The Early Life History of the Brooding Damselfish *Acanthochromis polyacanthus*: Effects of Environment and Ancestry

Thesis submitted by

Kathryn Diane Kavanagh
(B.A. *St. Mary's College of Maryland*, M.A. *The College of William and Mary*)

in October 1996

for the degree of Doctor of Philosophy
in the Department of Marine Biology
James Cook University of North Queensland

STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University of North Queensland will make it available for use within the University Library and, by microfilm or other means, allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

> In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author: and to make proper public written acknowledgment for any assistance which I have obtained from it.

Beyond this, I do not wish to place any restriction on access to this thesis.

16 June 97

(Date)

STATEMENT OF SOURCES
DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references in given.

16 June 97
(Date)

Table of Contents

Abstract

In complex life-histories, the timing of transitions between stages is of central importance in any consideration of ecological or evolutionary responses to environmental pressures. Understanding these interactions between environment, growth rate, developmental rate, and the timing of stage transitions is useful in predictions of the direction of ecological or evolutionary change in animals with complex life histories, such as frogs and fishes.

The primary aims of this study were to examine environmental correlates of growth, development, parental investment, and mortality rates for one species of coral reef damselfish (Pomacentridae: *Acanthochromis polyacanthus)* whose unique life history permits such site-specific demographic correlations. From literature references and measurements obtained from developmental series, these characteristics are compared with several other species of coral reef damselfishes. Field studies were conducted on the exposed and lagoonal reef zones surrounding Lizard Island, Great Barrier Reef. Developmental series were obtained from captive-reared animals kept under controlled temperature conditions in the lab.

Acanthochromis polyacanthus is highly unusual because it lacks a pelagic larval stage and exhibits extended biparental care of eggs and juveniles, in many ways similar to that of the substrate-brooding cichlid fishes. Hatching occurred during midday, in contrast to all other damselfishes which hatch at sunset. *Acanthochromis* have large, relatively well-developed hatchlings (5 mm SL). Dispersal from the nesting area is initiated by parents chasing their offspring away, which occurred 3-4 months after hatch (approximately 50 mm SL) at Lizard Island.

Parental effort was significantly greater in exposed reef zones than in the lagoon, and was greater in younger broods. This pattern was apparent in the analysis of defensive chases by parents, with more chases occurring in exposed reef zones and from parents with younger broods. Intruding conspecific adult *Acanthochromis* were the most frequently chased taxon (31.6% of all chases). Juveniles in a brood were also "tĕnded" (approached and/or herded back into the brood) significantly more often in exposed sites. Olfactory cues may be used by parents in detecting juveniles; a pilot study found that significantly more parents tested chose to spend time in water with the scent of their juveniles as opposed to plain seawater. Within a zone, parental care *per juvenile* did not change significantly as juveniles aged. Specialized juvenile behaviors included, most notably, glancing off the sides of the parents. Glancing rates did not differ between reef zones but significant differences between juvenile stages were found. Glancing rates were not significantly different in feeding and non-feeding juveniles, suggesting that this behavior is not a major source of nutrition. However, an experimental study indicated that ingestion of mucus did occur during glancing.

Production of broods was greater in front reef (exposed) sites but juvenile survival was greater in lagoon sites. There was a significant season/zone interaction with the greatest survival in the lagoon in early summer. Density of *Acanthochromis* adults was higher on front reefs. A significant positive correlation between adult density and brood density at all sites indicated that adult *Acanthochromis* prefer to live in front reef zones despite lower juvenile survival. The maximum size of *Acanthochromis* in exposed sites was consistently greater than in lagoon sites.

Under calm weather conditions, juvenile growth rates were generally lower in the lagoon than in exposed sites, however, growth rates of lagoon juveniles increased rapidly following strong winds (which potentially flush plankton-rich waters into the lagoon).

Exposed sites showed no difference in growth rates between calm and strong wind conditions. In contrast to increased growth rate, ossification rate was slowed in the lagoon juveniles after strong winds, suggesting that there is a trade-off between growth and development. No differences were detected in growth or development rates of lagoon juveniles that were provided with supplemental food.

Characteristics of *Acanthochromis* suggest that predation is an important selective force that affects the energetics and survival of early stages of fishes living on the reef. On ecological and evolutionary scales, spatial variation in environmental factors must influence the vital rates (*sensu* Houde, 1987) of young reef fishes; the interactions of these rates with the timing of stage transitions may allow predictions of the direction of change.

Acknowledgments

No matter what the book says, theses are never done independently. I had an enormous amount of support in order to complete this thesis: through time given in wonderful discussions of ideas, through plain hard work in helping me collect and analyze data, and, not insignificantly, through financial and emotional reinforcements in times of looming disaster.

I must first thank my supervisors Professor Howard Choat, Dr. Jeff Leis, and Dr. David Bellwood for their important contributions in stimulating and helping to shape my ideas about reef fish ecology and evolution. All of them were influential in this work. I am indebted to Howard Choat especially for supporting me and this work through its scattered beginnings, for his generous assistance in procuring funding for the project whenever he could, and for his initial support for my coming to Australia to study. I am grateful to Howard Choat and Dave Bellwood for their suggestion in 1992 that *Acanthochromis* might be a particularly interesting study subject. They were very right! I would like to thank Jeff Leis for his generosity and time during my Australian Museum visits, and for his prompt and useful critiques.

I am greatly indebted to Dr.Ross Alford for his influence in many ways: through interesting and fruitful conversations, for translating his froggy-minded insights across and into thoughts about the early life histories of reef-fishes, for his patience with my many requests about computers and statistics, and for lots of other general supervisory-type input. I also thank Drs. Julian Caley and Lin Schwarzkopf for their scientific advice and tough (but mushy on the inside) criticism of my papers. Their generosity extended far beyond the call of duty or friendship and had an enormous impact on my ability to complete this thesis.

I owe my thanks to many other people who ably assisted me with field, laboratory, or aquarium work. Without their collective assistance, this thesis would have been impossible. These include: Suresh Job, Jonathan Werry, Adam Felton, John Morrison, Don Booth (whom I also thank for providing cichlid larvae), Dave Stewart, Claudia Ludescher, Jean-Luc Solandt, Peter Nangle, Maya, Chad Lunow, Dirk Erler, Brad Smith, Simon Hawke, Lis Wilson, Bridget McCarty, Bryce Stewart, Andrew Cumming, John Ackerman, Con Lokkers, Jen McIlwain, Fabian Grutter, Glenn Wilson, Lexa Grutter, Brigid Kerrigan, Martin Gomon, Paul Southgate, Bob Riel, Leigh Winsor, and Heather Winsor. For computer and statistical help and/or for critiques on earlier drafts, I thank Dr. Hugh Sweatman, Natalie Moltschaniwskyj, and Laura Castell. For Amphiprion eggs, I thank the Wonderland Aquarium of Townsville. For assistance with my attempts at phylogenetic analysis, I thank Marty Cavalluzzi. For her beautiful drawings, I thank Lucy Smith. And for their excellent photographs, I thank Zoli Florian and Mark Johnson. I thank the Lizard Island staff, Lyle Vail, Anne Hoggett, Lance Pierce, and Marianne Pierce for their help in making my field work go smoothly. I am very grateful to Mr. Rod Thompson for his financial assistance. A special thanks goes to my officemate of these years, Steve Purcell, for being helpful, amusing, challenging, and a rude Aussie boy, all at exactly the right times. And I thank Christine Jones for giving me the steadiest of friendships outside my little scientific microcosm.

Finally, for their encouragement and support through the years, I thank my family, and my friends who have become family. A special dedication goes to Micaela Hellstrom for her passion and intellect which kept me going through some rough points.

My doctoral work was supported by an Overseas Postgraduate Research Award from the Australian Government, two James Cook University Scholarships, and two Australian Museum Postgraduate Research Grants.

Chapter One

General Introduction

Complex life histories, or those involving more than one stage, have been regularly used to develop and advance the theoretical framework for studying the evolution of life histories (Werner, 1986; Shine, 1978). In complex life histories, the timing of transitions between stages is of central importance in any consideration of the ecological or evolutionary responses to environmental pressures. Since transitions between stages are typically associated with a change in habitat, the duration of a particular stage may reflect the relative pressures on life stages in different habitats.

In analyzing life-history evolution, three approaches, demography, trade-offs, and the comparative method, are often used. Demographic parameters, such as mortality rates, growth rates, and size structure of populations, demonstrate the relative strengths of past selective pressures. They also provide the context for the responses to current environmental variability, and are the basic information necessary for examining traits of populations. A second approach, trade-offs among traits, is an important general concept in life history theory. Because resources are not infinite, animals must partition their limited energy into such things as somatic growth, movements and behaviors, number of offspring, etc., in order to maximize total reproductive output, or fitness. The pattern of trade-offs provides information on relative pressures on particular traits. A third approach to analyzing life histories is through the comparative method. The way that selection acts on individual traits, and patterns of trade-offs between them, is affected by the phylogenetic history of the taxon in question. The past history of the lineage (e.g. gene flow rates, bottlenecks, separated populations remixing, rapid vs. slow speciation) will affect the ability of the taxon to respond. Instead of comparing "apples and oranges", comparing a group of

phylogenetically-related species for trends among traits is one way to assess lineage-specific patterns of change without the problem of differing ancestries. The approaches of demography, trade-offs, and comparisons within a lineage will be used and discussed in parts of this thesis to assess patterns of life-history change.

The study of life history evolution can provide a new level of insight into the patterns observed in nature. Although these studies are increasing, marine systems are vastly underrepresented in the literature. Fishes and amphibians are the only vertebrates to have complex life histories, and thus the body of literature available on amphibians can be consulted for studies on fishes. In this thesis I examine ecological, morphological, ontogenetic and behavioral characteristics of species within the damselfish family (Pomacentridae), a group of coral-reef fishes. The group is particularly interesting because of the unusual life history of one of its members, *Acanthochromis polyacanthus*.

While typical damselfishes, and indeed nearly all marine teleost fish species, have a complex life cycle including a pelagic larval stage and a benthic juvenile/adult stage, one species of coral reef damselfish *Acanthochromis polyacanthus* has uniquely (among damselfishes) eliminated the pelagic larval stage. Instead of releasing larvae to live independently in the open sea, *Acanthochromis* (a monospecific genus) spends its entire life on the reef, brooding its young in this environment for months (Robertson, 1973; Allen, 1975; Thresher, 1985). This level of offspring care is qualitatively different from that of any other damselfish species, all of which spend only a few days guarding each clutch of eggs which hatch into pelagic larvae. The existence of the monophasic *Acanthochromis* life history is remarkable because of its radical departure not only from the norm of the vast majority of marine fishes, but also from that of all of its closest relatives, the 300+ species of damselfishes.

Pomacentrid Life Histories

Damselfishes are relatively small, demersal, site-attached reef fishes. They are found in all tropical seas, and a few genera (*Parma, Hypsypops, Chromis*) exist on temperate reefs. Among species, trophic niches range from territorial herbivore to "near-schooling zooplanktivore" (Leis and Rennis, 1983). Many species are trophically flexible and take advantage of the availability of plankton, algae, or small invertebrates. Most damselfishes are protogynous and the males are typically larger than the females (Thresher, 1984). In most species, the male prepares the nesting site, attracts one or more females to it to spawn, then defends the eggs. Nesting characteristics vary among species. Pomacentrine damselfishes typically lay single-layer demersal clutches of approximately 2,000-10,000 eggs attached to semi-protected cleaned areas of rubble or other areas of hard substrate, while chromine damselfishes defend areas of exposed algal turf or seagrass and lay eggs which are not in a clearly-defined mass. Anemonefishes (amphiprionine damselfishes) are commensal with sea anemones and lay eggmasses of about 200-1000 eggs on cleaned areas of coral rock near the anemone. Anemonefishes are protandrous and their social structure is exceptional among the damselfishes. On each inhabited anemone, there is one mature female, the largest fish on the anemone, and one mature male; all other fish are juvenile males. Males predominantly care for the eggs, but females contribute some care. Among the other damselfishes, the only example of biparental care of offspring is *Acanthochromis polyacanthus*, which extends this care into the juvenile stage. All pomacentrid eggs are guarded from predators, fanned, and cleaned until they hatch. Except for *Acanthochromis,* parental care ends at hatching, and the larvae leave the reef environment. The larvae spend approximately 2-5 weeks in the open ocean feeding on zooplankton, then return to the reef to settle in an appropriate habitat. Estimates of mortality rates during the pelagic larval stage of pomacentrids do not exist, but

overall are estimated to be high in reef fishes (16% to 20% per day (Houde, 1987); review in Leis, 1991). Levels of damselfish recruitment to reefs are highly variable in time and space (Doherty, 1991; 1994).

Among coral-reef fishes in general, the larval stage is one of high risk, with the three major elements of mortality being starvation, predation, and loss due to transport away from suitable habitat. Predation and starvation could potentially occur in either pelagic or reefal habitats at various levels, but the risk of not finding a suitable habitat is eliminated if larvae stay on the reef. Coral reef habitats are tiny islands of suitable habitat in the middle of large areas of ocean. Why then do nearly all coral reef fishes take the risk of dispersing away from a proven settlement site? The success of the *Acanthochromis polyacanthus* life-history begs the question.

Hypotheses about the Predominance of Occurrence of the Pelagic Larval Stage in Coral-Reef Fish Life Histories

Barlow (1981) reviewed the evidence for three major hypotheses for why coral-reef fishes have pelagic larval stages. These are 1) the food hypothesis, 2) the anti-predation hypothesis, and 3) the dispersal hypothesis. The food hypothesis suggests that food availability for larvae is greater in the ocean, and larvae are less susceptible to starvation by feeding through the critical early stages out at sea. The anti-predation hypothesis proposes that predation levels for larval fishes on the reef are greater than in the ocean, thus larvae must grow past a critical size before settling to the reef. The dispersal hypothesis proposed that the species that survive through time (sea-level rising and falling) are those that have developed dispersive larvae which chance upon new areas of reefal growth.

While different authors argue for each of the different hypotheses as the main selective pressure contributing to the maintenance of the pelagic larval stage as integral to reef-fish life histories, the available evidence is inconclusive (Doherty et al., 1985; Barlow, 1981; Johannes, 1978). Because of difficulties in controlling for historical effects, a method for definitively testing any of these hypotheses directly is as yet unimagined, and our evidence must remain circumstantial. However, with this in mind, if one were to conceive of an "evolutionary experiment" in the form of a species which could give us insights into the necessary traits required to bypass the pelagic larval stage, *Acanthochromis* is an invaluable example. All of its closest relatives have pelagic larvae, and they vary among species in many characteristics of early life.

Ancestry obviously plays a large role in the basic life-history of any species. Adaptive explanations must be viewed as overlaying the past history of each lineage. For *Acanthochromis*, this may include freshwater relatives.

The Cichlid Connection

The remarkable similarity of the brooding behavior of *Acanthochromis* with that of most of the substrate-brooding cichlids is immediately striking. Both taxa have biparental care of young, and even share complex parent/juvenile interactions such as the juveniles glancing (quickly touching) the sides of the parents. This style of brooding is unique in these fishes among all other taxa. Is there a connection?

The family Pomacentridae are currently placed within the order Labroidei. Two systematic assessments of groups within the Labroidei are used currently, and both suggest that that the Pomacentridae and the Cichlidae are sister-taxa (Stiassny and Jensen 1991; Kaufman and Liem, 1982). Although far from definitively resolved (G. D.

Johnson, Smithsonian Inst., pers. comm.), this probable ancestral connection is especially intriguing in this case. Is *Acanthochromis* a basal taxon retaining an ancestral condition shared by cichlid and pomacentrids, therefore making dispersive larvae in pomacentrids a *derived* trait? Or are cichlids and *Acanthochromis* a derived clade, thereby rendering "Pomacentridae" paraphyletic? Or, alternatively, are the cichlid and *Acanthochromis* life-histories and brooding behaviors independently derived? These questions cannot be convincingly answered without a systematic assessment of the group. Relationships within the Pomacentridae are currently unresolved, despite recent attempts using morphological and behavioral characters (Fitzpatrick, 1992; Kavanagh and Cavalluzzi, unpubl. data). However, even a basic description of the early life stages and details of the brooding behavior in *Acanthochromis* are lacking in the literature. More information for comparisons of the two groups may prove insightful. With this in mind, the first part of this thesis is descriptive and attempts to fill in some of the gaps in knowledge about the life cycle, morphology, and ecology of this species.

The Aim of the Study

The general aim of the studies presented in this thesis is to explore the ecological and evolutionary environment which has shaped the unusual early life-history of the brooding damselfish *Acanthochromis polyacanthus*. I attempt to assess some of the impacts that the elimination of the pelagic larval stage has on the ecology, behavior, and development of this coral-reef species.

The information gained from this special case, and from comparisons with other taxa, will advance our understanding of the factors which influence the ecological and evolutionary directions of change within coral-reef fishes, and the patterns of life-history change in general.

Chapter Structure

This dissertation is organized into six chapters: this general introduction, four independent studies followed by a general discussion.

The following chapter (Chapter Two) provides a description of the ontogeny, life history, parental care behavior, and external morphology of *Acanthochromis*. Comparisons of growth rates of related species are given. This information is discussed in comparison with other taxa and forms the basis for further inquiries into particular traits.

Chapter Three examines parental care expenditure and parent/juvenile interactions during brooding and is divided into three parts. In Part I, I investigate whether parental care effort varies among different reef zones and whether parental care increases with increasing offspring age. Part II explores the functional significance of "glancing" behavior shown by *Acanthochromis* juveniles. Part III presents the results of a pilot study on the use of olfactory cues in the recognition of young by *Acanthochromis* parents.

In Chapter Four, production of broods and survival of juveniles in different seasons and reef zones are measured. I present data on density and size structure of the *Acanthochromis* population on Lizard Island reefs. I test the hypothesis that more broods will be produced in areas where and when survival of juveniles is greatest.

Habitat effects on field growth and developmental rates of juveniles are examined in Chapter Five. Responses of growth and development to wind strength, reef zone, and food levels are tested.

Chapter Six gives an overall discussion of the major results and interprets them in the context of current views about the ecology and evolution of coral-reef fishes.

The Coral Reef Environment at Lizard Island, Great Barrier Reef, Australia

Most of the field work in this thesis was carried out on the reefs surrounding Lizard Island on the Great Barrier Reef (Fig. 1-1). Lizard Island (14°40'S, 145°27'E) is a mid-shelf island in the 60-km wide Great Barrier Reef lagoon. Predominantly southeast winds drive the relatively high wave action on the exposed sides of the reef, forming an exposed "front-reef" zone. A shallow (10m) lagoon is formed by smaller islands and reef flats surrounding a lagoon of approximately 2 km^2 to the south of Lizard Island. Reefs in the back-reef zone are also exposed to the open waters, but are typically in the lee of the winds.

Food supply for damselfishes may vary among zones, but availability of plankton and algae is not well-studied. Because the front-reef receives water directly from the Great Barrier Reef Lagoon, the planktivorous fish community there has access to a constant supply of oceanic plankton (see Hamner et al, 1988). In contrast, the lagoonal plankton supply must first pass over the reef crest and flat areas (thus potentially decreasing as it passes through their planktivore communities) or else be produced in the lagoon itself. Zonal differences also exist for availability of algae (S. Purcell, J.C.U., pers. comm.).

Predators on damselfishes also vary among zones, in abundance and in species distribution. Although it is dependent on the taxon, higher numbers of predators are generally found on the front-reef than in the lagoon (Beukers, 1996; Stewart, unpubl. data; Syms, unpubl. data). These include some of the small wrasses such as *Thallasoma lunare* (B. Stewart, unpubl. data; Fig. 1-2) or the dottyback *Pseudochromis fuscus* which are known predators of *Acanthochromis* juveniles or small damselfish settlers (pers. obs.).

Figure 1-1: Study sites at Lizard Island, Great Barrier Reef.

