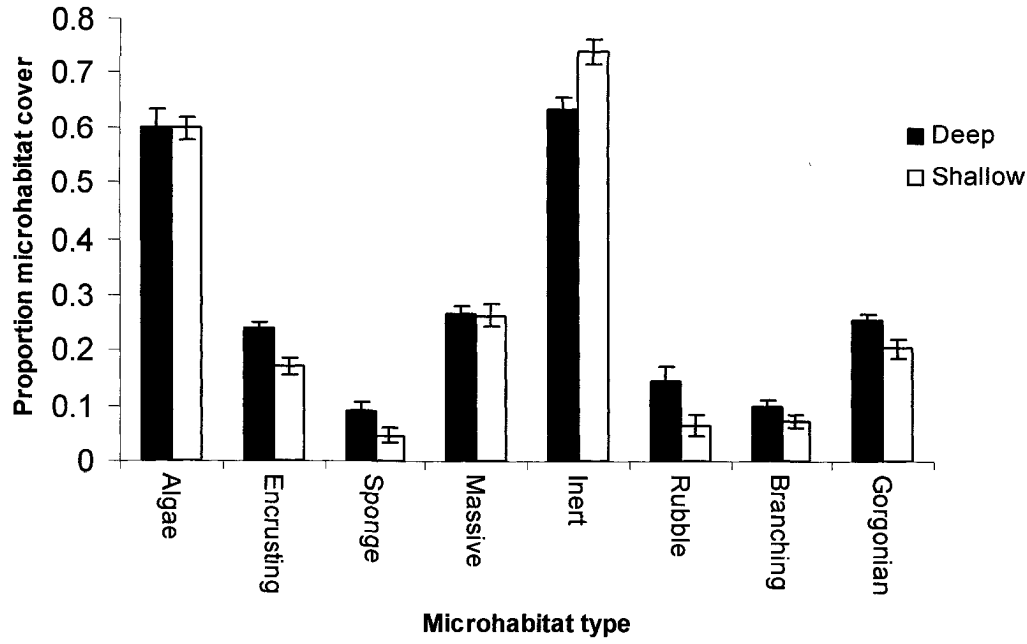
**Figure IV-1.** Total number of *C.cyanea* recruits settling to deep and shallow positions within the 7 sites of Turneffe Atoll, Belize across 2002 and 2003 (n=1169). Significantly more recruits were found to settle to deep positions ( $p<0.05$ ).



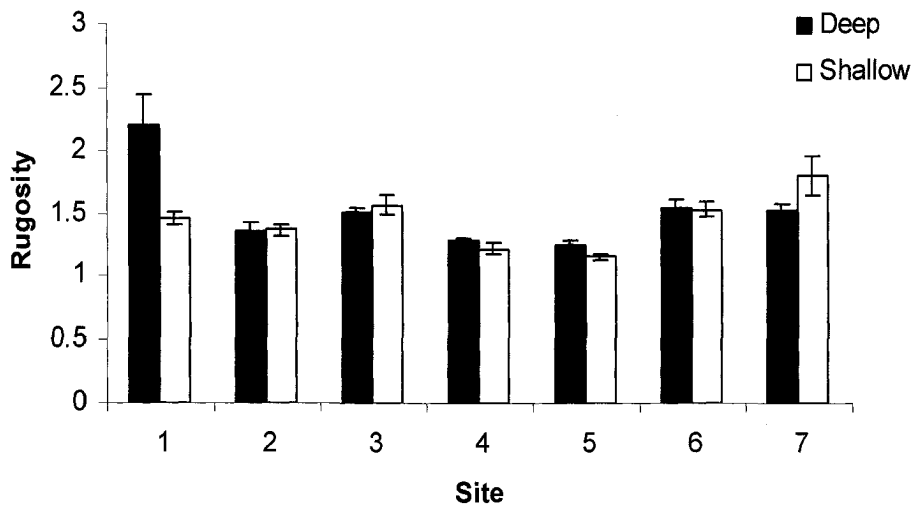
**Figure IV-2.** Arcsine transformed microhabitat cover proportions per site for algae, encrusting coral, sponge and massive coral ( $\pm$ S.E.).