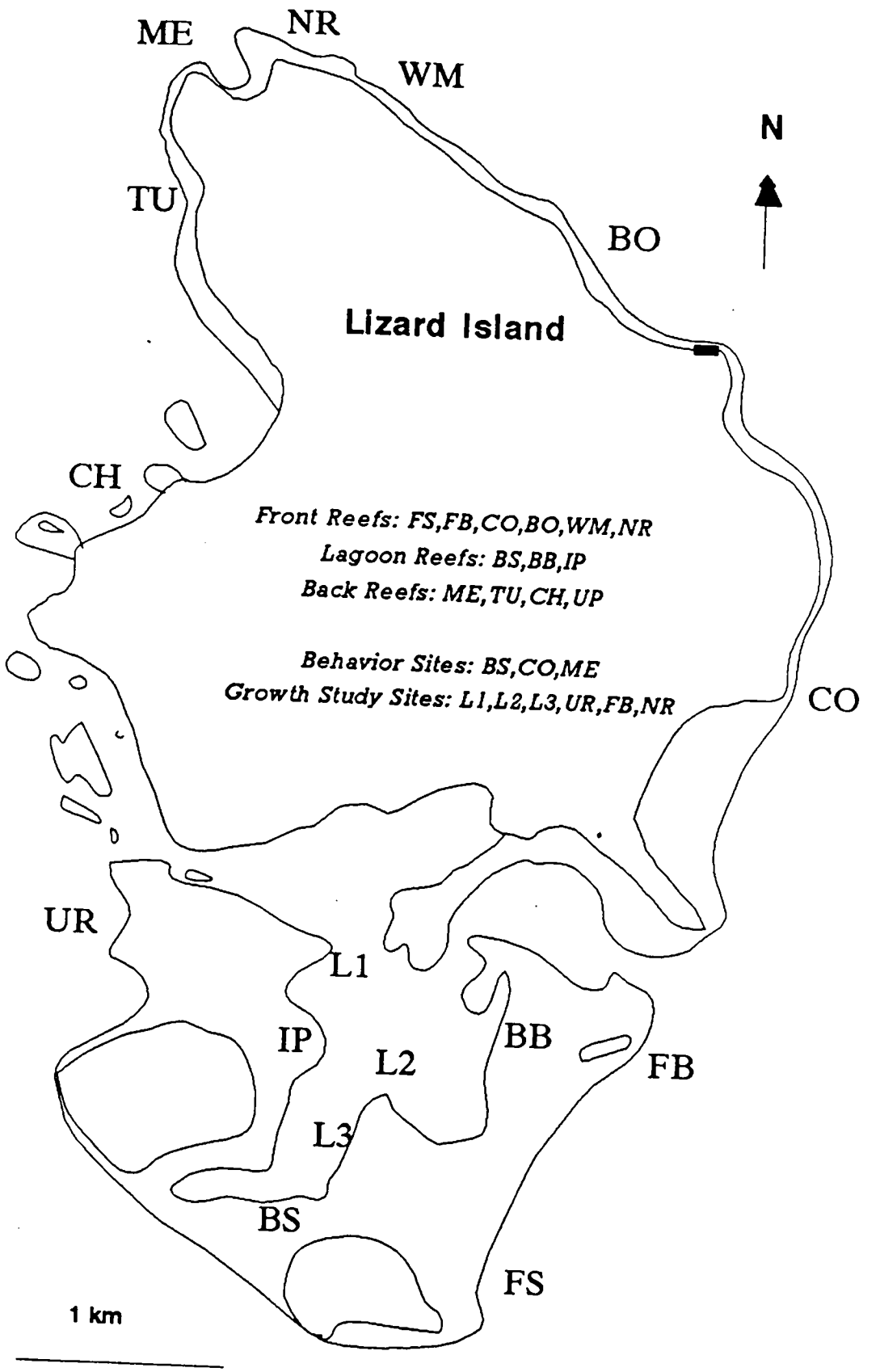
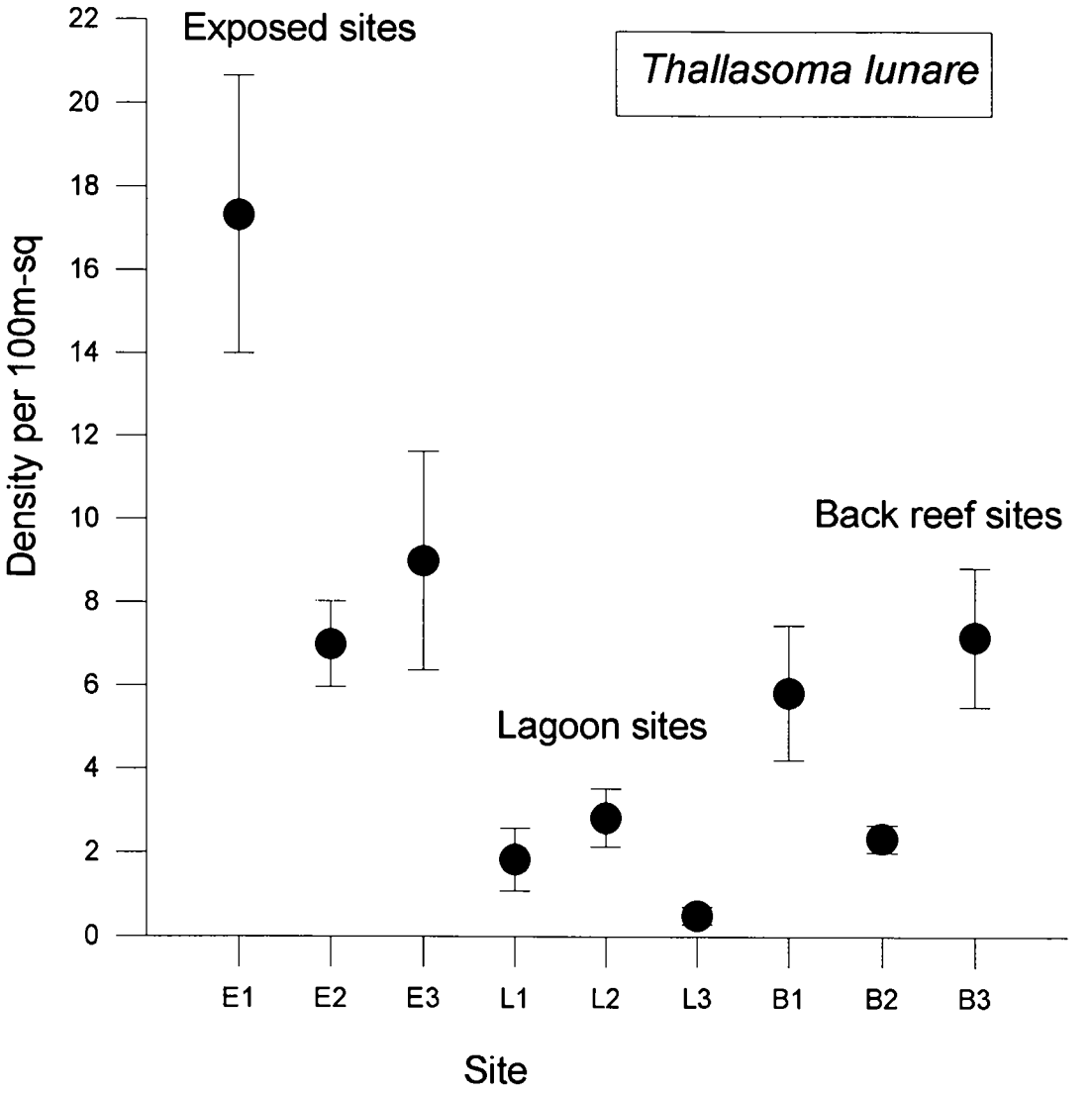

ME
NR
WM
N
TU
BO
Lizard Island
CH
Front Reefs: FS,FB,CO,BO,WM,NR
Lagoon Reefs: BS,BB,IP
Back Reefs: ME,TU,CH,UP
Behavior Sites: BS,CO,ME
Growth Study Sites: L1,L2,L3,UR,FB,NR
CO
UR
L1
IP
L2
BB
FB
L3
BS
FS
1 km

Figure 1-2: Density of the moon wrasse *Thallasoma lunare* at exposed, lagoon, and back reef sites at Lizard Island, Great Barrier Reef. Data from B. Stewart, James Cook University.


Exposed sites
Thallasoma lunare
Back reef sites
Lagoon sites
Density per 100m-sq
22
20
18
16
14
12
10
8
6
4
2
0
E1
E2
E3
L1
L2
L3
B1
B2
B3
Site

Chapter Two

Natural History and Ontogeny of the Brooding Damselfish, *Acanthochromis polyacanthus*, with Comparisons of Pomacentrid Early Growth Patterns

Introduction

The life history of the brooding damselfish, *Acanthochromis polyacanthus*, is rare among coral-reef fishes in that it lacks a pelagic larval stage. Because its early life stages are non-dispersive and site-attached, several studies have used *Acanthochromis* as a model species for ecological research on coral-reef fish dynamics (Thresher 1983, 1985a,b ;Connell 1995). Despite this reasonably high profile and the relative accessibility of all life stages, surprisingly little is known about its ontogeny, and about important segments of its life cycle. This is particularly remiss in this species, since its early stages are potentially informative about the requirements of early life on the reef as opposed to the open ocean. By correlating its unusual life-history pattern with other biological characteristics of the species, *Acanthochromis* can act as an "evolutionary test" species for hypotheses about coral-reef fish life-histories. Furthermore, since many morphological and behavioral characteristics show a range of variability within the pomacentrid family, these characters are potentially useful in systematic analysis.

Over the past two decades, several studies have focused on aspects of the reproductive behavior of *Acanthochromis*, site-specific demography at One Tree Island, and population genetics along the Great Barrier Reef. Information about the life history of the species can be extracted from these studies. These are briefly summarized below.

Acanthochromis is sexually monomorphic and appears to form monogamous long-term pairs (Robertson, 1973; Allen, 1975). However, if one of the pair dies or is removed, another ripe adult is nearby to take its place almost immediately (Nakazono, 1993). *Acanthochromis* nests in caves in the reef (Thresher, 1985) and has biparental care of eggs and juveniles

(Robertson, 1973). The eggs are relatively large (4.5 mm; Thresher, 1984). Robertson (1973) was the first to report on the unusual brooding behavior shown by *Acanthochromis*, where juveniles remain with the parents for several months, until they are 30-40 mm SL (Nakazono, 1993). Parents defend the school of juveniles from small predators. Juveniles show an unusual glancing behavior, where they swim up and touch the sides of the parents frequently during brooding (Robertson, 1973). Brood abandonment has been found to occur under several conditions. When one parent was removed in experiments at One Tree Island, the remaining parent found another partner quickly and drove off or preyed upon the old brood (Nakazono, 1993). In this same population, Thresher (1985) observed that *Acanthochromis* parents occasionally drive off their young (1-2 week old) broods early in the season, and suggested that this enabled a second brood to be produced. By a size frequency analysis, Thresher (1985) estimated age at maturity as approximately 2-3 years.

Although regional differences in genetic population structure and in color patterns has been found among populations throughout its geographic distribution (Doherty et al, 1994), color pattern is typically consistent within a population. It appears that there is often strong sexual selection for mates of a similar color pattern (Planes and Doherty, submitted, a), however in some interesting hybrid zones, these distinct color morphs come in contact and interbreed successfully in narrow zones of overlap (Planes and Doherty, submitted,a,b).

Despite these varied studies, many aspects of the biology of *Acanthochromis* are still unknown. This chapter aims to fill in some of the gaps in knowledge for this important species, and herein I describe my observations of the life cycle, ontogeny, and behavior. These observations may help in the interpretations of results from other studies on this species, as well as adding some insight into how early life stages of reef fishes might survive on the reef. I divide up my observations into five categories of the life cycle: 1)

eggs and embryos, 2) hatching and hatchlings, 3) brooded juveniles and parental care, 4) post-brooding dispersal and subadults, and 5) sexual maturity and reproduction.

In addition, comparisons of early growth of *Acanthochromis* and other pomacentrid species with varying durations of egg and larval stages are presented. These comparisons are a first attempt at correlations of early life history characteristics within the family using known-age specimens reared under controlled conditions. Studying trends in growth rates and the timing of life-history stage transitions will help in understanding the interdependence of these central characteristics of early life.

Methods

Acanthochromis were observed on Lizard Island, central Great Barrier Reef, over several trips during the period of Dec 1992 to Dec 1995, during which the majority of field work was conducted for this thesis. Most data on feeding, parental care, and parent/juvenile interactions were collected by observing *Acanthochromis* pairs and broods over 30-min periods at sites in the lagoon and exposed reefs of Lizard Island (Fig. 1-1; all sites). Observations were also made on occasional trips to other areas of the GBR: Orpheus Island, Magnetic Island, and Davies Reef (central Great Barrier Reef), and Hyde Reef and Heron Island (southern Great Barrier Reef). Notes about reproductive behavior, parental care, juvenile and subadult behaviors, and dispersal were recorded over approximately 250 hours of observations. The temperature in the field during this time varied seasonally from approximately 25-29C.

In addition, *Acanthochromis* pairs from Magnetic Island and Lizard Island were brought back to James Cook University Aquarium facilities and kept in large (100-1000 L) aquaria where eggnests, embryos, hatching behavior, and juveniles could be observed. Mean length-at-age was determined for embryos and juveniles from 14 broods reared in the aquarium facilities at

approximately 26-28 C. In the following description, ages are presented as either days after fertilization (d.a.f.) or days after hatch (d.a.h.).

A morphological description of the embryonic and juvenile stages is based on observations of known-age, captive-bred broods from Magnetic Island. Specimens were preserved in 10% formalin and examined using a dissecting microscope. Developmental series of embryos and juveniles were cleared and stained following methods of Potthoff (1984) to observe skeletal development.

For comparisons, rates of growth in length, muscle, and eye diameter were recorded for four pomacentrid species (*Chromis atripectoralis*, *Pomacentrus amboinensis*, *Premnas biaculeatus*, and *Acanthochromis polyacanthus*). In tables and figures, these species will be referred to as species A (*Chromis atripectoralis)*, B (*Pomacentrus amboinensis*), C *(Premnas biaculeatus*), and D (*Acanthochromis polyacanthus*) in order of increasing egg stage duration. These four species vary in egg stage durations from 2 to 16 days, and in larval stage durations from 0 to approximately 23 days (Table 2-1). Age is given as days after fertilization (d.a.f.) or days after hatch (d.a.h.). Developmental series were obtained through rearing larvae in large (100-2000 L) aquaria at a constant temperature of 28-29°C with ad libitum feeding. Specimens were collected daily at approximately 1700 hr, and fixed in 10% formalin. Larval *Chromis atripectoralis* could not be reared past 10 days, and therefore several wild-caught, otolith-aged, pre-settlement larvae that had been collected when sea temperatures were likely to be near 28° C were also examined (Murdoch, 1995). In addition, a few reared *Chromis viridis* larvae were also examined to increase sample sizes where possible. Combining data on *C. viridis* and *C. atripectoralis* was considered to be acceptable at the level of comparison in this study because of the close phylogenetic relationship of these species (Randall et al., 1985), their very similar larval development, as well as the similarity of their life-history stage durations (pers. obs.; Thresher et al, 1989;

Wellington and Victor, 1989). Specimens were examined from fertilization through approximately 30 days-after-fertilization (d.a.f.), and were taken from several separate eggmasses and parents per species to reduce genetic or tank effects. Chorion membranes were removed from preserved eggs to allow easier examination of embryos.

To compare growth rates, morphometric measurements of notochord length (NL) for preflexion larvae, standard length (SL) for postflexion larvae, muscle area (MA), and eye diameter (ED) were taken using a computer image-analysis system. Muscle area was measured by outlining the total area from a lateral view of the larva excluding head, gut, yolk, or fins. Weight could not be used as an estimate of growth because drying destroyed specimens for further analysis and in some cases the numbers of specimens were limited. Muscle area measurements were square-root transformed to linearize the data. Analysis of covariance was used to test whether growth rates differed significantly between species. Because there is potential for differences in prey capture, energetic demands, and growth rate due to morphological and behavioral changes through ontogeny (Fuiman, in press; Hunter, 1972), growth rates for pre- and post-flexion larvae were examined separately within each species.

Results

Eggs and Embryos

In observations of eggnests of captive-bred pairs, the eggs were attached individually to the substrate, upside down on the exposed undersurface. The clutches from Lizard Island, Magnetic Island, and Heron Island pairs consisted of a roughly circular patch of approximately 250-550 eggs. Some of these pairs were able to produce new clutches of eggs within days after removal of a newly-hatched brood. The eggs were 3.7-4.3 mm in length and 1.4-1.5 mm in width. No consistent differences among sites were apparent. Egg sizes differed among females (n=5) (Fig. 2-1).

Initially (3 d.a.f.), the embryo forms on the end of the egg closer to the substrate, with the head facing the substrate. This orientation is similar to that observed for many substrate-brooding cichlids (pers. obs.). At 5 d.a.f, the head of the embryo has migrated to the outer edge of the egg, with the tip of the tail just touching the substrate end of the egg (Fig. 2-2a). The embryo stays in this orientation (head-out) until hatching, although some variability was observed (<5%) wherein late-stage embryos were oriented head-down.

Acanthochromis embryos have a large head with a blunt snout (Fig. 2-2b). At 6 d.a.f., no mandible is present, but by 11 d.a.f., the jaw is fully formed (Fig. 2-2c). Under a dissecting scope, the heart and gills can be observed to be functioning at 5-6 d.a.f. The eye first shows pigment at 6-7 d.a.f. The dorsal and anal fin pterygiophores appear at approximately 8 d.a.f., and develop from the middle of the fin outwards. Two predorsal bones develop in embryos at about 14 d.a.f. Notochord flexion is completed during embryonic development, at approximately 10 d.a.f. (Fig. 2-2b). Pectoral fin buds are the first fins to develop and form early in the embryonic stage (6 d.a.f.). In cleared and stained specimens, the first features to ossify were the cleithrum and the pharyngeal teeth, which ossified about 1 day before hatching.

The first pigmentation (3 d.a.f.) consists of evenly spaced small melanophores over the entire surface of the yolk, with a small concentration around the animal pole (end near substrate). As the embryo migrates toward the outer edge of the egg (by 5 d.a.f.), the concentration of pigment moves with it. On the 5-day-old embryo, melanophores are large and concentrated on the fore and hind brain, becoming lighter until about halfway down the notochord (Fig. 2-2a). A series of ventral midline melanophores, two dorsal, and one lateral are the only body pigmentation. The yolk sac has dense pigment, sometimes darker at the head end. The midline of the hindbrain is free of pigment. Shortly after this, pigment concentrates on the dorsal side of the notochord and a line of lateral melanophores develops (Fig. 2-2b). The dorsal pigment eventually (11 d.a.f.) forms two lines. At this time, the mandible, branchiostegal and gular regions develop pigment, and the ventral melanophores are lost.

Hatching and Hatchlings

Five broods were observed closely over their hatch day(s) to observe hatching. The hatchlings left the egg after a "cap" opened up on the non-adhesive end of the egg. Hatching occurred during the early daylight to midday hours, not before 8 am or after about 2pm and over many hours for a single clutch. If all the eggs had not hatched by mid-afternoon, hatching did not continue overnight, but waited till the following midday.

After hatching the young emerged from the nest cave, began swimming immediately and stayed in a close group guarded by the parents. Feeding began within 24 hours of hatching, although yolk was present in dissected juveniles aged two or three days.

At hatch, the dorsal and anal-fin rays have begun to extend, and spines are just forming (Fig. 2-3a). The caudal fin is well-formed at hatch. Caudal-fin rays are truncate at hatch but gradually develop a fork over the next few days. All pectoral rays are present. Pelvic buds are

not visible during the embryo stage, but begin developing just after hatching (17 d.a.f.). The majority of the skeleton was not ossified at hatching.

Juveniles and Parental Care

Juveniles remained in an aggregated group, defended by the parents, for up to four months after hatching at Lizard Island. Bottom feeding was observed in all stages of development, including very young juveniles. A brief gut analysis of a few juvenile fish confirmed that algae and small benthic invertebrates were actually ingested.

Cleared and stained *Acanthochromis* specimens had 29 or 30 vertebrae: 13-14 precaudal and 16-17 caudal (Table 2-2). Ctenoid scales are formed between 12 and 17 d.a.h. (28-35 d.a.f). Procurrent spines on the caudal fin typical of other chromine damselfishes (sensu Leis and Rennis, 1983; pers. obs.) were not apparent in juvenile *Acanthochromis*.

At 4 d.a.h., melanophores increase on the dorsal midline and decrease on ventral gut region. Shortly thereafter, a stripe forms through the eye and a few more melanophores appear laterally. A yellow spot appears on the caudal peduncle at this time, or, in some populations (e.g. Davies Reef) , a yellow pigment stripe along the side is seen (5 d.a.h.). Melanophores then increase on dorsal and lateral surfaces, and some form over the anal fin (Fig 2-3b). Pigment forms on the pectoral fins, premaxilla, and around the mouth about 10 d.a.h., and a concentration of pigment appears around the anus (Fig. 2-3b,c).

Staging of Brooded Juveniles

Juveniles grow from 5 mm to approximately 50 mm SL before fledging from the nest area. During this lengthy period, they undergo gross changes in shape, pigmentation, and behavior which are useful for field staging of brooded juveniles; these stages will be referred to throughout this thesis. Stage 1 juveniles are newly-hatched, and stay in a tightly aggregated ball close to the coral reef. They do not have any yellow pigment and their caudal fin is truncate (Fig. 2-3a). By Stage 2, juveniles have a yellow lateral stripe or a large spot on the caudal peduncle (Fig. 2-3b). By Stage 3, they significantly increase in body depth and are typically in a much looser aggregation (Fig. 2-3c). Stage 4 juveniles have lost the yellow pigment, and developed black edges on their dorsal, anal, and caudal fins (Fig. 2-3d). Stage 5 juveniles have the coloration of the adult (e.g. black with white posterior body and tail), but are still brooded (Fig. 2-3e). Average sizes and ages for each of these stages, along with these criteria, are given in Table 2-3. These stages are based on field observations of Lizard Island juveniles.

Post-Brooding Dispersal and the Subadult Stage

Dispersal behavior of juveniles was deduced from repeated observations of late-stage broods over several days. Stage 4 or 5 juveniles were seen to gradually spread out from the nesting site, by associating with coral heads increasingly farther away. Sometimes parents were observed to drive the juveniles from the immediate nesting area (1-3 m). In areas with high wave energy, juveniles often joined large groups of other planktivores feeding in the current off the reef. No major dispersal events (entire brood leaves) were recorded from the repeated observations of over 50 late-stage broods. No territoriality was observed until pairs were established. Aggregations of subadult and unpaired adult *Acanthochromis* were commonly seen feeding in currents off the crest or wandering, individually or in smaller groups, over reef flats.

Sexual Maturity and Reproduction

Size at maturity, approximately 65 mm SL, was determined from estimates of size of the smallest paired adult seen with a brood. Age at maturity was approximately 9 months, determined from juveniles (from Magnetic Island parents) hatched and reared in captivity until they paired and spawned.

In the populations observed, male and female of a pair rarely differed in length even though a large range of sizes of fish were present in the area (see Fig. 4- 6). Of 205 pairs from Lizard Island in which size was estimated, only 5 were estimated to be of detectably different length. Of those pairs that differed, the mean difference in size between mates was 7 mm, or 5% of standard length (range 1-9%; n=5).

Courtship of *Acanthochromis* was observed in this study several times. The courtship pattern was similar to that described for other *Chromis* spp (Thresher 1984), with the (presumed) male swimming on his side with median fins erect towards the (presumed) female, circling then leading the female towards a nest site repeatedly. Sometimes the male would swim slowly with an exaggerated wiggle.

One set of observations was particularly interesting, as it recorded the end of the care of one brood, reformation of the pair, and the defense of the new nesting site. Initially, I observed a pair with a late-stage (stage 5; Table 2-3) brood interacting as a family group (parents defending brood; juveniles glancing off parents). The individual parents were identifiable by spots or rips in their fins. When they were observed two days later (day 3), the male was vigorously chasing its own juveniles away from the immediate nest area (about 1 meter) and very defensively avoiding being glanced. The female continued to interact with the juveniles, tending them and allowing them to glance. The male also chased intruders of any species away from the nesting site, and was observed courting

three females in the area, sometimes leading two at a time back towards the nest cave. They were never seen to enter the nest cave in over an hour of observation. When observations on this family group resumed the next afternoon (day 4), the male was paired up with his original mate (female parent of the stage 5 brood), and both were chasing away intruders from the nest area. This time, both were seen to chase away juveniles of their previous brood. Over the next few days, the renewed pair was seen to aggressively defend the nesting cave and refuse any interaction with their own juveniles. They spent minutes at a time inside the cave. It was observed that the majority of the stage 5 juveniles of this pair remained in the area, within 10 m, for at least the next week (when observations ceased.) As a estimate of effort, I counted number of chases/courtship swims per min associated with the establishment of this nest site. Over two hours of observation on three days, a total of 93 aggressive chases and 14 courtship swims were recorded for the pair.

Behavior-Induced Color Changes and a New Color Morph

In both field and laboratory conditions, I observed color patterns of both "all-black" (black with a small white or gray edge to the tail) and black-and-white color morphs (Plates 1 and 2) change under different conditions. At night, *Acanthochromis* adults and juveniles sheltered in coral rubble and developed a vertical white bar against an all-black background, or, in Lizard Island (black-and-white morph) fish, they were seen to acquire a reversed coloration pattern (white with black posterior body and tail) as they began their day/night transition. Under stress, various color changes in shades of black, grey, and white were observed, including these nocturnal patterns. In addition, field observations indicated that black-and-white fish (Lizard Island) changed the intensity of their black color on different days, from a dull grey to a deeper black. However, the overall black-and-white color pattern of the fish was consistently recognizable in these same fish during the day.

As reported in numerous papers, adult coloration patterns (diurnal) differ between separated reefs (Planes and Doherty, 1996a,b; Doherty et al, 1994; Allen, 1975). While all previous color morphs have included pigmentation produced only by melanophores (black, gray, or white), this study found a new color morph in which the pelvic fins, pectoral fin base, and ventral area of the body are bright yellow (Plate 3). This color morph was found on Magnetic Island, an inshore reef near Townsville, Australia. The color of the Magnetic Island fishes were otherwise similar to that referred to by Planes and Doherty (submitted, a) as the most common morph of the central Great Barrier Reef (black with white posterior body and tail).

Comparisons among growth rates in four damselfish species

For each measurement of growth rate within a species, the total number of specimens available for examination ranged from 40 to 236 for growth measurements. The total number of batches (independent clutches) examined for each measurement ranged from 2 to 8.

Hatching times of each species were consistent with previous observations at this temperature (Doherty, 1983; Thresher, 1985; Kerrigan, 1995): 2 d.a.f. for *Chromis atripectoralis* (A), 4 d.a.f. for *Pomacentrus amboinensis* (B), 7 d.a.f. for *Premnas biaculeatus* (C), and 15-16 d.a.f. for *Acanthochromis polyacanthus* (D) (Table 2-1). Settlement varied somewhat: 23-27 d.a.f (21-25 days after hatching) for *C. atripectoralis/viridis*, 24-26 d.a.f. (20-22 days after hatching) for *P. amboinensis*, and 21 d.a.f. (14 days after hatching) for *Premnas biaculeatus*. *Acanthochromis* has no pelagic stage and is settled at hatching (16 d.a.f.).

ANCOVA indicated significant differences in slopes and intercepts between species for preflexion growth rates. Pairwise comparisons found that Species C and D had higher intercepts than the other two species, suggesting their earliest growth (single cell to first

appearance of notochord) was faster. Starting from the earliest measurable embryonic length, Species B and D had higher rates of preflexion growth in length than A and C (Table 2-4; Fig. 2-4). While all other species appeared to accelerate or maintain the same growth rate at (and following) flexion (approximately 10 d.a.f.), Species D nearly stopped its growth in length between 10 and 16 d.a.f. (incidentally between notochord flexion and hatching in this species). ANCOVA indicated significant differences in slopes and intercepts of postflexion growth in length among species. Postflexion growth was again fastest in Species B, Species D was slowest, and C and A were intermediate (Table 2-4; Fig. 2-4). Pairwise comparisons indicated that B>C>D for slopes, and B>C=D for intercepts. No difference could be detected between Species A and any other species, likely due to small sample sizes.

The pattern among species for rate of growth in muscle area differed for preflexion larvae, but postflexion larvae showed the same pattern as they had for growth in length (Table 2-5; Fig. 2-5). ANCOVA indicated significant differences between species for slopes and intercepts. Among preflexion larvae, Species D had the highest rate of muscle gain, followed by B, C, and A. Pairwise comparisons found that C had a significantly greater intercept than the other species, indicating its early rate of muscle growth is greater than the other species (Table 2-5). At approximately 10 d.a.f., Species A, B, and C all accelerated their rate of muscle gain, while D slowed its rate (Table 2-5).

Significant differences in rate of eye growth for preflexion stages were found using ANCOVA. Species D had the highest eye growth rate followed by B, C, and A (Table 2-6; Fig. 2-6). Intercept differences were also significant. Species C and D had a greater intercept than B, indicating their earliest eye-growth rate is significantly higher. Although D continued to have the largest eyes at age until about 16 d.a.f., postflexion eye-growth rate was significantly slowed in D (Table 2-6). In contrast, eye-growth rate in B increased greatly

compared with its preflexion eye-growth rate. In Species C, postflexion eye-growth rate increased, but was surpassed by B and A (Fig. 2-6).

Discussion

This study provides a more detailed natural history of *Acanthochromis* than was previously available, the first description of its ontogeny, as well as a detailed comparison of growth rates in length, muscle area, and eye diameter among related species. Observations of life stages are discussed below.

Eggs, Embryos, and Hatchlings

Egg clutch sizes of the captive pairs in this study (central GBR) were up to 2-5 times greater than reported in the literature for Heron Island (southern GBR) pairs (Robertson, 1973). It cannot be assessed from available data whether this large difference is related to female size, or is a fixed life-history difference for these geographically-disparate and genetically-distinct populations. This interesting difference is worth further investigation. Thus far there is no evidence of regional variation in egg sizes.

The time of day at which hatching occurs in demersal eggs of reef fishes (and the time of spawning for broadcast spawners) are suggested to be adapted to minimize predation on the new hatchlings as they disperse away from the immediate reef environment (Robertson, 1991; Shapiro et al. 1988). Most damselfish eggs hatch very precisely at sunset (Doherty, 1980; Thresher, 1984), as a rapid response to darkened conditions (pers. obs.). Other demersal and broadcast spawners also appear to time the release of eggs or larvae into the sea with the day/night changeover period, suggesting this behavior may be adaptive (Robertson, 1991). The hatching time of *Acanthochromis*, in contrast, does not coincide with sunset, but instead they hatch preferentially in morning and midday. As new hatchlings are dependent on their diurnally-active parents for survival

(Nakazono, 1993; pers. obs.), this diurnal hatching time might also be seen as advantageous for the first hours of life on the reef for the non-pelagic young in this species.

Differentiation of the jaw and internal organs is relatively delayed in *Acanthochromis* compared with other pomacentrids (e.g. *Chromis atripectoralis* feeds at 4 d.a.f.; pers. obs.). Eye development also begins late, with pigment developing in the embryo several days later than confamilial species. The size at which scales form in other pomacentrids is variable, but they usually form before settlement (Leis and Rennis, 1983). The timing of scale formation in *Acanthochromis* is near the age at which most pomacentrids settle (~30 d.a.f.), but much later than when *Acanthochromis* juveniles "settle" (hatch) on the reef (~16 d.a.f.) suggesting scales are not critical to benthic survival.

The timing of notochord flexion (~10 d.a.f.) is similar to other pomacentrids (pers. obs). As in other pomacentrids, dorsal and anal fins begin to form just after flexion, with rays developing first. However, the ossification of the fins is much delayed. In the caudal fin, the 3rd and 4th hypural plate are fused. As the pattern of hypural fusions varies among pomacentrid species, this character may hold some systematic value (Potthoff et al., 1987; Fitzpatrick, 1992; pers. obs.).

The most remarkable feature of the skeleton of *Acanthochromis* is the high number of vertebrae (Table 2-2). Other pomacentrid species are reported to have 25 or 26 vertebrae; *Acanthochromis* has increased this number by 4-7 (this study; Fitzpatrick, 1992). It appears that the increase in vertebrae is concentrated in the precaudal region (Table 2-2). Because dorsal-spine pterygiophores tend to interdigitate with the neural spines of the vertebrae, the large number of dorsal spines (17), from which *Acanthochromis* derives its name, is probably coincident with the high precaudal vertebral count. The uniquely high count of precaudal vertebrae may provide a functional advantage. One possibility is that the enlargement of the precaudal area effectively translates to an increase in the body cavity. This larger body cavity

would allow *Acanthochromis* to hold a greater number of its relatively huge eggs. In reptiles, studies of allometrically increasing number of presacral vertebrae and body cavity area have been correlated with life history traits and interpreted as a means of maintaining a minimum critical clutch size (Griffith, 1990; Forsman and Shine, in press).

Parental care

The parental investment of *Acanthochromis* is qualitatively different than that of other pomacentrids. If calculated on a per-offspring basis, *Acanthochromis* clearly invests more energy in individual offspring than other pomacentrids. However, if calculated as overall energy/effort spent in parental care and reproduction, the gap between *Acanthochromis* and other pomacentrid species narrows substantially. Typical pomacentrids spend considerable energy in regular courtship and guarding multiple batches of eggs over a spawning season. If the activity level associated with courtship and establishing a nest-site in *Acanthochromis* (see above) is an indication of the energy required for these activities in all damselfishes, then the effort spent by the more typical damselfishes over a spawning season could be at least comparable to that exerted by *Acanthochromis* in caring for its one or two broods per season.

Dispersal

In this study, post-brooding dispersal (fledging) of *Acanthochromis* juveniles occurred at an exceptionally large size, about 40-50 mm SL, in broods observed on Lizard Island. Previous reports of dispersal sizes from One Tree Island (southern GBR) pairs indicate a smaller size at fledging, approximately 25-40 mm SL (Nakazono, 1993; Robertson, 1973). If this difference is demonstrated to be consistent among these separated populations, it would suggest a life-history response to the different

environmental conditions in the southern GBR reefs. For example southern GBR reefs experience cooler winter temperatures (ENCORE, Great Barrier Reef Marine Park Authority, 1996) and have fewer predators (Caley, 1995). Thus, one might predict that earlier fledging might be advantageous in southern reefs, because it would allow a second brood to be produced in the more restricted (cooler winter temperatures) spawning season. Comparative regional studies of these populations, in addition to ageing field-caught juveniles, would be useful for further testing these hypotheses.

Another contrasting observation regarding fledging in *Acanthochromis* is the mode of dispersal. No large dispersal events, or multiple-brood fledgings, were recorded in the repeated observations of late-stage broods in this study. Studies from One Tree Island suggest that the common mode of dispersal in those populations is for large groups of juvenile *Acanthochromis* to aggregate and disperse from an area (Thresher, 1985; Nakazono, 1993). Nearly all of the observations made on Lizard Island were on contiguous reef habitat rather than the isolated patch-reefs of Thresher's studies (1985), and this alone may account for the different conclusions. Studies in progress on isolated patch-reefs in the central GBR (Trunk Reef) indicate that large groups of juveniles from these *Acanthochromis* populations will in fact move between patch-reefs over distances on the order of 50-100 meters (A. Lewis, J.C.U., pers. comm.). These habitat differences in the mechanism of juvenile dispersal may have implications for population and community dynamics.

Adult Stage and Reproduction

Captive-bred *Acanthochromis* from Magnetic Island stock matured at a much younger age (9 months) than previously reported in the southern GBR population studies (2-3 years; Thresher, 1985). Although different methods were used in the southern GBR

studies (size frequency analysis), this substantial life-history difference could have significant impacts on population dynamics and ecology of the separated groups. This should be examined further.

Previous studies report positive assortative mating by color pattern in *Acanthochromis* (Planes and Doherty, submitted, a). The data in this study suggest that sexual selection is not only for the same color pattern but for similar-sized mates as well.

Courtship observations lead one to question the previous conclusions of long-term monogamy in *Acanthochromis*. If the observations of "extramarital" courtship in this study are taken with those of Nakazono (1993), which demonstrated that if one adult in a pair is removed, a new ripe partner is found almost immediately, these suggest that *Acanthochromis* is easily willing to reform pairs and monogamy may only last for the duration of a brooding period or a season.

Growth rate comparisons among species

While all preflexion growth rates in *Acanthochromis* were equal or higher than those of the other species, postflexion growth rates were typically lower. *Acanthochromis* goes through flexion inside the egg, thus growth in length and mass during this time would likely be constrained. The available energy in the embryos of this species may be better utilized in gaining competence, by differentiating tissues, rather than gaining additional mass. Early competence may be comparatively important for *Acanthochromis* hatchlings, as they, unlike their relatives, must survive through their early life in the reef environment where predation pressure is intense.

These variations among species in growth rate through the embryonic and larval stages resulted in larvae which reached settlement age at widely varying sizes. The idea that larvae need to achieve a minimum competence level before settling to the reef would suggest that rates of ontogeny need to be examined, in addition to rates of growth, in order

to explain more about the early life history patterns in the family, including the allocation of energy to growth or to ontogeny and adaptive implications of the timing of stage transitions such as hatching and settlement.

Early growth rates as well as life history comparisons indicate significant and biologically-interesting variability exists in the pomacentrid family suggesting the family's usefulness in testing many hypotheses about reef fish ecology and evolution. However in some critical features, *Acanthochromis* stands alone (parental care of hatchlings, no pelagic stage), and the lack of intermediate life-history types or of additional comparative species with similar life histories means that inferences are necessarily limited. Despite the interesting correlations of life-history, behavior, and morphology, the "test" has no degrees of freedom. Given this restriction, one fruitful path might be to correlate differences in morphological and life-history traits with environmental variability among separated and genetically-distinct populations of *Acanthochromis*. This opportunity exists along the Great Barrier Reef. In addition, a systematic analysis of the Pomacentridae would help in understanding patterns of change in early life history traits within the family, and would greatly facilitate interpretation of the significance of characteristics in *Acanthochromis*.

Table 2-1. Early life-history stage durations of four pomacentrid species at 28-29 C. Codes (A-D) are used in subsequent figures.

	Species	Egg stage duration	Larval stage duration	Total duration to settlement	Hatchling environment	Size at settlement (mm)
A	*Chromis atripectoralis*	2	21-25	23-27	pelagic	8.7-9.5
B	*Pomacentrus amboinensis*	4	19--21	23-25	pelagic	11.2-12.5
C	*Premnas biaculeatus*	7	14	21	pelagic	7.8-8.1
D	*Acanthochromis polyacanthus*	16	0	16	reef	5.0-5.5

Table 2-2. Range of meristic counts reported for species from the subfamilies of Pomacentridae.
Bold type indicates data from this study.

Meristics	Amphiprioninae	Pomacentrinae	Lepidozyginae	Chrominae	*Acanthochromis*
dorsal fin	VIII-XI,14-21[1]	XII-XV,10-17[1]	XII, 14-15[1]	XII-XV,10-16[1]	XVII,14-16[2]
anal fin	II, 11-15 [1]	II,10-18[1]	II,15-16[1]	II,10-16[1]	II,14-16[2]
pectoral fin	15-21 [1]	14-20[1]	21-22[1]	15-22[1]	17-18[1]
pelvic fin	I,5[1]	I,5[1]	I,5[1]	I, 5[1]	***I, 5***
caudal fin	?	7-8+6-7[1]	8+7[1]	8+7[1]	***8+7***
hypural fusions	***4,5 or 1,2+3,4,5***	***none or 4,5 or 1,2+3,4***	?	***none***	***3,4,5***
vertebrae	11+15=26 (1)	11+15=26[1]	11+15=26[1]	11+15=26[1]	***13-14+16-17=29-30*** Total=29-32 [3]

References:
1. Leis and Rennis, 1983; 2. Allen, 1975; 3. Fitzpatrick, 1992.

Table 2-3. Characteristics used for categorizing *Acanthochromis* broods.

Stage of brood (Functional Category)	Defining characteristics	Approx. age [1]	Size range, approx. (SL) [2]
1 (New)	Newly-hatched. Tight ball of tiny larvae. No yellow pigment yet.	1-10 days	5 - 11 mm
2 (Older)	Yellow stripes or spots along side. Still elongated body.	10-25 days	11 - 25 mm
3 (Older)	Body depth increases significantly. Still has yellow pigment.	25-45 days	25 - 35 mm
4 (Dispersing-Age)	No yellow pigment. Black edges to posterior part of dorsal and anal fin, and on dorsal and ventral edges of caudal fin. Generally light gray color.	45-75 days	35 - 45 mm
5 (Dispersing-Age)	Adult coloration (white tail and posterior body), but still brooded.	75-90 days	45 - 55 mm

[1] Based on observations of captive-bred juveniles reared at 27-30 C.
[2] Based on field-caught specimens and captive-bred juveniles.

Table 2-4. Rankings and statistical comparisons of slope and intercept parameters for preflexion and postflexion rates of growth in length (SL).

Groups indicate the results of pairwise comparisons using ANCOVA (p=0.05) for differences among species.

Preflexion growth: Notochord length

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.210	3	|	1.195	4	|
B	*P. ambo.*	0.304	1	|	1.390	3	|
C	*Premnas*	0.172	4	|	2.205	2	|
D	*Acanth.*	0.298	2	|	2.444	1	|

Postflexion growth: Standard length

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.310	3	| | |	1.370	2	| |
B	*P. ambo.*	0.494	1	|	-0.820	4	|
C	*Premnas*	0.311	2	|	0.954	3	|
D	*Acanth.*	0.246	4	|	1.695	1	|

Table 2-5. Rankings and statistical comparisons of slope and intercept parameters for preflexion and postflexion rates of growth in muscle area (MA). Groups indicate the results of pairwise comparisons using ANCOVA (p=0.05) for differences among species.

Preflexion growth: Muscle area

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.041	4	|	0.289	2	|
B	*P. ambo.*	0.094	2	| |	0.170	3	|
C	*Premnas*	0.052	3	| |	0.563	1	|
D	*Acanth.*	0.174	1	|	-0.091	4	|

Postflexion growth: Muscle area

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.123	3	| | |	0.578	1	| | |
B	*P. ambo.*	0.227	1	|	-1.261	4	|
C	*Premnas*	0.130	2	|	-0.0370	3	| |
D	*Acanth.*	0.092	4	|	0.1002	2	|

Table 2-6. Rankings and statistical comparisons of slope and intercept parameters for preflexion and postflexion rates of growth in eye diameter (ED). Groups indicate the results of pairwise comparisons using ANCOVA (p=0.05) for differences among species.

Preflexion growth: Eye diameter

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.027	3	| |	0.099	4	|
B	*P. ambo.*	0.030	2	|	0.147	3	|
C	*Premnas*	0.023	4	|	0.244	1	|
D	*Acanth.*	0.054	1	|	0.189	2	| |

Postflexion growth: Eye diameter

	Species	Slope	Rank	Groups	Intercept	Rank	Groups
A	*C. atri.*	0.060	2	|	1.544	2	|
B	*P. ambo.*	0.064	1	|	-0.219	4	|
C	*Premnas*	0.044	3	|	0.035	3	|
D	*Acanth.*	0.036	4	|	0.250	1	|

Figure 2-1. Mean egg diameters (longitudinal axis) of *Acanthochromis* females from Lizard Island, Magnetic Island, and Heron Island (Great Barrier Reef).