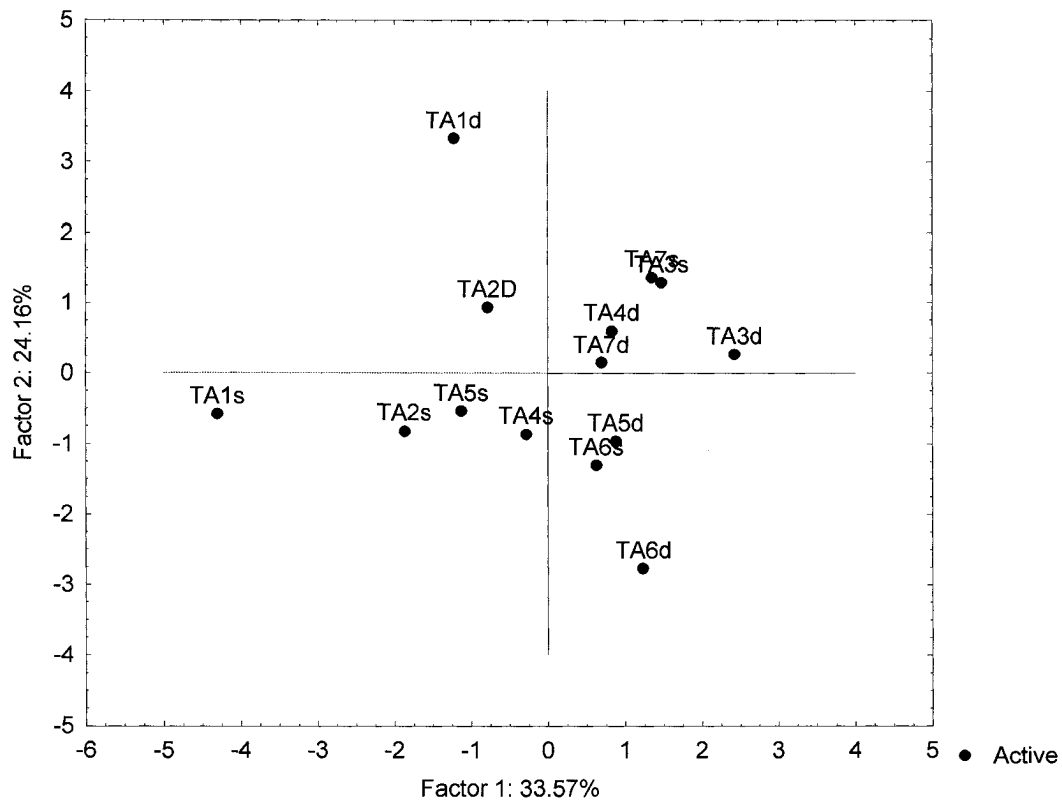
**Figure IV-3.** Arcsine transformed microhabitat cover per site for inert substrata, rubble, branching coral and gorgonian ( $\pm$ S.E.).



**Figure IV-4.** Average arcsine transformed microhabitat cover for all microhabitat types quantified at deep and shallow positions ( $\pm$ S.E.).

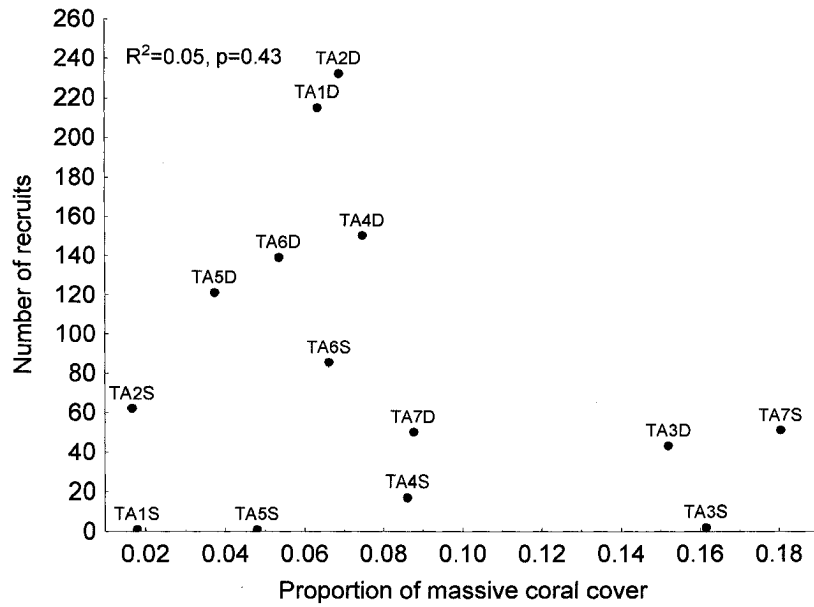
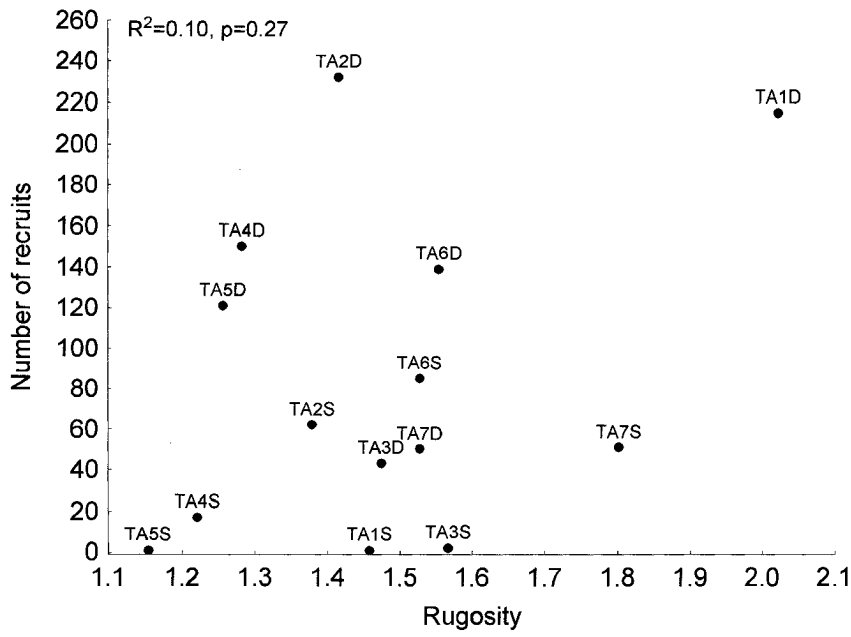