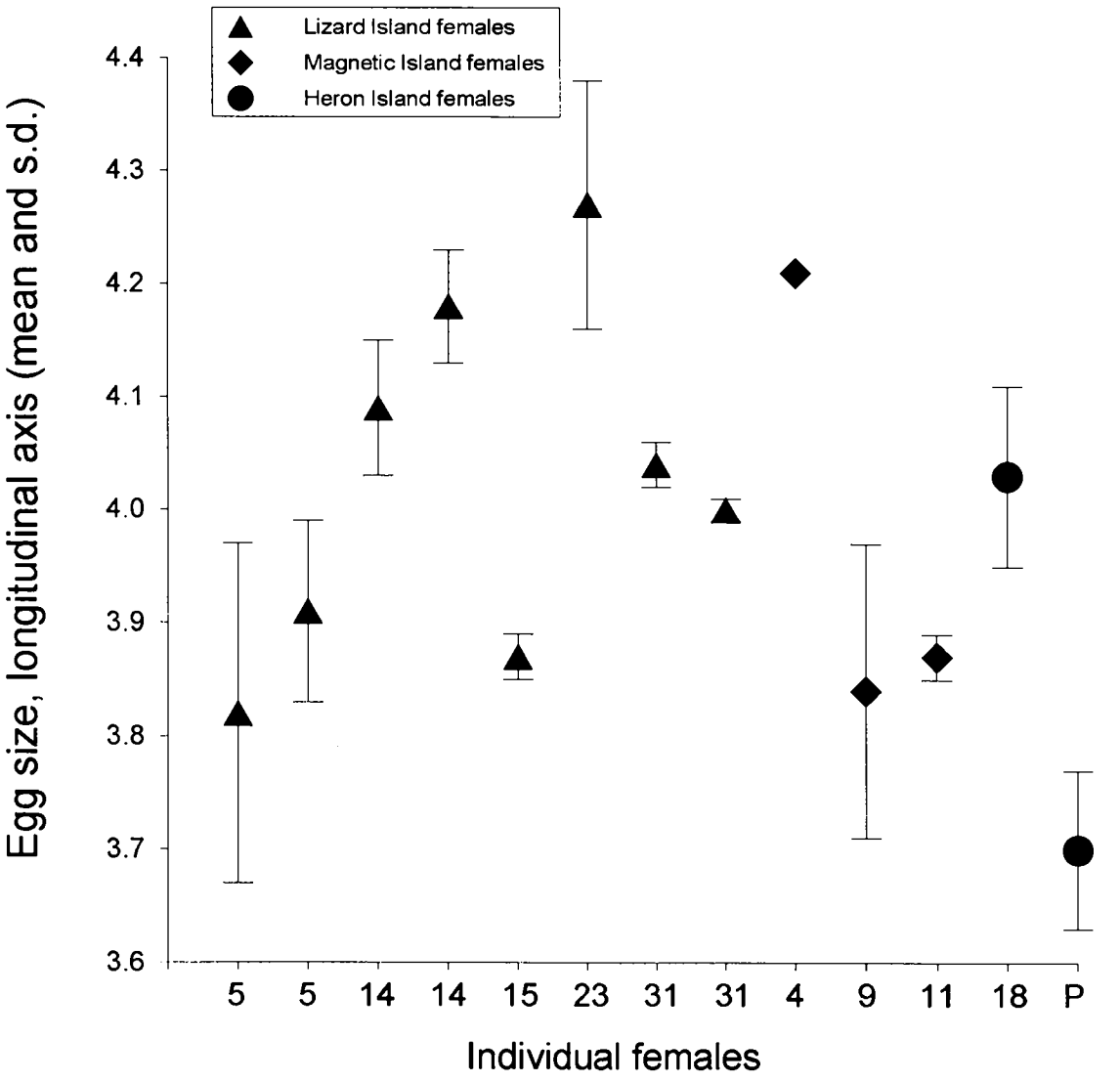
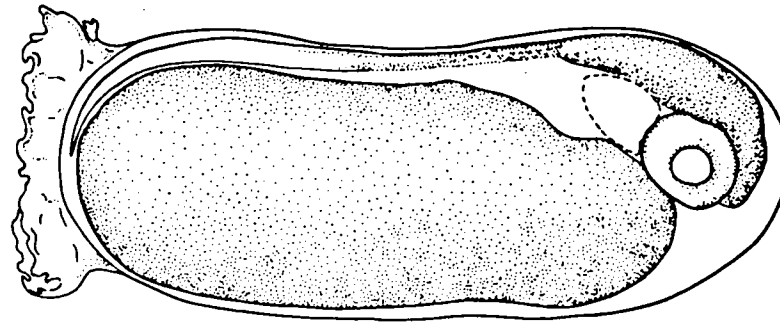
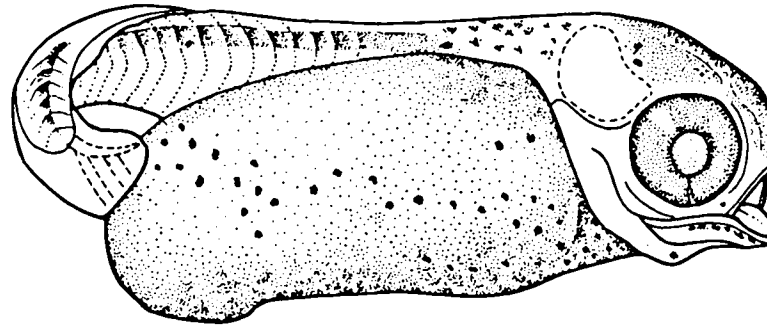

Lizard Island females
Magnetic Island females
Heron Island females
Egg size, longitudinal axis (mean and s.d.)
4.4
4.3
4.2
4.1
4.0
3.9
3.8
3.7
3.6
5
5
14
14
15
23
31
31
4
9
11
18
P
Individual females

Figure 2-2. Stages in the embryonic development of Acanthochromis polyacanthus spawned from Magnetic Island pairs held in captivity. Top figure is 6 days after fertilization (9 days before hatch); egg length 3.9 mm; approximate notochord length 3.6 mm. Middle figure is 9 days after fertilization, 6 days before hatch; notochord length is approximately 3.9 mm. Bottom figure is 12 days after fertilization, 3 days before hatch; standard length is approximately 5.4 mm.





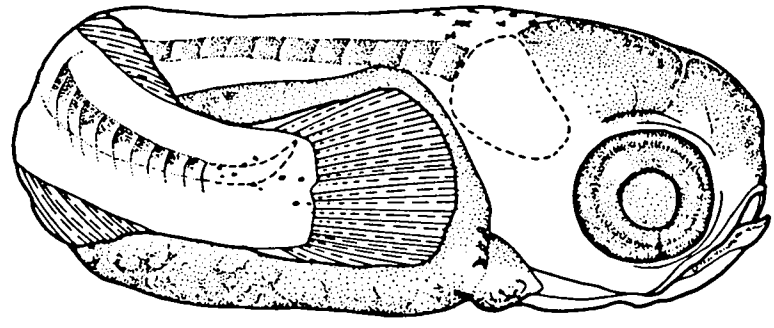


Figure 2-3. Stages in the development of juvenile *Acanthochromis polyacanthus*. Newly-hatched (Stage 1) spawned from Magnetic Island pairs held in captivity. Others are collected from wild populations at Lizard Island, Great Barrier Reef. Lengths, from top to bottom, are Stage 1(newly-hatched): 5.7 mm SL; Stage 2: 12.0 mmSL; Stage 3: 19.5 mm SL; Stage 4: 29 mm SL; Stage 5: 47 mm SL.

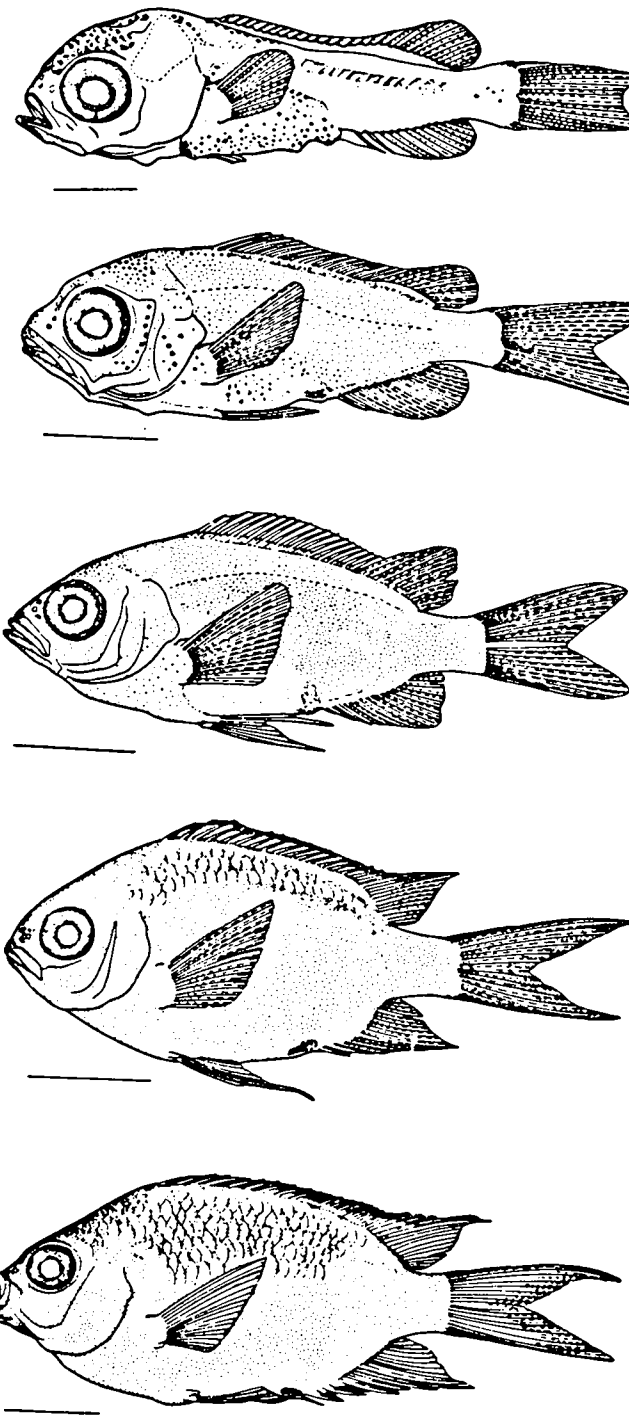


Figure 2-4. Linear regressions of pre- and postflexion rates of growth in length for *Chromis atripectoralis* (A), *Pomacentrus amboinensis* (B), *Premnas biaculeatus* (C), and *Acanthochromis polyacanthus* (D). Light and dark arrows indicate approximate times of hatching and settlement, respectively.

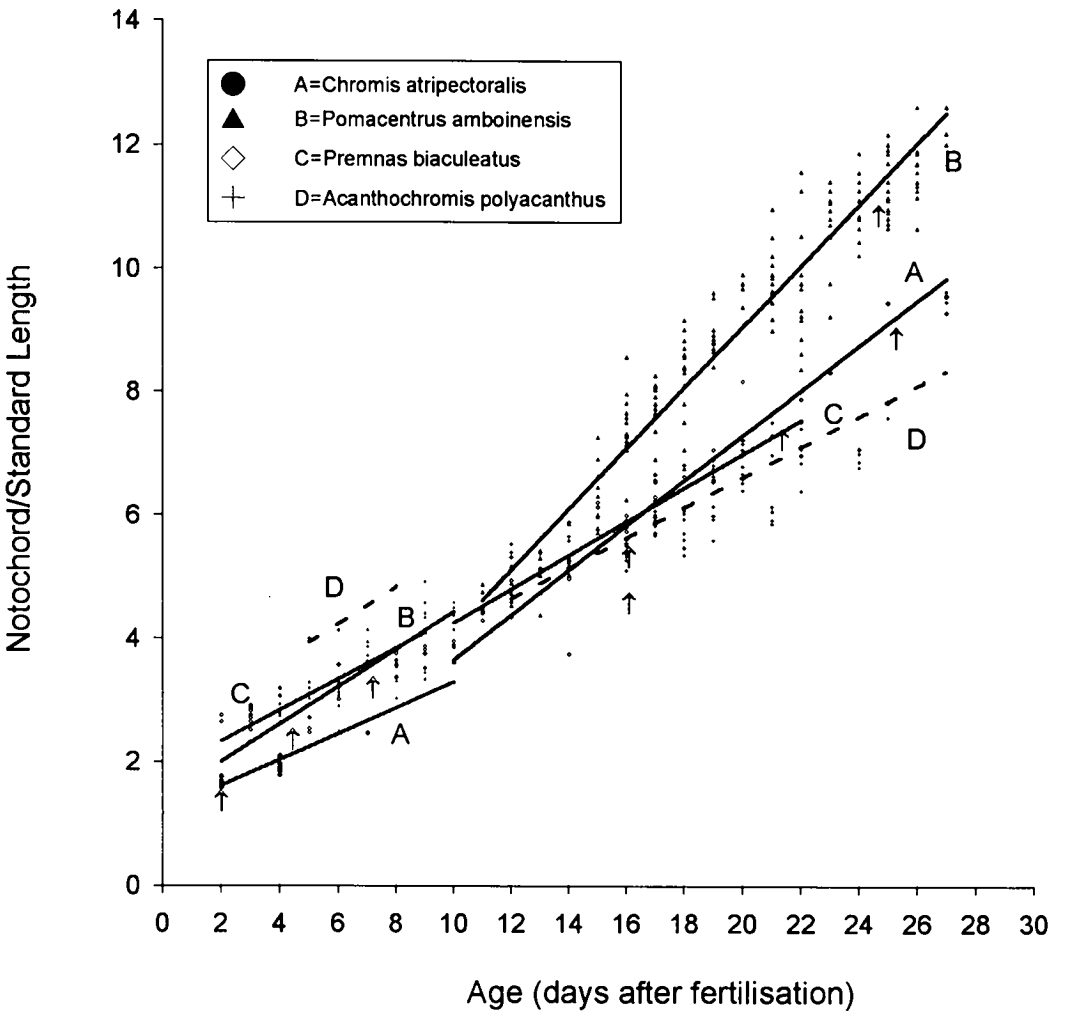

A=Chromis atripectoralis
B=Pomacentrus amboinensis
C=Premnas biaculeatus
D=Acanthochromis polyacanthus
Notochord/Standard Length
Age (days after fertilisation)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
A
B
C
D

Figure 2-5. Linear regressions of pre- and postflexion rates of increase in muscle area (square-root transformed) for *Chromis atripectoralis* (A), *Pomacentrus amboinensis* (B), *Premnas biaculeatus* (C), and *Acanthochromis polyacanthus* (D). Light and dark arrows indicate approximate times of hatching and settlement, respectively.

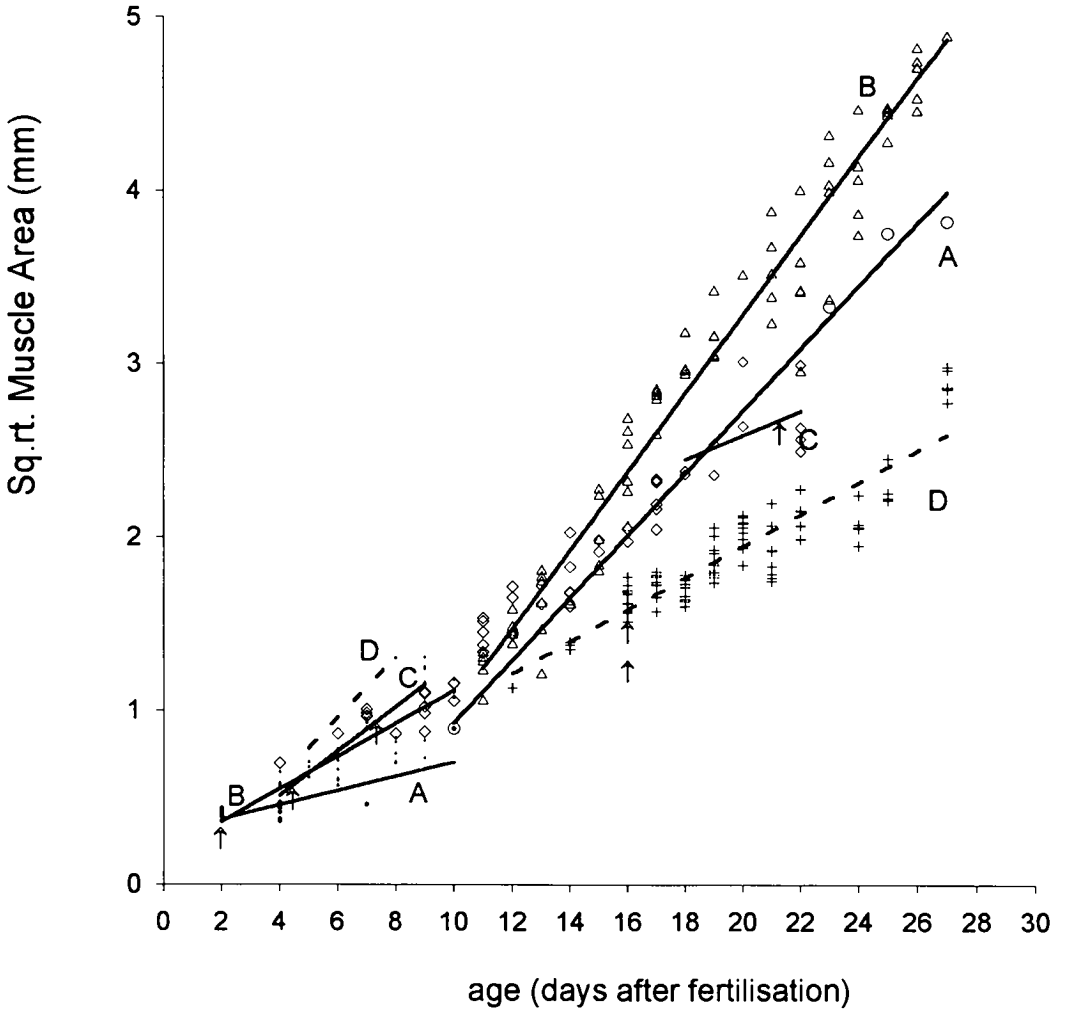

Sq.rt. Muscle Area (mm)
0
1
2
3
4
5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
age (days after fertilisation)
A
B
C
D
A
B
C
D

Figure 2-6. Linear regressions of pre- and postflexion rates of growth in eye diameter for *Chromis atripectoralis* (A), *Pomacentrus amboinensis* (B), *Premnas biaculeatus* (C), and *Acanthochromis polyacanthus* (D). Light and dark arrows indicate approximate times of hatching and settlement, respectively.

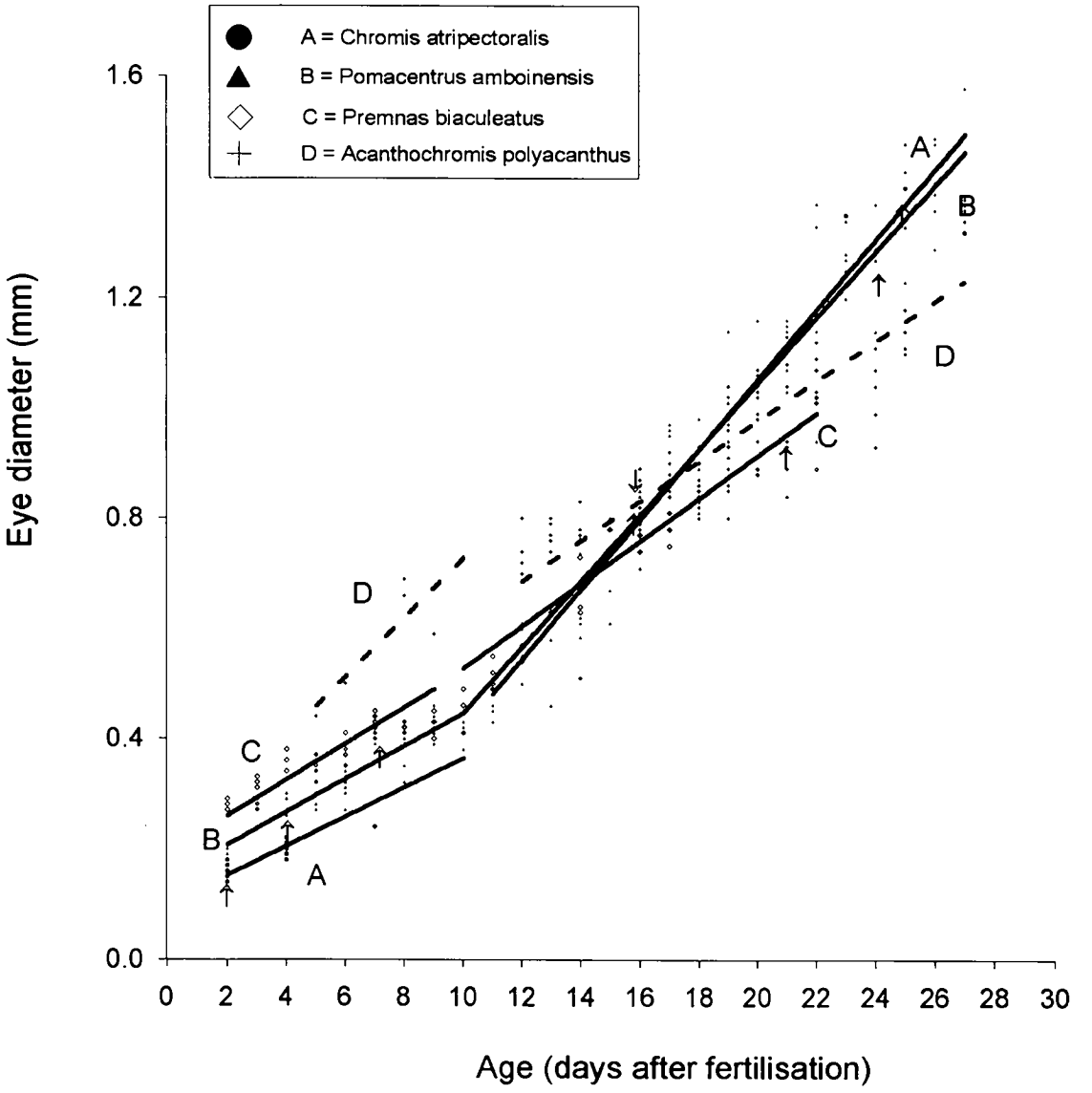

A = Chromis atripectoralis
B = Pomacentrus amboinensis
C = Premnas biaculeatus
D = Acanthochromis polyacanthus
Eye diameter (mm)
1.6
1.2
0.8
0.4
0.0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Age (days after fertilisation)
A
B
C
D

Plate 2-1. *Acanthochromis polyacanthus* parent with stage 4 juveniles, from Lizard Island, Great Barrier Reef.

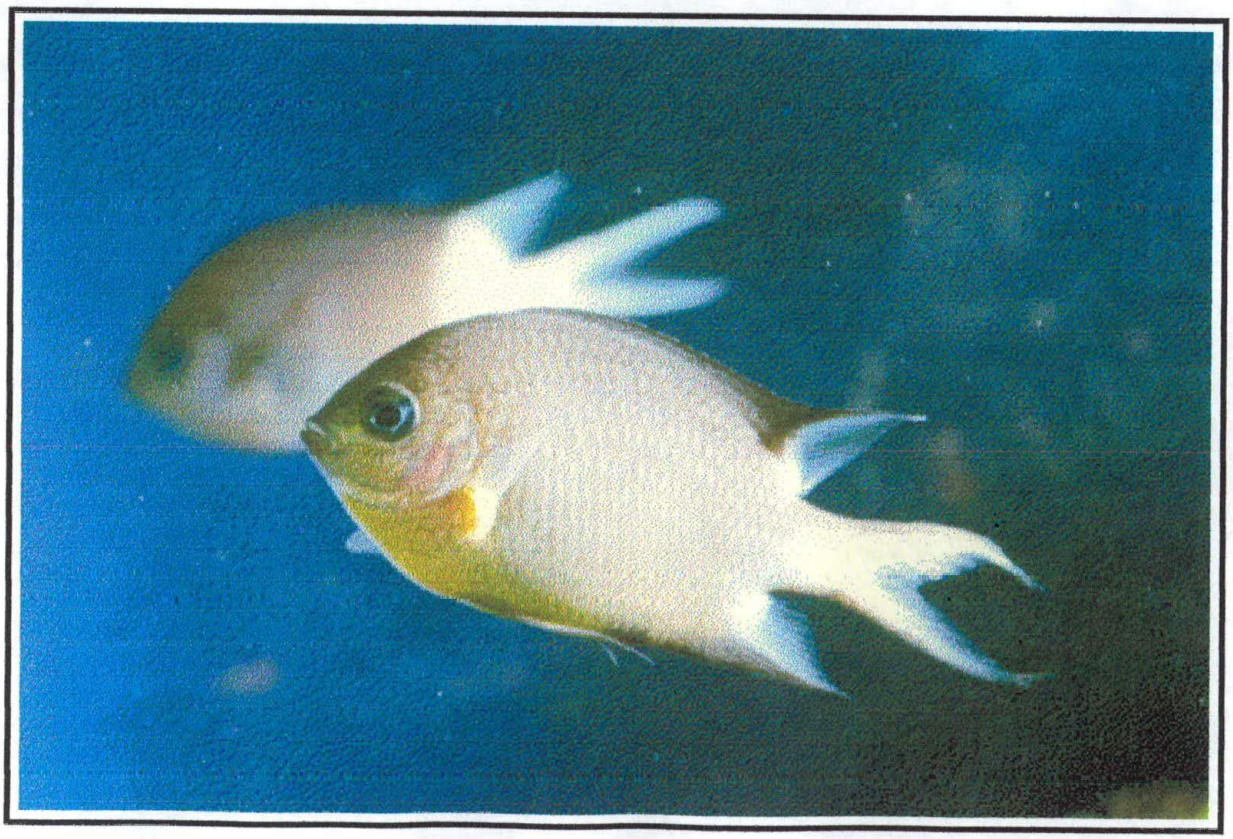
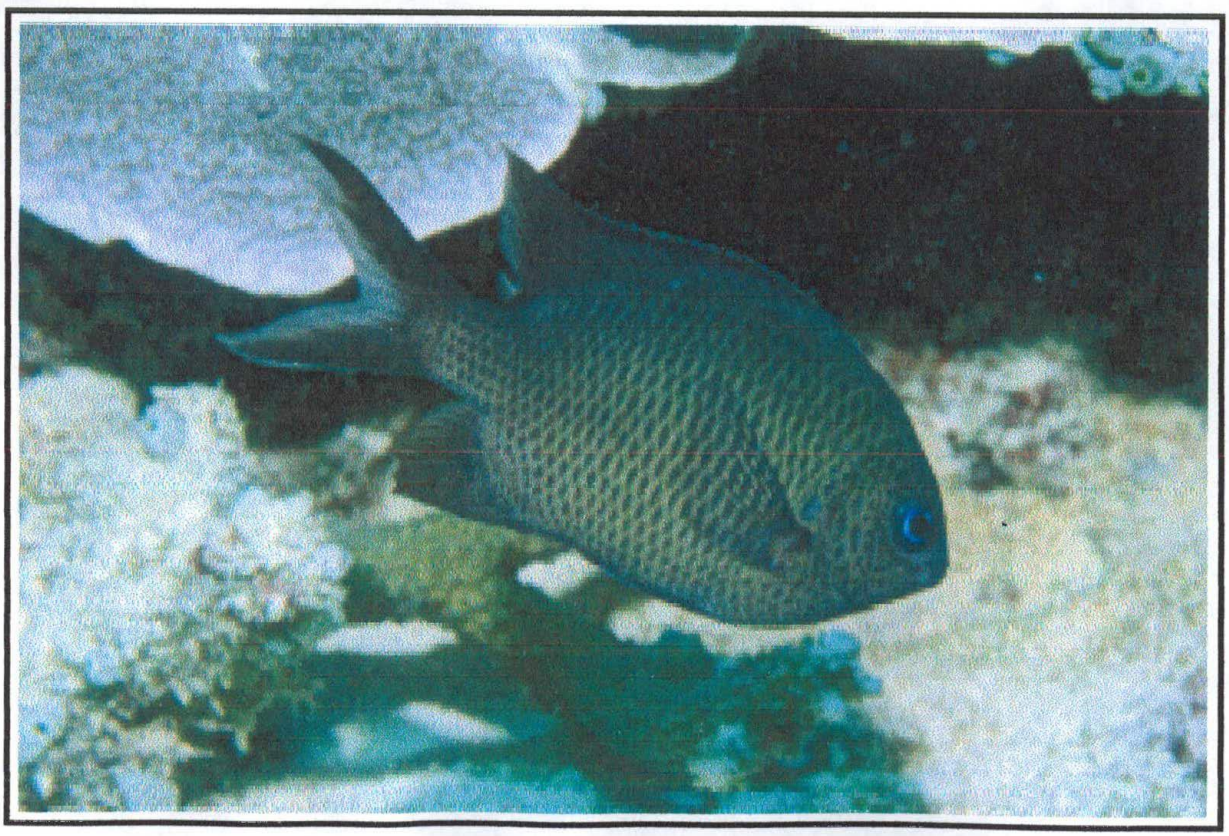


Plate 2-2. *Acanthochromis polyacanthus* from Heron Island, Great Barrier Reef.

Plate 2-3. *Acanthochromis polyacanthus* from Magnetic Island, Great Barrier Reef.



Chapter Three

Intensity and function of post-hatch parental care behaviors in the brooding damselfish *Acanthochromis polyacanthus*

Introduction

Along with the elimination of the dispersive larval stage, brooding behavior is one of the most conspicuous characteristics distinguishing *Acanthochromis* from its closest relatives. The success of the *Acanthochromis* life history is linked closely with this extended parental care, as it has been demonstrated that mortality of young juveniles is high and rapid without parental care on the reef (Robertson, 1973; Allen 1975; Nakazono, 1993; pers. obs.). The characteristics of the species' parental care therefore hold important information contributing to our understanding of the evolution of this unique life history in the coral reef environment. This chapter examines several aspects of parental care behavior in *Acanthochromis*, and is divided into three parts. Part I reports on a field study which compared the intensity of parental care behaviors in different environments and through ontogeny of the juveniles. Parts II and III then present the results of laboratory experiments which examine the functions and possible proximate causes for particular behaviors.

Part I:

Effects of Local Environment and Offspring Age on Parental Care Effort

Introduction

A central consideration in discussions of life-history evolution concerns the pattern of allocation of limited reproductive resources into individual offspring (Stearns, 1992;

Harvey and Pagel, 1992). Allocation of energy into parental care of eggs or juveniles is one way that individuals can invest more resources into each offspring. Increased parental care is associated with particular environments: harsh or unpredictable conditions, or high rates of predation, parasitism, or intense competition with conspecifics (review in Clutton-Brock 1991). Many behaviors, including those associated with reproduction, are known to vary adaptively among populations in response to predation risk (Magurran and Seghers, 1994; Huntingford and Wright, 1991; Reznick and Endler, 1992; Endler, 1994). Thus, an animal's overall fitness is likely to be affected by energetic or behavioral costs (Zoran and Ward, 1983; Lamon and Ward, 1983), particularly those associated with selection for heightened parental care and/or anti-predator responses (Huntingford and Torricelli, 1991; but see Reist, 1983).

Marine teleost fishes typically have low investment per offspring and little or no parental care (Breder and Rosen, 1966). Parental care of larvae or juveniles is particularly rare among marine fishes (Clutton-Brock, 1991), however one species of coral reef damselfish *Acanthochromis polyacanthus* broods its free-swimming young for months in reefal habitats (Robertson, 1973; Thresher, 1983). This life history stands in striking contrast to that of its closest phylogenetic relatives, which have only a few days of egg care followed by an independent pelagic larval stage. *Acanthochromis*' parental care behavior has been described in general in several sources (Robertson, 1973; Allen, 1975; Thresher, 1985). However, nothing is known about spatial and temporal variation in parental care intensity, duration, or complexity, despite the high potential for local adaptation in this species (see Doherty et al, 1995).

Some predictions about the variations in parental care can be made based on comparative studies with other taxa. Several freshwater families of fishes (e.g., Cichlidae) show extended parental care which is similar to the behavior exhibited by *Acanthochromis* ,

and, since they have been the focus of a large body of work on the evolution of parental care, they serve as useful models for developing hypotheses. In these families, the degree of parental care is related both to environmental conditions and to offspring age. In brood-caring freshwater fishes, the extent of parental care is found to increase among intraspecific populations with increased predation risk (Tulley and Huntingford, 1987) or with increased food supply for the parents (Townshend and Wootton, 1984). In addition, the level of care is modified as offspring age and their competence, food or space requirements, and/or "reproductive value" changes (Noakes and Barlow, 1973; Ward and Barlow, 1966 Quertermus and Ward, 1969). Adaptive arguments have been made for both increasing and decreasing of brood care as juveniles age, and it is not clear which pattern is more prevalent in brooding fishes. Increased investment in offspring might be expected as juveniles age because they become more valuable; that is, older juveniles are more likely to reach sexual maturity since (in most cases) they have survived through a large proportion of the average total mortality in their life cycle. On the other hand, decreased investment in individual offspring though time might be expected if the relative effects of parental care on older offspring are lower. Predictions are often difficult because the relative importance of these two opposing effects are unknown (Clutton-Brock, 1991). In some species of cichlids, parental care intensity increased as juveniles aged (Ward and Barlow, 1973), while in others it decreased (Noakes, 1979) or stayed the same (Noakes and Barlow, 1972).

Acanthochromis lives and broods its young on coral reefs, an environment which is typically thought to have high and variable predation levels among habitats (Jones et al, 1991; Kingsford, 1992; Connell, 1994; Beukers, 1996). At One Tree Island in the southern Great Barrier Reef, mortality rates of juvenile *Acanthochromis* were found to vary significantly among sites differing in predator levels (Connell, 1995; Thresher, 1983). In

the reefs surrounding Lizard Island (central Great Barrier Reef), where this study was conducted, *Acanthochromis* occurs across reef zones reported to differ in several ways: in levels of predators (Beukers, 1996; M. Emslie, B. Stewart, and C. Syms, unpubl. data) including major predators of *Acanthochromis* juveniles such as *Thallasoma lunare* (pers. obs; Robertson, 1973; Stewart, unpubl. data) and in juvenile and adult reef-fish mortality rates (Aldenhoven, 1986; Gladstone and Westoby, 1988). As increasing the diligence of parental care is one way of reducing juvenile mortality rates, these data suggest the level of parental care could be strongly affected by the local environment. Therefore it is predicted that *Acanthochromis* will exhibit a greater level of parental care in habitats with more predators.

Acanthochromis broods its young for an extended period, which inhibits further reproduction by parents during brooding. Thus, the relative extent and intensity of care through time also has fitness consequences for the parents. The dispersion area of *Acanthochromis* is observed to increase as juveniles age, thus the effectiveness of parental care may be reduced as parents cannot easily guard the whole brood at once. *Acanthochromis* parental care (investment per offspring) may decline as offspring age if this pressure is important.

The purpose of this study is to describe how parental care in *Acanthochromis* varies among reef zones and as juveniles age, thereby providing a comparative assessment of the energetic cost of parental care, as measured by the intensity of parental care behaviors. In reef zones with higher predation risk (the "exposed" zones), the effort given in parental care by *Acanthochromis* parents is expected to be greater. As offspring age, parental care may either increase or decrease as individual offspring are more or less likely to benefit.

Methods

Repeated observations of a total of 28 *Acanthochromis* broods with parents were made at Lizard Island for this study. During February 1994, 20 broods were selected for observation. This first field study examined broods in two zones, lagoonal (BS) and exposed reefs (CO) (Fig. 1-1). Within each zone, broods of different ages (=stages 1 to 5) were observed. Stages were assigned using criteria based on morphology and pigmentation (see Table 2-2).

In each zone, ten family groups (both parents and a brood) were observed for 30-min periods. These included two replicate broods at each stage of development in each zone. These broods were repeatedly visited (every 2-3 days) over several weeks, for a total of 126 observation periods. In July 1994, eight more broods (two stage 3, three stage 4, and three stage 5) were observed in the same manner, but in this case only these later stages of juveniles were present because it was not peak spawning season (Ch. 4). On this trip, the exposed-reef site previously visited (in February) could not be used because of rough weather, so another site (ME) was chosen in a back-reef area sheltered from prevailing winds (Fig. 1-1). This site was also reported to have greater numbers of predators than lagoon sites (Beukers, 1996). The lagoon site visited on this trip was the same one that was used during the previous observation period (BS). Observers sat still approximately 3 meters from the brood and recorded interactions between parent and juvenile, any aggressive encounters with conspecifics or other species, and the area of dispersion of the brood. To calibrate estimates of area of dispersion, a meter-stick was used to measure brood dispersion after the observation period was over by holding it against landmarks marking the edges of the distribution of the brood. Number of juveniles in the brood (brood size) was also estimated and recorded. The calibration curve for this

estimation is reported elsewhere (Fig. 4-9). Because male and female parents could not be distinguished, counts of behaviors are recorded for the pair.

The variance-ratio test was used to test for equality of variances among zones (Zar, 1984). Data with unequal variances were log-transformed after rescaling (from counts-per-minute to counts-per-hour) and adding 1 to be able to transform counts of 0. I used a 2-factor ANOVA to test for differences among brood stage and reef zone, for each behavior quantified. The mean number of behavioral manoeuvres observed per minute was termed "effort". This was an estimate of how much energy parents put into care for a brood. To get an estimate of how much care an individual juvenile received (integrated across the brood), this measure of parental effort was divided by the number of juveniles in the brood, and again analysed by brood stage and zone.

Results

Recorded observation time of selected broods on the reef totalled 46 hrs. Brood size decreased as juveniles aged, from a mean of 120 at stage 1, to a mean of 25.7 at stage 5 (Table 3-1).

The area of dispersion of broods significantly increased with age, and there were no significant differences among zones in the dispersion area of broods by stage (Fig. 3-1; Table 3-2). Newly-hatched broods were dispersed over an area of approximately 30 cm^3. By stage 5, the average brood dispersion area had increased to 2.5 m^3. Although numbers of juveniles per brood decreased over time (Table 3-1), the average area occupied by each individual increased as they grew, from 0.45 cm^3 at hatching to 3 cm^3 at stage 5.

Most of the time spent in parental care by *Acanthochromis* involved defending juveniles. On average, parent *Acanthochromis* with new broods chased away intruders about 16 times over a 30-min period. ANOVA detected highly significant differences

between brood stages and reef zones (Tables 3-3a and b). Mean number of chases per min (defensive effort) decreased as broods aged, and mean chasing frequency in exposed sites appeared to be higher than lagoonal reefs for earlier stages (Fig. 3-2). A post-hoc Tukey's test confirmed this trend was significant.

In contrast to the trends in total chasing frequency, mean defensive effort per juvenile (number of chases per min per juvenile) was similar between stages of juvenile, and for reef zone (Fig. 3-2; Table 3-3). However, ANOVA detected a significant stage/zone interaction. Examination of trends in the data suggest that this significant interaction comes from the higher number of chases in exposed zones in early stages (Fig. 3-2).

Observers also recorded the taxon chased, and results were summarised into major categories (Table 3-4). The abundance of these groups in the local community was not assessed, thus relative frequency of chases do not necessarily reflect selective aggression, but rather how much effort is spent by the parents in activity that is likely to be related to predation avoidance, territoriality, or expelling unrelated *Acanthochromis* juveniles. The highest percentage of chases for any individual species (31.6 %) involved an intruding *Acanthochromis* adult (Table 3-4). Unrelated conspecific juveniles were chased relatively infrequently (6.9%). Damselfishes as a group were the most frequently chased, comprising 67.3% of all chases. Obligate piscivores and known predators of *Acanthochromis* juveniles were chased relatively infrequently (13.9%) compared with the other categories, however it was informally noted on data sheets that these species were often chased longest and most vigorously.

Two types of behavioral interactions between parent fish and their juveniles were recorded: glancing and tending. Glancing results will be presented in Part II of this chapter as part of a separate analysis of this behavior. During "tending" interactions, one parent

swam up behind a juvenile, then both paused for a moment, and frequently the parent then gently swam behind the juvenile, herding it back into the main brood. This same motor pattern (see Ward and Barlow, 1966) was eventually used more aggressively to drive the older juveniles (stage 4 or 5) from the brooding site and was also used to chase away unrelated juveniles from the brood. No significant differences were detectable in average number of tending observations between stages of brood (Fig. 3-4; Table 3-3). However, juveniles were tended significantly more often in exposed sites (Table 3-3). In contrast, no differences between brood stage or zone were detectable in tending frequency-per-juvenile, although means were consistently higher in exposed sites for each stage (Fig. 3-3; Table 3-3).

Total parental effort was calculated by summing number of chases and tends over time, for each brood stage and zone. Highly significant differences in parental effort were detected between stages and between zones (Fig. 3-4; Table 3-5) with greater parental effort observed in exposed sites and in younger broods. In contrast to total parental effort, effort per juvenile did not differ between brood stage within a zone, or between zones (Fig. 3-4; Table 3-5).

Discussion

The results of this study indicate that the intensity of parental care can vary depending on the behavior involved, the brooding site, and the age of offspring. From a parents' perspective, more effort in general is given to younger broods and in exposed reef zones. Since parents use significantly less effort in lagoon sites to raise broods, these zones may be a better choice for nesting. Effort per juvenile neither increased or decreased as juveniles aged; individual juveniles received approximately equal amounts of parental care through the brooding period.

Because defensive chases are frequent and involve vigorous swimming, chasing appears to be the most energetically demanding behavior performed by the parents. During observations, it was clear that these chases often served to deter predators. Although this was not quantified, aggressive chases varied in their intensity and the distance chased. Lizardfishes (Synodontidae), small wrasses such as *Thallassoma lunare* (Labridae), trumpetfishes (Aulostomidae), and rockcods (Serranidae) were most vigorously pursued, sometimes over meters. *Thallasoma lunare* is a known predator of juvenile *Acanthochromis* (Nakazono, 1993; Robertson 1973; pers. obs.). On Lizard Island, the differences among reef zones in parental care effort are correlated with zone differences in the abundance of some of the known and probable predators of *Acanthochromis* juveniles (Beukers, 1996; Syms and Stewart, unpubl. data). This suggests that, in addition to the probability of greater mortality of juveniles, it is more energetically expensive to brood in areas with higher numbers of predators. This correlation makes a case for further experiments aimed at isolating the effect of predation on parental effort in these habitats.

The frequency with which intruding conspecific *Acanthochromis* juveniles and adults were chased indicates the importance of brooding territoriality, conceivably aimed at preventing other adults or juveniles from disrupting the brood. For the youngest broods, other *Acanthochromis* adults could also represent a predation threat. Further studies examining territoriality among adults and closely-spaced broods in a site might be useful for understanding how social interactions affect the intensity of behaviors. If density of adult *Acanthochromis* differs among sites, then these brooding behaviors might also be affected; this correlation of higher adult *Acanthochromis* density with higher numbers of predators and/or mortality rates may be relevant in the Lizard Island situation (e.g. Ch. 4). The "tending" behavior recorded here may also serve to increase juvenile survival, however its function remains unclear. It appears to be associated with the parents maintaining the

integrity of the brood, possibly through identification of their own juveniles as distinct from those of another brood. Both herding juveniles into a defendable group size and aggressively defending these groups would serve to decrease the probability of predation.

From an individual juvenile's perspective, approximately the same amount of care is received each day throughout their entire developmental period until they leave the nesting area, but individual juveniles on average received more care in exposed sites at every stage (Fig. 3-4). Post-hatch parental care of individual broods in *Acanthochromis* lasts for months, but the level of energy required by the parent changes through this period. The intense protection of newly-hatched broods abates as broods age, and parents can effectively resume "normal" feeding routines in later stages of brooding. However, it is interesting that the decrease in overall effort parallels the decrease in brood size, such that the effort per offspring remains constant throughout the months of brooding. One might reason that, because it requires such an investment of time and energy, the duration and intensity of parental care through the brooding period is likely to be optimized for greatest survival of juveniles. The guarding and tending efforts provided by parents for the large, nearly independent, later-stage juveniles is hard to understand in this context. If entire broods are removed (experimentally or through predation), *Acanthochromis* adults are easily capable of laying repeated clutches over short time periods (days; pers. obs.), so it seems the extra effort spent on these older stage juveniles must be worth the delay of the next spawning.

It is clear that differences exist among reef zones in total parental care effort, and it is likely that the same pattern holds when examined on an individual juvenile basis. The correlation of this behavioral variation with particular environmental gradients, is corroborated by similar relationships found in freshwater and terrestrial habitats (Endler, 1994; review in Clutton-Brock, 1991). It would be interesting to consider these results

along with other traits which might vary among reef zones (e.g. body size, and rates of growth, development, fecundity, or mortality) to further understand the interaction between life-history traits and the fitness consequences of living and reproducing in different zones of the coral reef.

Part II:

Notes about the frequency and function of glancing behavior in juvenile *Acanthochromis*

Introduction

Parent-contacting or "glancing" behavior is a peculiar and rare type of interaction between parent fish and their offspring in which the free-swimming juveniles occasionally swim towards and rapidly touch the sides of the parent. This behavior has been most often recorded in members of the family Cichlidae; 24 out of 28 species known to exhibit parent/juvenile physical contact of any kind are freshwater cichlids. Of the four non-cichlid species, two are freshwater catfishes (Bagridae) that have elongate filliform processes on the ventral surface of the male which secrete a milky proteinaceous substance on which the young feed (Sundararaj, 1962; Noakes, 1979). Another species is an Amazonian osteoglossid (*Arapaima gigas*) whose parent-juvenile contact behavior is vaguely referred to in the literature, but is apparently under dispute; no specific juvenile behaviors are described for this species (in Noakes, 1979). The fourth non-cichlid species, and the only marine species, is *Acanthochromis polyacanthus* (Pomacentridae). The glancing behavior of *Acanthochromis* juveniles on their parents bears a superficial resemblance to that recorded for cichlid species such as *Etroplus maculatus* or *Cichlasoma citrinellum* (Noakes and Barlow, 1972; Ward and Barlow, 1966).