**Figure IV-5.** Mean rugosity ( $\pm$ S.E.) for deep and shallow positions within sites at Turneffe Atoll.



**Figure IV-6.** PCA factor plot of habitat features quantified at each depth for all 7 sites within Turneffe Atoll.





**Figure IV-7.** Rugosity and massive coral cover versus total recruitment of *C. cyanea* for deep and shallow positions within each of the seven sites in Turneffe Atoll for 2002 and 2003.

## TABLES

**Table IV-1.** Microhabitat types quantified within Turneffe Atoll, Belize.

Microhabitat type
algae
branching coral
encrusting coral
inert
gorgonian
massive coral
rubble
sponge

**Table IV-2.** Results of two-factor ANOVA of recruitment. Significant p-values are bolded.

Source	Df	MS	F	p
Site	6	57.54	4.18	<b>&lt;0.001</b>
Position	1	459.55	33.42	<b>&lt;0.001</b>
Site x Position	6	18.25	1.33	0.24

**Table IV-3.** Results of two-factor ANOVA site x position interactions for microhabitat characteristics measured across Turneffe Atoll (Df=13).

Habitat	MS	F	p
Algae	0.11	7.82	<0.001
Branching Coral	0.008	1.75	0.07
Encrusting Coral	0.032	9.10	<0.001
Gorgonian	0.038	8.59	<0.001
Inert	0.07	5.77	<0.001
Massive	0.053	9.65	<0.001
Rubble	0.091	10.30	<0.001
Sponge	0.042	12.45	<0.001
Rugosity	0.42	8.85	<0.001

**Table IV-4.** Component loadings from principal components analysis of microhabitat characteristics for position/site measurements.

	PC1	PC2	PC3
branching	0.65	0.36	0.34
algae	-0.50	0.74	-0.04
encrusting	0.93	-0.11	-0.25
sponge	0.38	-0.57	-0.13
gorgonian	0.83	-0.02	0.33
massive	0.74	0.43	0.02
rubble	0.20	-0.15	-0.88
inert	-0.17	-0.76	0.48
rugosity	0.09	0.59	0.06

## DISCUSSION

The spatial analysis of recruitment revealed that site 2 received significantly more recruits than its southern adjacent site, site 3. Leeward site 6 also received significantly more recruits than site 3, in addition to southern atoll site 5. It is difficult to interpret differences in recruitment between sites 2 and 3, as no other windward sites showed significant recruitment differences (i.e. sites 1, 4 and 5), and an upstream/downstream recruitment effect resulting from the south to north current flow (Tang et al.) was not found. In addition, spatial variability in recruitment could not be explained by differences in microhabitat (see below). However, site 6 is a leeward site with high predicted water retention relative to windward site 3 and south site 5 (Tang et al. 2006). If the sources of recruits to leeward site 6 are independent of the source of recruits to windward sites (which are predicted to receive recruits from a southeastern source), this may in part explain this difference in recruitment.