The actual functional significance of glancing behavior in any species remains unclear. In studies of cichlids, various ways that glancing may be important have been suggested. These include: 1) as a nutritional supplement (through ingesting mucus or parasites) (Noakes and Barlow, 1972), 2) for chemical or tactile cues for identification of individuals, 3) as a tactile induction of parental care (Quertermus and Ward, 1969; Noakes, 1979), 4) as a fright response (Ward and Barlow, 1966), or 5) for transfer of growth hormone (Schuetz, 1994). In *Etroplus maculatus* (Cichlidae), ingesting mucus from glancing was necessary for normal growth and development of juveniles (Noakes and Barlow, 1972). It is apparent that glancing behavior varies in style and may serve different purposes in different species (Noakes, 1979).

The few studies which mention glancing behavior in *Acanthochromis* hypothesise that it provides a source of nutrition for the juveniles (Robertson, 1973; Allen, 1975). However, it has not yet been established that any ingestion occurs during contact, and if so, what relative quantity of supplemental food is provided. Furthermore, it has been reported that glancing in *Acanthochromis* juveniles is most frequent in young juveniles and appears to diminish with age (Robertson 1973; Noakes, 1979), however no data are presented which provide evidence for variable rates of glancing. In this study, I quantify glancing behavior in *Acanthochromis* juveniles, and examine its potential role as a source of supplemental nutrition.

Methods

Rates of glancing, planktonic feeding, and bottom feeding by juveniles were obtained during 30-min behavioral observations of broods in lagoonal and exposed reef zones as described above (Part I: Methods). Glancing frequencies were analysed for differences among reef zone and juvenile stage, as in Part I. Because of difficulties in

reliably distinguishing individual predation events on plankton or bottom substrate, individual broods were recorded as either feeding or non-feeding during each observation period. To test whether glancing rate changed when juveniles were feeding independently (not glancing off parents), glancing rates for feeding and non-feeding broods were calculated for each stage of juvenile, then a two-factor analysis of variance was used to test for significant differences in glancing frequency for feeding and non-feeding juveniles of each stage.

To determine if juveniles were only touching the parents or whether they were actually ingesting mucus, juveniles and one of their parents were brought into the laboratory. The parent was held briefly out of the water and painted on its flanks with diluted Alcian Blue, which stains mucus (Cook, 1974). The fish was placed into a separate tank for 5 minutes to allow excess stain to rinse off, then placed into another aquarium with eight of its juveniles. The fish were observed in order to record glancing activity by the juveniles. After two hours the juveniles were removed and frozen, then dissected for evidence of Alcian Blue in their guts. As a control, 8 juveniles were placed in a separate tank to which Alcian Blue stain had been added until the water was a pale blue color. No parent was added. After two hours, the juveniles were sacrificed and frozen for later gut examination.

Results

Over all observations, frequency of glances by a brood ranged from 0 to 72 per 30-min period. The glancing frequency was remarkably similar between zones, but varied among brood stages (Fig. 3-5; Table 3-6). Significant differences were detected between brood stages, with a relatively low frequency of glancing in stage 1, the highest frequency always in stage 2 broods, and steadily decreasing mean frequencies through stages 3-5

(Fig. 3-5). ANOVA detected significant differences in frequency of glancing by individuals as juveniles aged, but glancing frequency-per-juvenile was similar in both habitats (Fig. 3-5; Table 3-6). The mean rate of glancing by individuals was 0.010 glances/min/juvenile (s.d.= 0.009). Assuming that juveniles will glance over normal daylight hours, that indicates that each juvenile glances only 5 or 6 times per day.

Seventy-seven percent of juveniles were recorded as feeding during observation periods. Of these 17% were observed feeding off the bottom substrate and 100% were plankton feeding. Bottom feeding was observed in stages 2 through 5, but not in stage 1 juveniles. No differences were detected in glancing rates between feeding or non-feeding juveniles for any stage of development (Table 3-7; Fig. 3-6).

Six out of eight juveniles removed from the tank after two hours with an Alcian Blue-painted adult had stain in the anterior part of their guts. None of the control juveniles showed evidence of blue stain in their guts.

Discussion

While the results of the Alcian Blue experiment indicate ingestion of surface mucus occurs during glancing, the frequency data suggests that extremely low quantities of mucus are ingested. Furthermore frequency of glancing does not appear to be influenced by whether the juveniles have been recently feeding. Because of these results, it appears unlikely that the function of glancing is merely to provide additional nutrition.

The question remains, then, what is the important function of this complex interaction? Because ingestion does occur during at least some of the glances, transfer of some substance from parent to juvenile occurs. Transfer of growth hormone during glancing has recently been reported in one cichlid species (Scheutz, 1994) and could

encourage faster growth -- possibly an advantage on the reef. This seems a good avenue for further investigation.

Part III:

The use of olfaction for detection of juveniles by parents

Introduction

Because broods of *Acanthochromis* are often living in close proximity to each other, *Acanthochromis* parents must have some method for identifying their own young. This appears to occur during parent/juvenile interactions called tending. Parental tending or herding of juveniles has been described for other species of brooding fish (Fryer and Iles, 1972; Tulley and Huntingford, 1987), and can require substantial effort and have the important function of maintaining brood integrity. The tending behavior is also suggested to prepare juveniles for later encounters with predators (Tulley and Huntingford, 1987). The ability to identify juveniles should be essential for making sure parental effort is directed towards one's own brood, and for driving away intruding juveniles of other broods. During the tending interaction, the parent pauses behind the juvenile for a moment, before either herding it back to the brood, chasing it away, or just ignoring it. Because of the apparent ability of parents to discriminate among juveniles that at least appear (to human observers) similar (Robertson, 1973; pers. obs.), it is possible that olfactory cues are used.

Chemical cues have been demonstrated to be used by fishes in detection of conspecifics (Sweatman, 1988) and food (Davis and Olla, 1995), and in affecting social behaviors (Davis and Olla, 1995; Knutsen, 1992; Pawson, 1977). It has been repeatedly suggested that olfactory cues may be important in illiciting brooding behaviors in cichlids, although no studies have specifically tested this hypothesis (Keenleyside, 1991). It seems

logical that *Acanthochromis* might also require special sensory abilities to identify their young. Using field-caught parents and their broods, an experiment was set up to test whether *Acanthochromis* parents could detect their juveniles using only olfactory cues.

Methods

A 100-l glass aquarium which was covered with black plastic on three sides, and three small pieces of coral rubble were placed equidistantly inside to provide substrate. On either side of this aquarium, a smaller aquarium was placed at a slightly higher level, and also covered with black plastic (Fig. 3-7). The aquaria were filled with seawater and left static for the experiments. A short length of 5-mm tubing attached to a hypodermic needle was used to drip water from the small aquaria into the sides of the larger one. To determine how fast the introduced water would diffuse through the tank, beet juice was used to stain the water in one of the small tanks, then it was dripped into the large tank, and diffusion time measured using a stopwatch, until the leading edge of the stain penetrated two-thirds of the tank.

For each trial, one parent was placed in the center third of the aquarium and encouraged to associate with the center piece of coral by temporarily blocking off the side corals with plastic boards. The parent's brood was placed in one of the smaller side-tanks, randomly chosen. The other side-tank was filled with only seawater. The fish were left to acclimate for 30 minutes with no disturbances. Trials were run outdoors in shaded mid-day light. After acclimation, a siphon was started, dripping water from the tank on either end, one presumably saturated with the exudate from the brood, and the other containing only seawater. An observer seated 2 meters away from the experimental tank kept track of how much time was spent in the third of the tank from which the brood-water was being introduced, as a fraction of the total time until the brood-water would have diffused through

to the third of the tank opposite from where the cue was introduced. Each parent fish was used in only one trial. Between trials the tanks were emptied and completely flushed with seawater.

A chi-square analysis was used to test whether fish spent more time than expected in the one-third closest to the introduced brood-water.

Results and Conclusions

Eight trials were run each with a naive parent. Parents spent from 0 to 100% of their time in the one-third of the tank closest to where brood-water was being introduced (Table 3-8). The mean time spent in this section averaged over all parents was 46.7% of total time, while the randomly expected fraction of time would be 33.3%. A chi-square analysis was used to detect significant departures from random in the number of trials in which the parent spent more time than expected (greater than 33.3%) in the section into which brood-water was being introduced. Six parents spent more time than expected in the one-third on the tank with the stimulus. The chi-square analysis detected a highly significant departure from random, indicating more parents chose to spend a greater amount of time in water containing the scent of their juveniles, as opposed to plain seawater. These results indicates the potential for parents to identify juveniles in the field using only olfactory cues. Further studies might include investigating the ability of parents to distinguish between their juveniles and those of other broods, and the ability of siblings in a broods to identify each other and their parents. While the results of this study are preliminary, they support previous findings that olfactory cues are likely to be important in reef habitats (Sweatman, 1983,1985 ; Miyagawa, 1989; Fricke, 1974).

Table 3-1. Mean and standard deviation of brood sizes for each brood stage, in broods observed for parental care behaviors. n = sample size.

Stage	Mean	S.D.	n
1	120.0	12.7	4
2	81.7	28.7	4
3	71.1	47.9	7
4	47.6	28.5	7
5	25.7	13.0	7

Table 3-2. Results of two-factor ANOVA for dispersion area of *Acanthochromis* broods, by juvenile stage and reef zone. Data were log-transformed. * means statistically significant difference detected. A. Brood dispersion area for entire brood. B. Brood dispersion area divided by brood size.

A. Brood dispersion area

Factor	df	Type III SS	F	p
stage	4	234526	9.53	0.0001 *
zone	1	1997	0.32	0.5700
s*z	4	22438	0.91	0.4600
error	113	695573		

B. Dispersion area per juvenile

Factor	df	Type III SS	F	p
stage	4	24.85	2.98	0.0221 *
zone	1	0.056	0.03	0.8701
s*z	4	8.39	1.01	0.4072
error	113	235		

Table 3-3. Results of two-factor analysis of variance for parental care behaviors exhibited by Acanthochromis, for each brood stage and reef zone. * means statistically significant difference was detected at $p<0.05$.

A. Chases per minute

Factor	df	Type III SS	F	p
stage	4	11150	14.21	0.0001 *
zone	1	1110	5.66	0.0190 *
s*z	4	1420	1.81	0.1315
error	113	22160		

B. Chases per minute per juvenile

Factor	df	Type III SS	F	p
stage	4	1.74	1.94	0.1080
zone	1	0.16	0.72	0.3991
s*z	4	2.26	2.54	0.0438 *
error	113	25.2		

C. Tends per minute

Factor	df	Type III SS	F	p
stage	4	1793	1.90	0.1153
zone	1	2048	8.68	0.0039 *
s*z	4	503	0.53	0.7117
error	113	26663		

D. Tends per minute per juvenile

Factor	df	Type III SS	F	p
stage	4	0.335	0.33	0.8567
zone	1	0.9235	3.65	0.0587
s*z	4	0.2496	0.25	0.9113
error	113	25.2		

Table 3-4. Summary of taxa chased by *Acanthochromis* parents away from broods, grouped by major categories. Total number of chases observed and percentages are given.

Category	Chases	Percent
Acanthochromis adults / subadults	184	31.6
Acanthochromis juveniles (other broods)	40	6.9
Damselfishes (other)	168	28.8
Obligate piscivores	81	13.9
Facultative piscivores / other	110	18.8
Total	583	100

Table 3-5. Results of two-factor analysis of variance for parental effort shown by *Acanthochromis*, for each brood stage and reef zone. Effort is the sum of the frequency of defensive chases and tends (see text) per minute. * means statistically significant difference was detected at $p<0.05$.

A. Parental effort per minute

Factor	df	Type III SS	F	p
stage	4	19285	10.38	0.0001 *
zone	1	6175	13.29	0.0004 *
s*z	4	1063	0.57	0.6834
error	113	52499		

B. Parental effort per minute per juvenile

Factor	df	Type III SS	F	p
stage	4	1.9	0.82	0.5181
zone	1	1.85	3.16	0.0780
s*z	4	2.6	1.11	0.3543
error	113	66.1		

Table 3-6. Results of two-factor analysis of variance for glancing behaviors by juvenile *Acanthochromis.*, by juvenile stage and reef zone. Data were log-transformed. * means statistically significant difference detected. A. Glances per hour. B. Glances per hour divided by brood size.

A. Glances per minute

Factor	df	Type III SS	F	p
stage	4	71656	12.66	0.0001 *
zone	1	13	0.02	0.9286
s*z	4	731	0.11	0.9772
error	113	180728		

B. Glances per minute per juvenile

Factor	df	Type III SS	F	p
stage	4	24.85	2.98	0.0221 *
zone	1	0.056	0.03	0.8701
s*z	4	8.39	1.01	0.4072
error	113	235		

Table 3-7. Results of two-factor ANOVA for glancing frequency of *Acanthochromis* broods, for feeding and non-feeding juveniles of each stage. No significant differences were detected.

Factor	df	Type III SS	F	p
feeding	4	0.0000073	0.01	0.9323
stage	1	0.00316	0.79	0.5370
f*s	4	0.00065	0.16	0.9570
error	61	0.06		

Table 3-8. Percent of time spent by *Acanthochromis* parents in the 1/3 of the experimental tank closest to where the olfactory scent of their juveniles was released. Total time for each trial was 4 minutes. Expected time if parents were randomly selecting a position in the tank is 33.3%. Chi-square analysis indicate a significant deviation from expected, with a higher number of parents spending more time than expected in the 1/3 closest to brood-water.

Parent #	Side of tank with juveniles	% of time spent in 1/3 of tank closest to brood-water
1	L	43.5
2	R	76.0
3	L	51.3
4	L	0
5	L	74.8
6	L	75.4
7	R	3.5
8	R	100

Figure 3-1. Dispersion area (means and standard deviations) of *Acanthochromis* broods observed at Lizard Island sites. Stages are defined in Table 2-2.

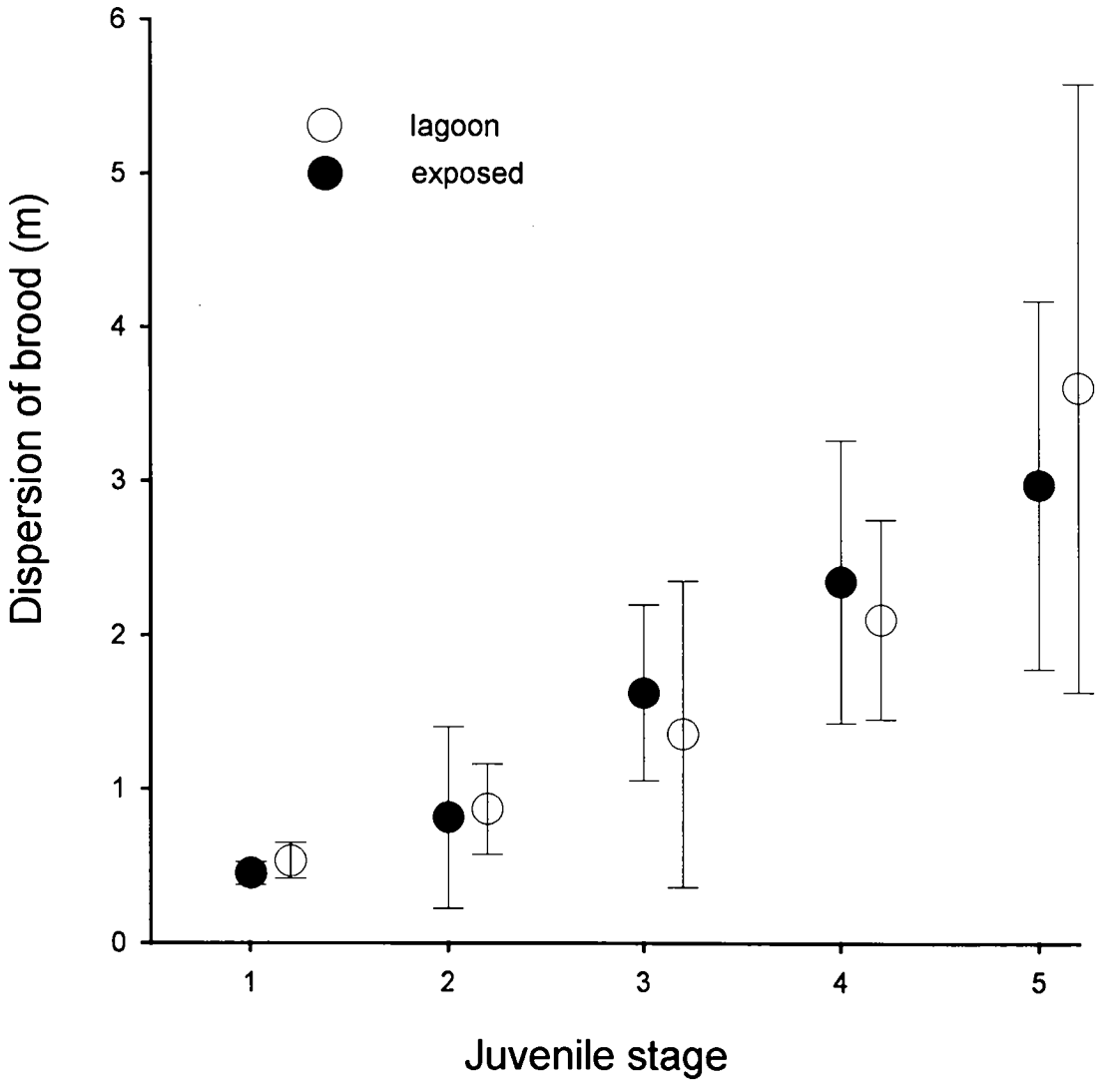

Dispersion of brood (m)
0
1
2
3
4
5
6
lagoon
exposed
1
2
3
4
5
Juvenile stage

Figure 3-2. Aggressive behavior exhibited by *Acanthochromis* parents and juveniles in family groups observed in exposed and lagoonal reef sites at Lizard Island, GBR. Top graph gives means and standard deviation for the entire brood (total number of chases observed per minute of observation), while the bottom graph gives means and standard deviations for number of chases per juvenile (total chases per minute divided by brood size). Stage of brood is defined in Table 2-2.

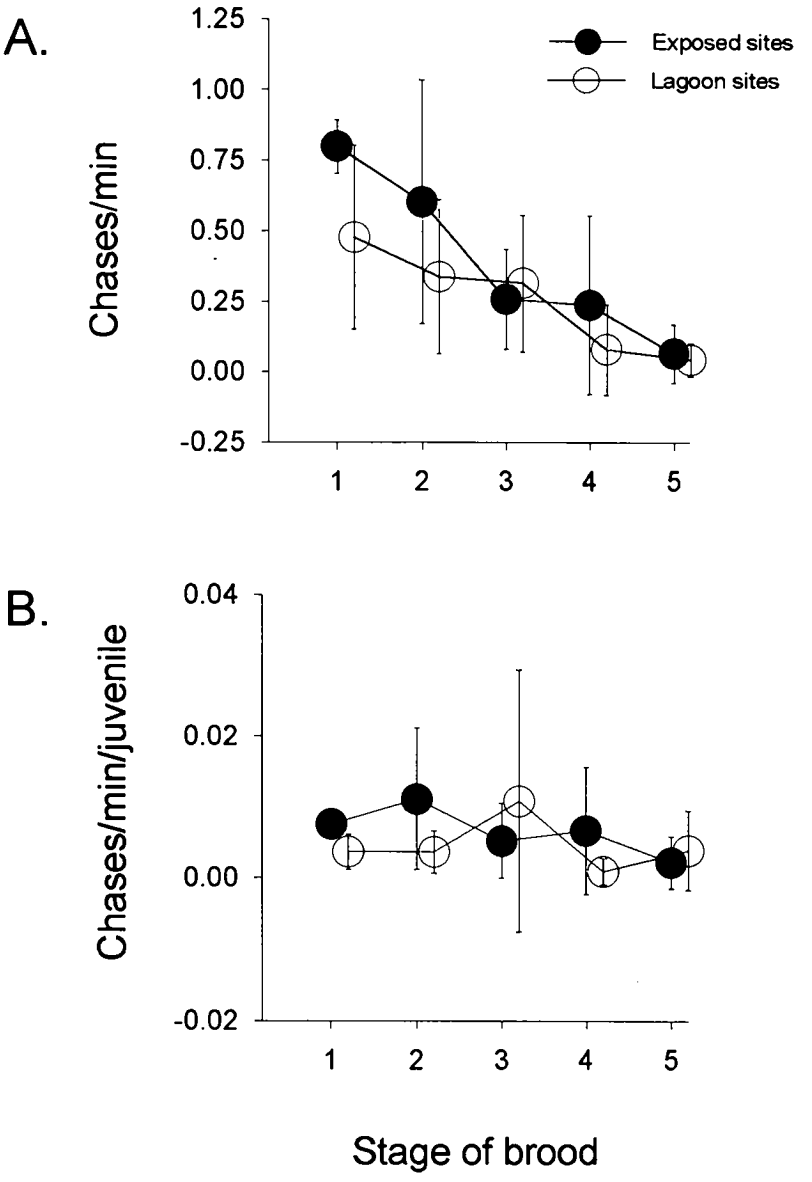

A.
Chases/min
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
1
2
3
4
5
Exposed sites
Lagoon sites
B.
Chases/min/juvenile
0.04
0.02
0.00
-0.02
1
2
3
4
5
Stage of brood

Figure 3-3. Tending behavior exhibited by *Acanthochromis* parents and juveniles in family groups observed in exposed and lagoonal reef sites at Lizard Island, GBR. Top graph gives means and standard deviation for the entire brood (total number of chases observed per minute of observation), while the bottom graph gives means and standard deviations for number of chases per juvenile (total chases per minute divided by brood size). Stage of brood is defined in Table 2-2.

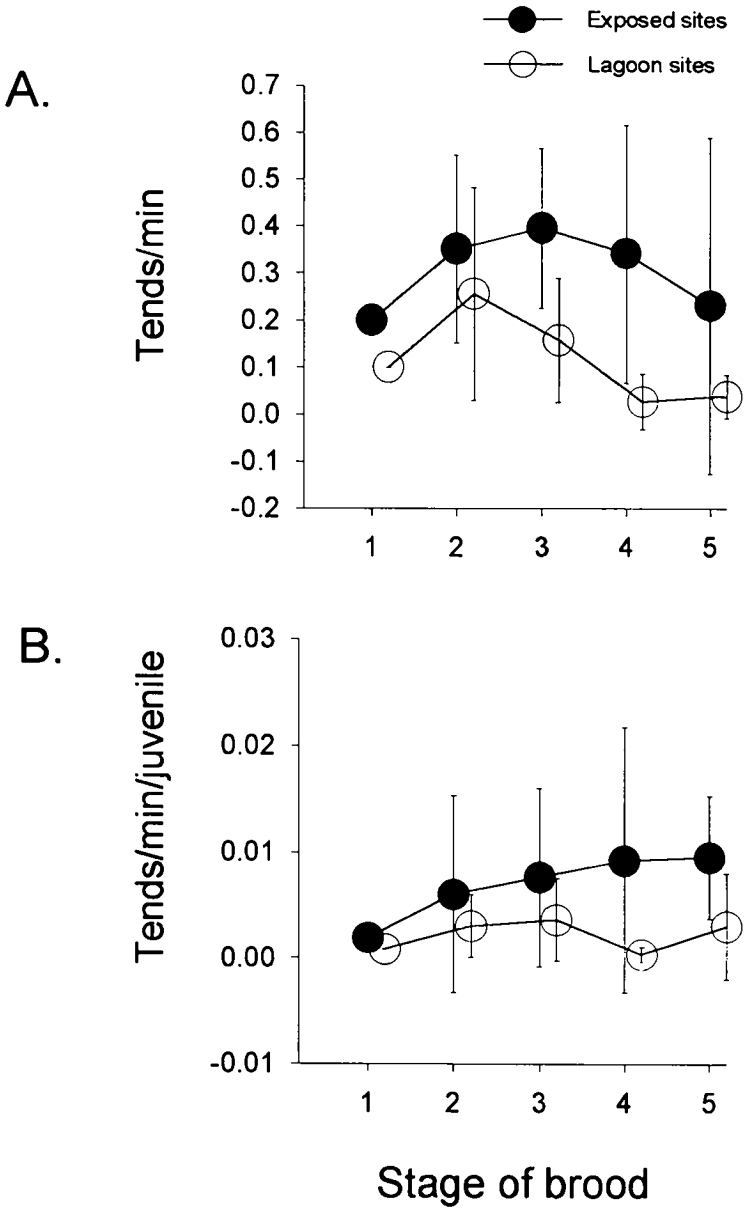

A.
Exposed sites
Lagoon sites
Tends/min
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
1
2
3
4
5
B.
Tends/min/juvenile
0.03
0.02
0.01
0.00
-0.01
1
2
3
4
5
Stage of brood

Figure 3-4. Parental effort (sum of chases and tends for *Acanthochromis* parents observed in exposed and lagoonal reef sites at Lizard Island, GBR. Top graph gives means and standard deviation for the entire brood (total number of chases observed per minute of observation), while the bottom graph gives means and standard deviations for number of chases per juvenile (total chases per minute divided by brood size). Stage of brood is defined in Table 2-2.

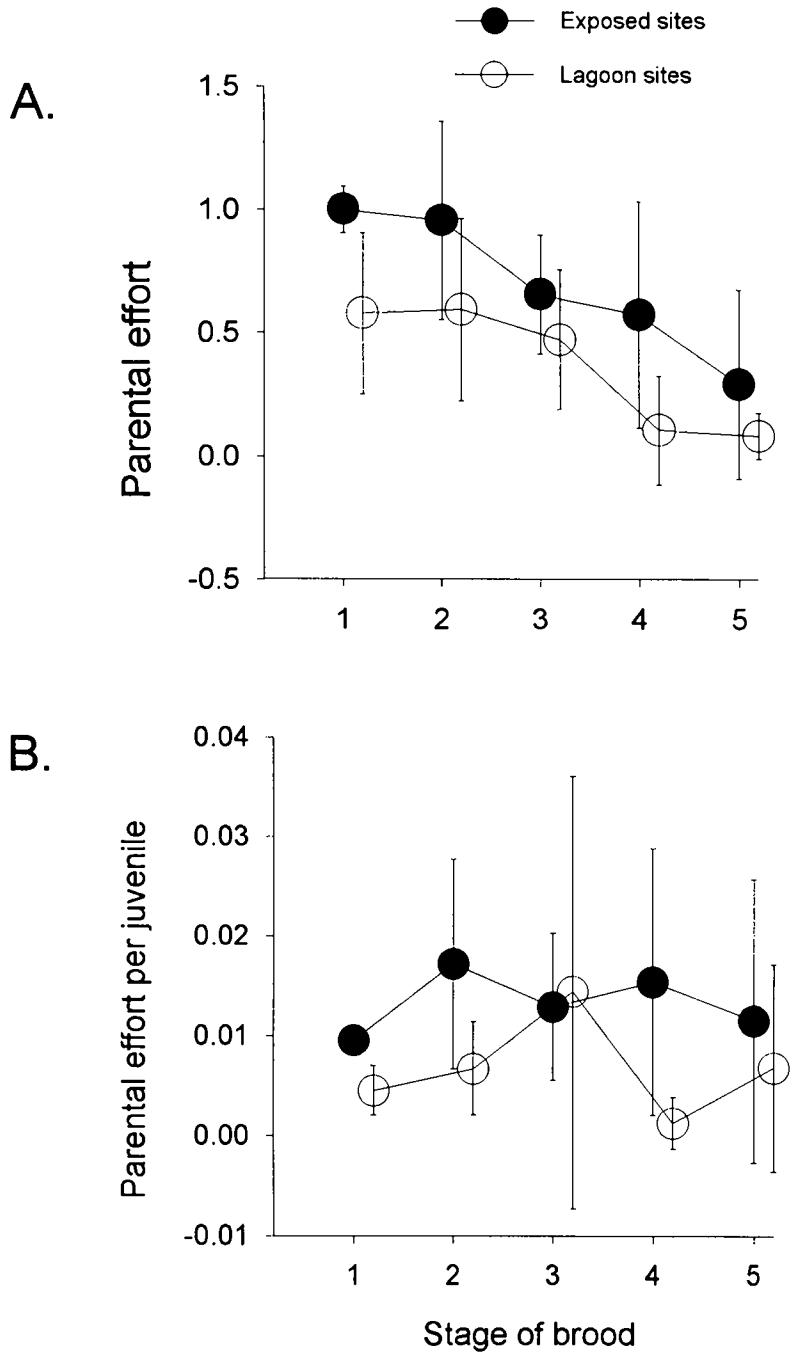

A.
Exposed sites
Lagoon sites
Parental effort
1.5
1.0
0.5
0.0
-0.5
1
2
3
4
5
B.
Parental effort per juvenile
0.04
0.03
0.02
0.01
0.00
-0.01
1
2
3
4
5
Stage of brood

Figure 3-5. Glancing behavior exhibited by *Acanthochromis* parents and juveniles in family groups observed in exposed and lagoonal reef sites at Lizard Island, GBR. Top graph gives means and standard deviation for the entire brood (total number of chases observed per minute of observation), while the bottom graph gives means and standard deviations for number of chases per juvenile (total chases per minute divided by brood size). Stage of brood is defined in Table 2-2.

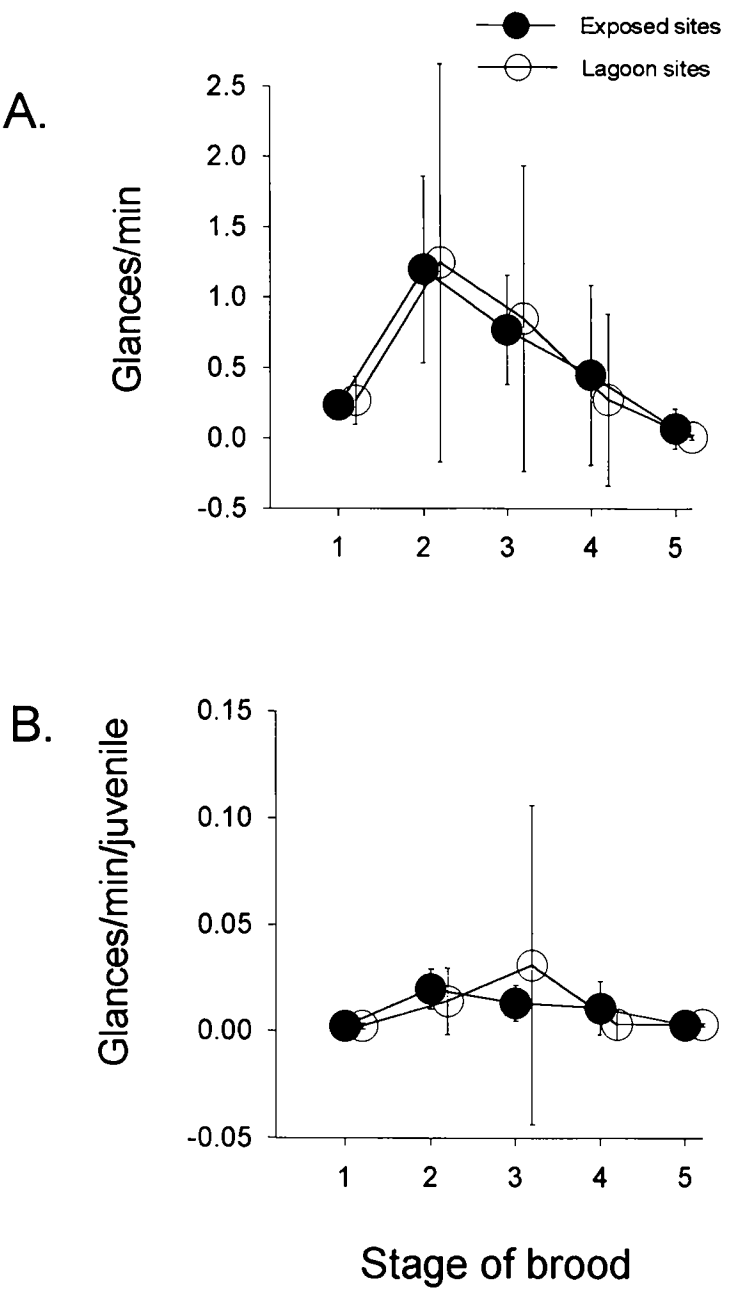

A.
Exposed sites
Lagoon sites
Glances/min
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
1
2
3
4
5
B.
Glances/min/juvenile
0.15
0.10
0.05
0.00
-0.05
1
2
3
4
5
Stage of brood

Figure 3-6. Glancing rate (glances per min per juvenile) for feeding and non-feeding *Acanthochromis* broods. (Pooled observations across reef zones.) Stage of brood is defined in Table 2-2.

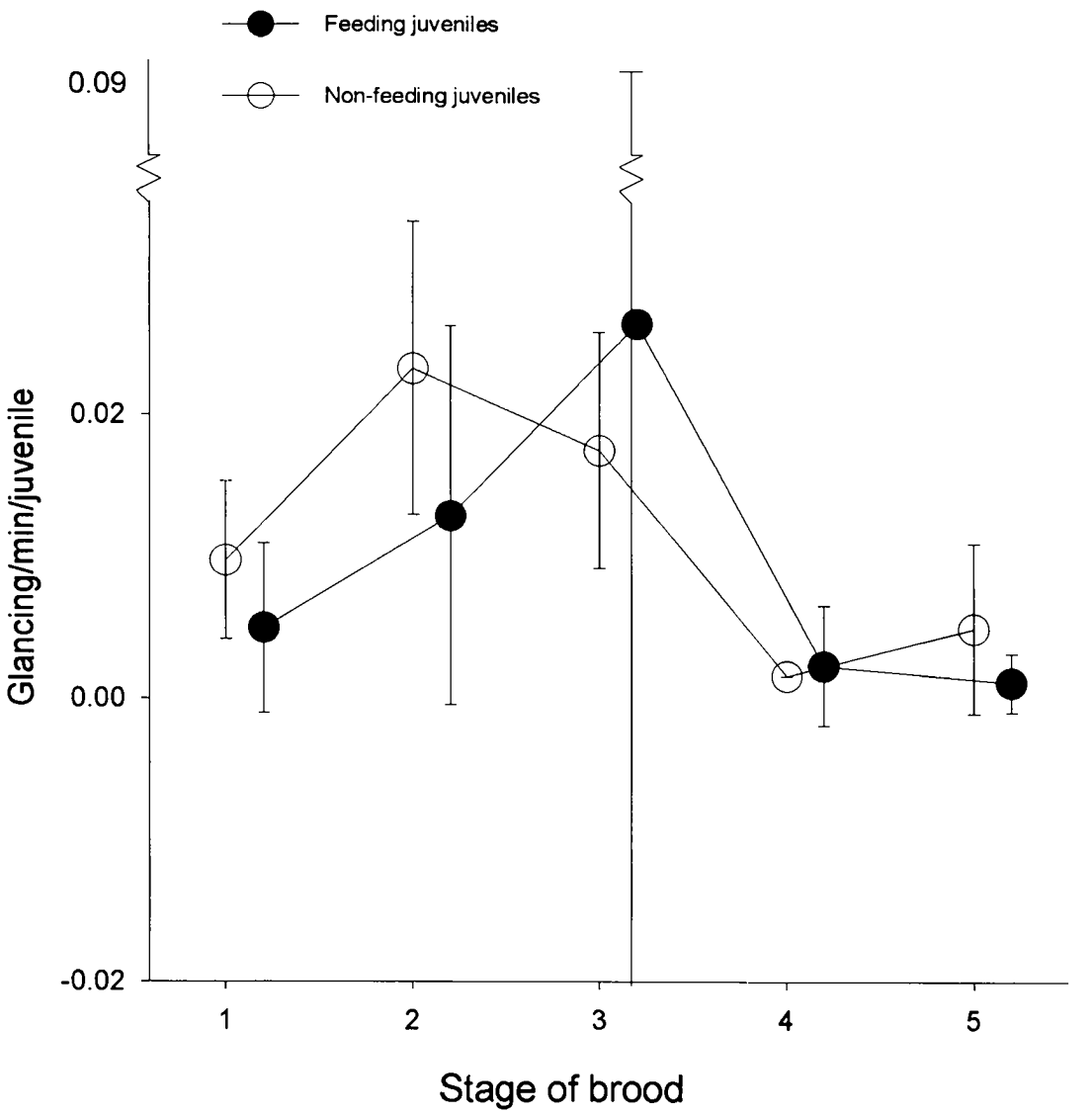
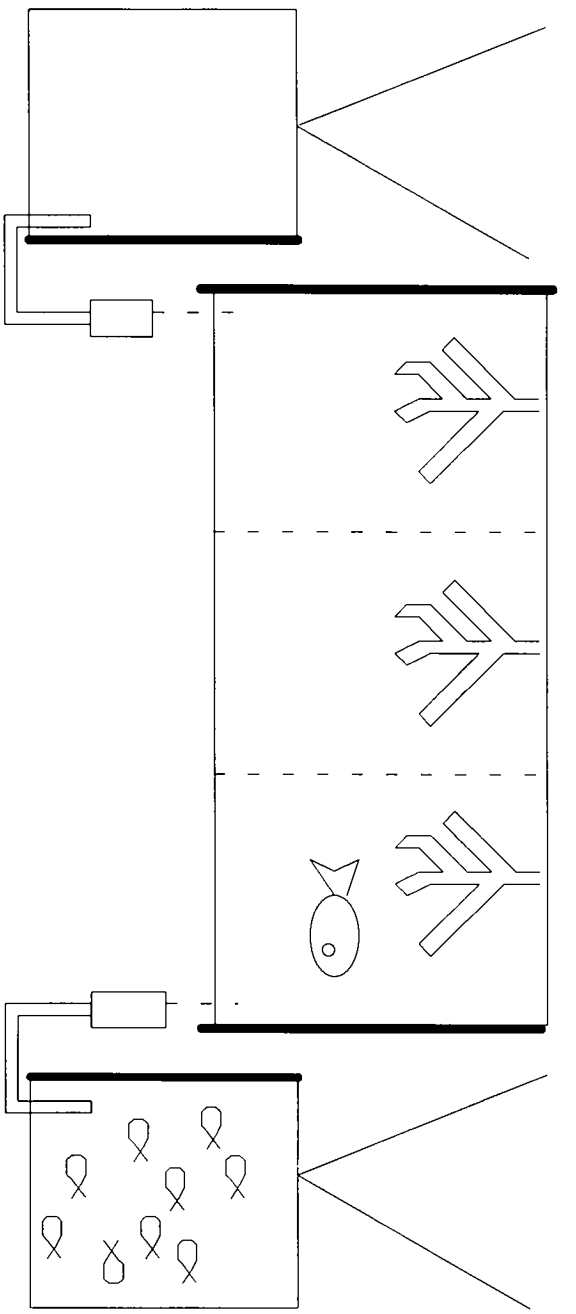

Feeding juveniles
Non-feeding juveniles
0.09
0.02
0.00
-0.02
Glancing/min/juvenile
1
2
3
4
5
Stage of brood

Figure 3-7. Experimental set-up for testing whether parent *Acanthochromis* can detect their juveniles using olfactory cues.



Chapter Four

Seasonal and zonal differences in rates of juvenile production and survival in the damselfish *Acanthochromis polyacanthus* at Lizard Island, Great Barrier Reef

Introduction

For coral reef fish, spawning can involve such energy-intensive behaviors as long-distance migrations to a spawning aggregation (Serranidae: *Epinephalis* spp.), daily movements between reef zones (Acanthuridae; Labridae), selection and defense of a demersal nesting site (Pomacentridae; Balistidae), or synchronization of spawning in seasonal, lunar, or daily cycles (review in Robertson, 1991). Because energy for reproduction is necessarily limited, current theory suggests that these behaviors have a strong fitness value: they are a result of the partitioning of reproductive resources into spatial and temporal patterns that produce the most surviving offspring. However, the striking variability in these behaviors among species, and among populations within species, suggests that other factors may have influenced locally observed spawning patterns other than a straightforward fitness response. These might include conditional behavioral responses to local environments, "copying" from previously established individuals (Warner 1995), selection for other factors that do not relate directly to survival of offspring (Shapiro et al, 1988; Robertson, 1991), or an adaptive response to historical environmental factors that no longer exist.

Attempts to understand the ultimate cause of these reproductive patterns has generated many adaptive hypotheses for their evolution (Johannes, 1978; Barlow, 1981; Doherty 1983; Warner, 1995). Most of these hypotheses assume the overriding importance of larval/juvenile biology in controlling characteristics of reproduction. However others present alternative hypotheses suggesting that the limits or requirements of adult biology may be just as important in the evolution of reproductive patterns (review: Robertson, 1991; Shapiro et al,

1988). For example, spawning of reef fishes may be timed to coincide with full-moon so that larvae will be competent to settle around the following new moon when they cannot be seen as easily by predators (control by larval/juvenile biology) (Christy, 1978; Kingsford, 1980); alternatively, spawning at full-moon may allow ripe adults to find mates easier and ensure a greater fertilization success (control by adult biology) (see Robertson, 1991). Testing these hypotheses is difficult however, because spatial and temporal variation in spawning and mortality rates are notoriously hard to obtain. Most reef fishes have open populations and tiny dispersive larvae, and thus far it has proved impossible to follow cohorts from a single spawning, or even an entire reef, to estimate survivorship. Comparative mortality rates for juvenile and adult stages of coral reef fishes are becoming available in the literature, and several recent studies have made it clear that differences in mortality rates exist on a wide range of spatial and temporal scales (Doherty 1980; Kingsford, 1982; Aldenhoven, 1986; Eckert, 1987; Gladstone and Westoby, 1988; Connell, 1994; Caley, 1995a,b; Booth, 1995). Correlation of spatial and temporal patterns in spawning frequency with subsequent mortality rates of particular life history stages would be a useful beginning to understanding the ecological and adaptive significance of certain reproductive behaviors. Although several studies have measured both spawning frequency and recruitment rates at sites, these measurements are unlinked (Gladstone and Westoby, 1988; Robertson et al, 1988). Because we do not know the extent of recruitment "feedback" that open reef-populations receive, it is currently impossible to link spawning and subsequent mortality for most reef fishes.

Fishes that lack a dispersive stage are unusual in that they have more control over the particular conditions their juveniles will encounter than do fishes with the more typical dispersive larval stage. Their life history also makes them useful study animals for questions about the importance of different life stages in determining patterns of reproduction. In these

species which can more readily determine the environment that their offspring encounter, one would predict that if juvenile survival was strongly dependent on the time and place of nesting/brooding, these fishes would select nesting sites and spawn in seasons which optimize juvenile survival.

Because it broods its young conspicuously on the reef for months, and occurs over a range of reef zones, *Acanthochromis polyacanthus* is a good species to choose for investigating temporal and spatial variability in rates of production of offspring and their subsequent mortality. Because the juveniles can be approximately aged by external characteristics and size, mortality rates can be estimated through numbers of "known-age" juveniles per brood. This chapter examines whether the time and place where *Acanthochromis* broods are most frequently produced is also the time and place where juvenile *Acanthochromis* survival is highest. The time scale I examine is across seasons, and the spatial scale is across major reef zones at Lizard Island.

Some background information is required in order to address this question. Parent size is known to affect both clutch size (James and Bruton, 1992) and survival of brooded juveniles in other species (Wisendon and Keenleyside, 1995), thus consistent differences in parent size between zones and/or seasons need to be evaluated. Furthermore, to compare production of broods in different zones, one needs to examine whether the differences in numbers of broods are due to the differences in numbers of potential parents (inferring habitat selection), or due to differences in number of broods produced *per* parent (suggesting increased fecundity). Therefore, data on adult size and density were collected concurrently with brood production and juvenile survival estimates.