Recruitment was also found to be significantly higher at deep than shallow positions, as I found from the ANOVA and multiple regression analysis. A number of other studies have similarly found depth to be an important determinant of recruitment (Williams et al. 1983, Sale et al. 1984, Steele 1997, Leis et al. 2002) the spatial distribution of species on the reef (Luckhurst and Luckhurst 1978, Bell 1983). Depths may differ in habitat, water movement, light, and food availability (Keast and Harker 1977), and may have differential effects on mortality, as would be reflected in recruitment measures. Jones (1986) found that *Pomacentrus amboinensis* settling to deeper areas experienced greater survivorship over the first 9 months of benthic life. Given that habitat was found to have no effect on recruitment, any differences

in habitat between depths cannot explain differences in recruitment. However, any of the other mentioned factors may have influenced the recruitment of *C.cyanea*.

Finally, variability in recruitment could not be explained by differences in microhabitat characteristics across sites and depths. This finding supports a number of studies that have found no recruitment-habitat relationship when scaling up (Tolimieri 1995, Casselle and Warner 1996, Sale et al. 2005), suggesting that larvae settle to a reef through processes unrelated to habitat at scales of tens of kilometers in this case. Caselle and Warner (1996) suggest that hydrographic features, among other factors, may determine patterns of recruitment. Reef fish ecologists are currently in the early stages of incorporating hydrodynamics with the study of large-scale recruitment (e.g. Cowen et al. 2000, 2006, Shanks et al. 2003), and these studies will be necessary in allowing us to gain a better understanding of reef fish recruitment.

As Shima (2001) suggests, reef fish ecologists often apply correlational findings as general ecological phenomena, with a lack of consideration of scale. In contrasting the findings of Chapter III, where microhabitat influenced the small-scale recruitment of *C.cyanea*, this study has highlighted the importance of multi-scale approaches in ecological studies. Studies of reef fishes lacking multi-scalar approaches should be considered significant only on the scale at which the ecological system has been studied.

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## GENERAL DISCUSSION

The central problem of ecology is recognizing and understanding the factors that influence the distribution and abundance of species. Numerous interacting factors typically determine a species spatial distribution and abundance, making it particularly difficult to determine the influence of single factors independently. In addition, influencing factors often vary on spatial and temporal scales, adding to the complexity of ecological studies (Levin 1992). Ecology is filled with a history of studies focusing on single factors at single scales. Although these studies have been essential in gaining an overall greater understanding of the distribution and abundance of organisms, multi-factor, multi-scalar approaches provide a broader ecological perspective and are necessary for applications in species conservation (Noss 1992, Lapin and Barnes 1995, Rotenberry and Knick 1999, Poiani et al. 2000, Beck et al. 2001).

Reef fish ecologists continue to study and debate the effects of both pre- and post-settlement factors in influencing the distribution and abundance of reef fishes. Coral reefs are multi-scalar systems, and although the importance of multi-scalar and multi-factor approaches to studying reef fishes is recognized (Sale 1998), studies still often focus on the effects of single factors at single scales (Shima 2001), that may be unsuitable for the effect being evaluated.

In the three studies carried out here, I have attempted to determine the effects of multiple factors influencing the distribution and abundance of the coral reef fish *Chromis cyanea* at small and large spatial and temporal scales. In addition, in

focusing on a single species, I was able to eliminate potential species-specific differences for the pre and post settlement factors evaluated.

### *Large-Scale Recruitment*

Large-scale recruitment to Turneffe Atoll was evaluated for *C.cyanea* in 2002 and 2003. In Chapter II, I evaluated spatial and temporal variability in recruitment, finding that recruitment to site 2 was significantly higher than to sites 3,5,6 and 7 in 2002, while recruitment to site 2 was significantly higher than to site 4 in 2003. It is important to note that recruitment was analyzed for all seven sites in 2002 during 4 census periods (1,2,3,6), whereas recruitment was analyzed for 3 sites (2,4,7) during 3 census periods (1,2,5) for 2003. Between-year differences in recruitment found within Chapter II can therefore not be reliably made.

However, the relatively high recruitment to site 2 was a trend found from both the spatio-temporal analysis in Chapter II and the spatial analysis in Chapter IV. Tang et al.'s (2006) retention index and circulation model provided no evidence to suggest that site 2 recruitment should be high relative to other sites. From chapter II, it was also evident that recruitment showed little within-year temporal variability, as only one census period (5 vs. 1) difference was found for Turneffe Atoll 2003, and no census period differences were found in 2002. Neither larval traits nor large-scale habitat differences could explain the variability in recruitment:

### *Pelagic Larval Duration and Larval Growth Rate*

As the study of larval life history traits and the environmental variables affecting them are continually studied, it is becoming increasingly evident that the pelagic life of tropical reef fishes has important potential implications as to their distribution and abundance in the reef environment (Bergenius et al. 2002, Wilson and Meekan 2002, Sponaugle and Pinkard 2004).

Although I was able to find a correlation between mid stage larval growth and pelagic larval duration, where faster growing larvae settled at a younger age, I was unable to find a relationship between either growth rate or larval duration and recruitment, suggesting that these life history characteristics did not influence the survivorship and subsequent settlement of *C.cyanea*. I did, however, find that PLD showed little within-site temporal variability but high among-site variability in Turneffe Atoll. This suggests that the PLD of individuals settling within a site is fairly consistent, which may imply that the source of recruits may also be somewhat consistent if ocean currents transport larvae to the same sites through time.

In evaluating larval growth rates, a consistent pattern was found only within Turneffe Atoll in 2002, where individuals settling during the mid to late summer experienced faster growth than individuals settling during the early summer. This variability may be due to the typical within-season temperature differences during the sampling period. If temperature or other factors influence the growth rate of fishes, this will have implications for their dispersal, as individuals growing at a faster rate in the later summer will be expected to settle younger than slower growing individuals, and will thus have a lower potential dispersal distance.

As previously mentioned, few studies have tested the relationship of larval life history traits and recruitment in the tropics to date, and further research carried out at similar spatial and temporal scales is required. In addition, environmental variables are known to influence the growth of larval fish (e.g. Sponaugle et al. 2006), and studies evaluating these effects will allow us to gain a better understanding of larval growth, larval durations, and the subsequent dispersal of larvae. Also important yet still in its early stages of research is the incorporation of ocean circulation patterns (Schultz and Cowen 1994, Roberts 1997), which, together with larval life history and behavioral traits will enhance our ability to predict recruitment (Sale and Mora 2002).

#### *Microhabitat effects*

A number of studies have reported the influence of habitat on the settlement of coral reef fishes (e.g. Booth 1992, Wellington 1992, Sale 1984). The answer as to whether habitat influences the distribution and abundance of fishes is perhaps more apparent than the scale at which habitat affects fishes. The spatial effect of habitat on reef fishes is a particularly important consideration for conservation purposes. Marine protected areas are designed in part to protect fishes and the coral reefs they inhabit, and it is thus necessary to determine the scale that habitat will affect their distribution and abundance (Friedlander et al. 2003), and hence their recruitment. Large-scale differences in habitat will be an important determinant of the size and spatial distribution of MPA's (Dugan and Davis 1993, Friedlander and Parrish 1998,

Murray et al. 1999), and areas of “high quality” habitat may be those considered for protection (Schmitten 1996).

In studying the effects of habitat on the recruitment of reef fishes, I first determined that *C.cyanea* recruit to coral patches of high rugosity and massive coral cover. Although this study was carried out at the scale of the individual home range, it was important in revealing the habitat characteristics necessary for the recruitment of this species. In chapter IV, the same recruitment-habitat relationship was not found at a larger spatial scale of tens of kilometers. This contrasts the findings of Roberts and Ormond (1987) and Shima (2001) among others, who found that particular habitat features across large scales from hundreds of meters to kilometers, was a reliable predictor of recruitment. A number of studies have, however, found difficulty in detecting large-scale habitat effects on recruitment (Caselle and Warner 1996, Ault and Johnson 1998). Whether this is due to the variability in the methods used to study habitat effects, or whether habitat does not play a role in determining spatial patterns in recruitment at large scales is not known, and more large-scale habitat studies are required.

Through a recolonization experiment, I was also able to determine that the recruitment of *C.cyanea* was positively correlated with the presence of conspecific fish (see also Sweatman 1983, 1985, Booth and Beretta 1994), possibly due to the apparent benefit of avoiding predation (Sandán and Pacala 2005). In this case, fish may have been recruiting to coral patches where conspecifics were present, or alternatively, observed differences in recruitment to patches with conspecifics was a result of increased survivorship. In either case, my findings suggest that, in addition

to the direct negative effects of habitat degradation on recruitment, the removal of resident fishes from the coral reef environment may also have important consequences to reef fish recruitment (Öhman 1998).

From the recolonization experiment I found that the recruitment of *C.cyanea* was low over the duration of the study, as coral patches removed of resident fish remained largely unreplenished. This finding agrees with others supporting the recruitment limitation hypothesis (Doherty 1983, Victor 1986, Armsworth 2002), which contrasts the historical ecological view that populations remain close to their carrying capacity and are limited by resources (MacArthur 1972). If recruitment plays a major role in shaping reef fish populations, conservation strategies including the creation of marine protected areas must consider the connectivity of populations separated at scales of tens to hundreds of kilometers representative of the spacing of source and sink populations (Man et al. 1995).



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