Methods

Study sites and periods

Observations of *Acanthochromis* at Lizard Island, Great Barrier Reef were made over a total of four trips (="seasons"): Early Summer (October 1994), Mid-Summer (December 1994/January 1995), Late Summer (March 1993), and Mid-Winter (July 1993). Forty-eight transect sites were chosen to sample sub-populations from 3 reef zones (Front, Lagoonal, and Back Reefs) around the Lizard Island group (Fig. 1-1; FS, FB, CO, BO, WM, NR, TU, CH, UR, BS, IP, BB). Front Reef is defined as the zone where the reef is subject directly to the prevailing winds and typically has the highest wave action. Lagoonal Reef is a protected, relatively shallow area that only has open access to Great Barrier Reef waters through two channels and in a veneer of water over reef flats. Back Reef environments have access to the open waters, but are protected from the prevailing winds and thus are typically calmer. Although weather conditions did not allow all transect sites to be visited on every trip, a minimum of 8 fixed 50m X 4m transects were visited in each zone visited during each season.

Data collection

To determine size structure and density of adults and sub-adults in the population, all *Acanthochromis* along each transect were counted and total length of these fish was estimated visually by a diver (KK). Size estimates were calibrated at the beginning of each trip by visually estimating the total length of individual fishes, then capturing and measuring them. For each brood encountered along a transect, the number of juveniles in the brood and the total length of individuals within the brood were estimated, as was their stage of development (Table 2-2) and the size of the parents. Because error was high in estimation of length of smaller juveniles, staging of broods using coloration and morphology was used as an indication of size and age (Table 2-2). Although these characteristics allowed 5 stages of juveniles to be separated in the field, to simplify analysis juveniles were grouped into three

functional categories: New Broods (stage 1), Older Broods (stages 2 and 3), and Dispersing-Age Broods (stages 4 and 5; see below). Male and female of the pair were without exception of very similar size (<5 mm difference), so a single estimate was taken to represent the size of both parents.

Estimates of number of juveniles per brood (brood size) were calibrated by visually counting and recording the number of juveniles, then capturing and counting the entire brood. Several broods were observed repeatedly over the duration of the late summer and winter trips, and then again during subsequent trips. This allowed estimates of loss over time, and growth rate for a few individual broods.

Assumptions and statistical analyses

Size-at-maturity was taken as the smallest adult observed brooding juveniles. Non-brooded *Acanthochromis* smaller than the size-at-maturity were called subadults. Size frequencies were plotted for each reef zone for each season. Density of adults at sites were determined by mean numbers of *Acanthochromis* equal to or greater than size-at-maturity recorded over a transect, divided by area of reef surveyed (800 m^2). Densities of subadults were determined by a similar calculation based on abundance of individuals between the average size of a stage 5 juvenile and the size-at-maturity. Densities of adults and subadults were tested for significant differences between zones and seasons using a two-factor analysis of variance.

Numbers of broods observed on transects were examined for differences between seasons and zones. For each category of brood (New, Older, Dispersing-age), a two-factor analysis of variance was used to detect differences in numbers of broods per m^2 in each season and reef zone. A Tukey multiple comparison test was used to determine the source of significant results of the ANOVA.

To test whether zonal differences in brood abundance might be due to differences in adult density among reef zones, I looked at how adult density and brood density covaried. Total brood density (number of broods of all stages per m^2) was calculated and examined for the effect of adult density using an analysis of covariance with adult density as the covariate, and reef zone as a factor.

Because juveniles could be effectively staged, brood size at a particular stage was used as an estimate of age-specific loss. These estimates of loss were based on two assumptions about initial brood size: 1) clutch size at hatching was based on the relationship between female body size and clutch size from captive-bred *Acanthochromis* and 2) all juveniles in each brood observed were siblings from a single clutch. Because *Acanthochromis* lays its eggs deep in small caves in the reef (Thresher, 1984), field measurements of egg-clutch size were not able to be determined on Lizard Island. However, *Acanthochromis* pairs held in large (1000-L) tanks spawned regularly over two years; these pairs produced clutches of approximately 250-550 eggs, and showed a positive relationship with body size for the limited data available (Fig. 4-1). To approximate clutch size for field-observed parents, first, field estimates of parent size were adjusted by subtracting from each size estimate the mean error (calculated from the size calibrations). A clutch size was then calculated for each field-observed parent based on the clutch size/body size relationship from the captive parents (Clutch size = (5.27 (Body size)) - 273.17). The body size/clutch size regression was very weak (r^2=0.06), indicating that other factors have an important influence on observed clutch sizes in the range of female sizes observed. Because the data from captive-produced clutches was lacking clutches from the smallest females, the body size/ clutch size function is likely to be a conservative estimate of the effect of small body size (i.e., less subject to bias in overestimating survival rates of juveniles from small parents). It should be noted that although assumption of clutch size affects estimates of mortality of the earliest

stage (egg through newly-hatched juveniles), estimates of loss *between* juvenile stages are not influenced by this clutch size assumption.

The second assumption is based on the observation that no broods for this study ever exceeded 250 individuals or exhibited a bimodal size frequency, such as might happen if two or more clutches were combined (Ch. 2). Occasionally closely-spaced, unrelated, late-stage broods were mixed during observation periods (determined by size and staging differences in the aggregation): data from these broods were excluded from the analysis.

Loss of juveniles from a brood can happen through either mortality or dispersal. Observations of juvenile dispersal from broods indicate that dispersal does not occur before juveniles reach approximately 50-60 mm TL at Lizard Island (see Ch. 2). Furthermore no non-brooded juveniles under approximately 50 mm TL were ever observed on the reef, suggesting that even if they did disperse at a smaller size, they were preyed upon relatively quickly. Thus, it is assumed that the numbers of juveniles (brood size) in New (stage 1) and Older (stage 2 and 3) broods provide a measure of survival rate from a single clutch, while brood size for Dispersing-age broods (stages 4 or 5) could be a result of mortality or dispersal from the brood.

Percent survival for each brood was determined by dividing the observed brood size by the calculated initial clutch size (see above). Percent survival data were arcsin-square-root transformed to normalize the variance, and compared among zones and seasons using a two-factor analysis of variance for each category of brood (New, Older, Dispersing). A Tukey multiple comparisons test was used to test for differences within factor levels.

To assess whether larger parents were more or less successful in producing more fledglings, a regression of brood size on parental size was performed and tested for deviations from the hypothesis that slope=0.

Results

Density and size frequencies of adult and subadult Acanthochromis

Sizes of fish were typically overestimated by the observer (Fig. 4-2). With one exception (18.8%), error in estimating adult *Acanthochromis* was never greater than 10%. The smallest brooding adult observed, 90 mm TL, was taken to indicate size-at-maturity. The largest *Acanthochromis* observed was 175 mm TL.

Peak densities of *Acanthochromis* were reached at sites on the Front Reefs, with a mean of 0.74 adult fish/m^2 (S.E.=0.56). Lagoon densities were lower, with a mean of 0.59 adult fish/m2 (S.E.=0.35), and Back Reef sites were lowest in adult density with a mean of 0.46 adult fish/m2 (S.E.=0.20) (Fig. 4-3). A two-factor analysis of variance among seasons and zones indicated significant differences in densities of adult *Acanthochromis* existed among reef-zones (Table 4-1). No differences were detected among seasons (Fig. 4-4). A post-hoc Tukey multiple comparison test indicated differences in adult density between Front and Back Reef zones, but no differences were detected between Front and Lagoon, and between Back and Lagoon reefs. Subadult densities were calculated separately, and were not detectably different among zones or seasons (ANOVA: F=1.59; p=0.154; df=11).

A correlation of site-specific densities of subadults (60 -90 mm TL) and adults (<90 mm TL) showed positive correlations of densities of subadults and adults (Pearson's Corr. Coeff. = 0.3726, p=0.016) (Fig. 4-5).

Size frequencies showed definite size structuring around the island, with consistently smaller fish in the lagoon (Fig. 4-6). For example, for both Front and Back Reef environments in the summer, 34% of the adult fish (>90 mm TL) were over 150 mm TL. In contrast, in the lagoon only 2.5 % of adult fish were over 150 mm TL. Size frequencies from the winter transects showed the same pattern of smaller fish in the lagoon, but maximum size

of fish was slightly lower in all reef zones and the difference between zones was not as striking (Fig 4-6).

Brood production

A two-factor analysis of variance in New Brood abundance failed to detect differences among reef zones, but found significant differences among seasons and a significant season/zone interaction (Table 4-2; Fig. 4-7). A Tukey multiple comparison test indicated that most broods were present in Early and Mid-Summer (Early Summer = Mid-Summer > Late Summer > Mid-Winter), but no other differences were detected (Fig. 4-8). However, relatively young (less than approx. 1 month old) broods were observed regularly in Late Summer and occasionally in Mid-Winter, indicating that reproductive effort of *Acanthochromis* is concentrated, but not restricted, to summer at Lizard Island.

Analysis of variance of Older Brood abundance detected significant differences among season and zones, and a significant season/zone interaction (Table 4-2; Fig. 4-7). Although the highest abundance of broods was observed in the Lagoon in Mid-Summer, a Tukey multiple comparison test failed to detect differences among zones, but indicated that most Older Broods were present in Mid-Summer (Mid-Summer > Early Summer = Late Summer = Mid-Winter) (Fig 4-7).

Two-factor ANOVA of number of Dispersing-Age Broods (stages 4 and 5) failed to detect differences among zones, but found significant differences among seasons and a significant season/zone interaction (Table 4-2). Again, most broods were found in the Lagoon in Mid-Summer, but a Tukey multiple comparison test failed to detect differences among seasons (Fig. 4-7).

Analysis of covariance of adult density and brood density (number of broods per m^2) detected a significant positive relationship between adult density and brood density for each reef zone (Table 4-3).

Juvenile survival to fledging

Brood sizes were nearly always slightly underestimated, with 0-18% error, increasing with increasing brood size (Fig. 4-9).

An overall rate of survival for the Lizard Island population of *Acanthochromis* juveniles was calculated using brood size for each stage of brood (mean over all zones and seasons) and assuming an initial clutch size of 500. This calculation indicates that approximately 16.7 % of eggs laid survive until stage 3, and 6.4 % survive and are guarded until stage 5 (Table 4-4). Stage-specific mortality/loss is by far the highest in stage 1 (which assumes the inclusion of mortality from spawning up to approximately 1-10 days posthatch) and in stage 5 (which may include some dispersal). Relatively low mortality is recorded between stages 2 and 4 with >80% survival between stages (Table 4-4).

When seasonal and zone-specific survival rates of New, Older, and Dispersing-Age juveniles were examined, they were found to be generally higher in Early-Mid Summer and on Lagoonal reefs (Fig. 4-10). For New Broods, significant differences were detected among seasons and zones (Table 4-5). No significant season/zone interaction was detected ($p<0.09$). A post-hoc Tukey test indicated that Early Summer had significantly higher survival than Late Summer and Mid-Winter but no other spatial or temporal differences were detected with this test.

Older Broods showed significant differences in brood size between seasons and zones, with a significant season/zone interaction (Table 4-5). A Tukey multiple comparison

test indicated significantly greater survival in the Lagoon, but no differences were detectable for seasons (Fig. 4-10).

For Dispersing-Age broods, significant differences in loss rates (mortality plus dispersal) among seasons, and a significant season/zone interaction, were detected (Table 4-5). A post hoc Tukey test indicated the Lagoon had larger Dispersing-Age broods (Lagoon > Front Reef = Back Reef). The largest Dispersing-Age broods were found in the Lagoon in Mid-Summer (Fig. 4-10).

Parent size was typically smaller in the lagoon (ANOVA: $F=70.14$, $p=0.0001$; Tukey test: Lagoon < Front Reef = Back Reef). A correlation of parent size and brood size found no effect of parent size on survival of juveniles of any stage for any reef zone (Table 4-6).

Other estimates of mortality rate were obtained from repeated observations of individual broods over varying periods of time. Short-term observations (every 2-3 days for 12 days) of 26 broods through February and July 1993 showed no detectable differences in brood size for any brood with the exception of three Dispersing-Age broods. Observations over a longer period (between December 1992 and February 1993) could be made on only two broods at one lagoon site, and indicated a mean loss rate of 29% from stage 2 to 5 and a mean growth rate of .55 mm/day. This value is similar to the mortality calculated using mean new-brood size at age (Table 4-4). Other broods whose nest sites were flagged in Dec 1992 were gone by Feb 1993.

Discussion

Acanthochromis are spawned, hatch, and effectively "settle" in the same place. Their life cycle thus allows far greater control by parental choice of the offspring's environment than other coral reef fishes. If reproductive patterns were strongly influenced by offspring survival, times and places when survival of juveniles is likely to be greater should determine nesting

site. Although the interpretation of seasonality must be made cautiously because of unassessed interannual variability in each season, it appears that most broods were produced in Early - Mid Summer during 1993-1995 at Lizard Island. Thus, as predicted, more *Acanthochromis* broods were produced at Lizard Island during seasons when survival of brooded juveniles was greatest. Several factors that might affect mortality rate could also vary seasonally, such as predator levels (e.g. newly-settled lutjanids), food supply, and predator-swamping through increases in density of their prey (other juvenile fishes), and these might help explain the results. Per-capita protection from predation through high abundance of juveniles has been suggested in other studies of this species (Nakazono, 1993). It appears, then, that the timing of peak spawning in this species could have a selective advantage.

In contrast, no such positive relationship between brood production and survival was found among reef zones. In fact, data from Lagoonal reefs suggest an opposite effect, with fewer broods present but greater juvenile survival. If a lower density of adults existed in the lagoon, then that could account for a lower number of broods produced there. Differences in adult density were found among reef zones, and the density of adults was found to positively covary with density of broods. This is interpreted to mean that individual pairs produce about the same number of broods on average: fewer broods are found in Lagoon reefs because there are fewer pairs there. Thus adults appear to prefer Front Reefs to live and produce offspring, in preference to other zones. Because survival of broods appears to be lower in Front Reefs, the choice to spawn and brood young there does not appear to be selectively advantageous.

Two potential explanations of the unpredicted correlation of juvenile mortality and adult abundance among zones are discussed below. The first considers that nesting sites in the "'better", low-mortality, locations (Lagoon) may be limited and therefore some adults must nest

in suboptimal conditions (e.g. Front Reef). Because the body size of Lagoon adults is typically smaller than that of adults on the exposed (Front and Back) reefs, and because the density of adults is lower in the Lagoon, this interpretation would mean that a few of the smaller adults always get the best nesting locations. Limited nest-sites implies competition, but competition for lagoon nest-sites seems unlikely for two reasons: 1) because small adults would probably not consistently win the competition, and 2) because the covariance of densities of juveniles, subadults and adults among sites suggests that there is not space-limitation or obvious competition, but rather that some sites were consistently preferred by all sizes of *Acanthochromis*. If competition occurred, one would expect some "spreading out" into other reef locations, but instead, certain sites seem to have many more (or less) *Acanthochromis* of all ages.

Another potential explanation of the patterns observed in this study is that growth rates differ between lagoonal reefs and exposed reefs. Higher growth rates have been reported on exposed reefs in other studies (Gladstone and Westoby, 1988; Thresher, 1985; see Ch. 5). If growth rates are lower in lagoonal reefs, a trade-off may be set up, with higher juvenile and adult growth rates (on exposed reefs) measured against higher juvenile survival (in lagoon). Higher growth rates on exposed reefs could also account for the larger size of the adults there, presuming that fish spend a large portion of their life in the same place.

More information on movements, age structure, and growth rates among reef zones would be very useful in any interpretation of the results of this study. Both of the potential interpretations of the zonal differences depend on information about movements between reef zones. However, this information is very scarce. Attempts to tag and relocate *Acanthochromis* as part of this study proved unsuccessful. Previous literature suggests that *Acanthochromis* late-stage juveniles will move between patch reefs (Thresher, 1985; Nakazono,1993) possibly over distances of 100's of meters (A. Lewis, J.C.U., unpubl. data),

but other observations suggest they stay in the same area for at least a few weeks after being chased away from the nesting site by the parents (Ch. 2). Knowledge of variability in growth rates and age structure might help explain the variation in size structure, and possibly the advantage of nesting in an area where juvenile survival is relatively low. In the next chapter, I present results of a study in which juvenile growth rates were determined among these reef zones.

Because Acanthochromis juveniles receive parental care, their mortality rates are potentially different than newly-settled juveniles of other species lacking this care. Comparisons of mortality rates of newly-settled pomacentrids reported in other studies can be made. Rates extracted from these studies indicate approximately 50% loss over the first few months after settlement, but this value varies among studies: for example, 30% in first month, 40-60% by 6 months (Doherty, 1980); 8-30% in one month (Booth, 1995); 10-90% in one year (Beukers, 1996). The body size of the Older Broods (Stages 2 and 3) of *Acanthochromis* most closely correspond to the body sizes of newly-settled individuals of other pomacentrid taxa (approximately 8-15 mm SL). The mortality rates of *Acanthochromis* of these sizes are very similar to the reported average mortality rates for newly-settled pomacentrids (~14% in one month (stage 2 to 3); ~40% over 2 months (stage 2 to 4); Table 4-3). These relatively high mortality rates in early life on the reef suggest that this stage has important impacts on population size, however, this study indicates that other factors may override the concerns of juvenile biology.

Table 4-1. Results of 2-factor ANOVA for density of adult *Acanthochromis* in different seasons and reef zones.

Source	df	Type III SS	MS	F	p
Zone	2	0.1482	0.0741	5.51	0.0094 *
Season	3	0.0197	0.0066	0.49	0.6914
Z*S	6	0.0127	0.0021	0.16	0.9860
Error	29	0.39	0.013		

Table 4-2. Two-factor ANOVA results for number of new, old, and dispersing-age broods observed per 50-m transect, for seasons (early, mid-, and late summer, and mid-winter) and reef-zones (front, back, lagoon).

A. New Broods

Source	df	TypeIII SS	MS	F	p
zone	2	3032.66	1516.33	0.66	.5202
season	4	50010.22	12502.55	5.43	.0006*
z*s	6	30758.38	5126.4	2.23	.0485*

B. Older Broods

Source	df	TypeIII SS	MS	F	p
zone	2	16275.81	8137.91	4.39	.0161*
season	4	28655.20	7163.80	3.87	.0069*
z*s	5	22514.63	4502.93	2.43	.0436*

C. Dispersing-Age Broods

Source	df	TypeIII SS	MS	F	p
zone	2	3910.160	1955.08	2.30	.1067
season	4	28832.40	7208.10	8.48	.0001*
z*s	6	14153.91	2358.99	2.78	.0166*

Table 4-3. Results of analysis of covariance of brood density and adult density (adults/ m^2), for each reef zone.

Source	df	Type III SS	MS	F	p
Zone	2	0.0007	0.0004	1.05	0.3625
Adult Density	1	0.0020	0.0020	5.80	0.0222 *
Z * A.D.	2	0.0011	0.0006	1.65	0.2091
Error	31	0.0105	0.0003		

Table 4-4. Survival of *Acanthochromis* juveniles between stages. Stages defined in Table 2-1. Percent survival estimates are to the midpoint of each stage, e.g. egg to mid-stage 1; mid-stage 1to mid-stage 2; etc.

Stage	Mean (S.D.) Brood Size	% Survival (x/500)*100	% Survival Between Stages	n
1	118.69 (59.0)	23.7	23.7	41
2	97.3 (50.1)	19.5	82.1	51
3	83.4 (47.7)	16.7	85.7	64
4	58.7 (37.6)	11.7	70.4	55
5	32.0 (26.5)	6.4	54.5	42

Table 4-5. Results of 2-factor ANOVAs testing for differences in adjusted brood size (% surviving in New and Older Broods, % surviving and/or not dispersing in Dispersing-Age Broods; see text) in different seasons and zones. ANOVAs were performed on each age-category of juvenile (New, Older, and Dispersing-Age).
* = significant at p=0.05 level.

A. New Broods

Source	df	Type III SS	MS	F	p
Zone	2	0.19	0.10	4.81	0.011 *
Season	3	0.32	0.11	5.38	0.002 *
Z*S	5	0.20	0.04	2.00	0.088
Error	80	1.61	0.02		

B. Older Broods

Source	df	Type III SS	MS	F	p
Zone	2	0.46	0.23	11.33	0.0001 *
Season	3	0.23	0.08	3.85	0.0136 *
Z*S	4	0.23	0.06	2.91	0.0284 *
Error	62	1.26	0.02		

C. Dispersing-Age Broods

Source	df	Type III SS	MS	F	p
Zone	2	0.05	0.03	2.14	0.1251
Season	3	0.36	0.12	9.11	0.0001 *
Z*S	5	0.20	0.04	3.05	0.0146 *
Error	76	1.01	0.013		

Table 4-6. Means and standard deviations of parent size and brood sizes for each reef zone, and results of Pearson's Correlation Analyses between parent size and brood size for each stage/zone combination.

		Parent size		Brood size			
Stage	Zone	Mean	S.D.	Mean	S.D.	Corr. Coeff.	p
New	Back	150.2	12.0	116.5	73.0	0.166	0.524
New	Lagoon	128.7	13.2	111.7	59.5	0.290	0.108
New	Front	147.3	11.5	97.1	42.4	0.226	0.131
Older	Back	152.3	9.8	70.4	49.1	-0.077	0.761
Older	Lagoon	124.4	16.9	100.6	56.9	0.268	0.253
Older	Front	149.5	14.6	69.9	38.0	0.171	0.278
Disp	Back	149.5	12.3	45.9	28.6	0.385	0.076
Disp	Lagoon	119.6	16.7	70.1	52.5	0.371	0.118
Disp	Front	146.9	12.6	36.5	28.5	0.002	0.990

Figure 4-1. Egg clutch sizes for captive female *Acanthochromis polyacanthus*.

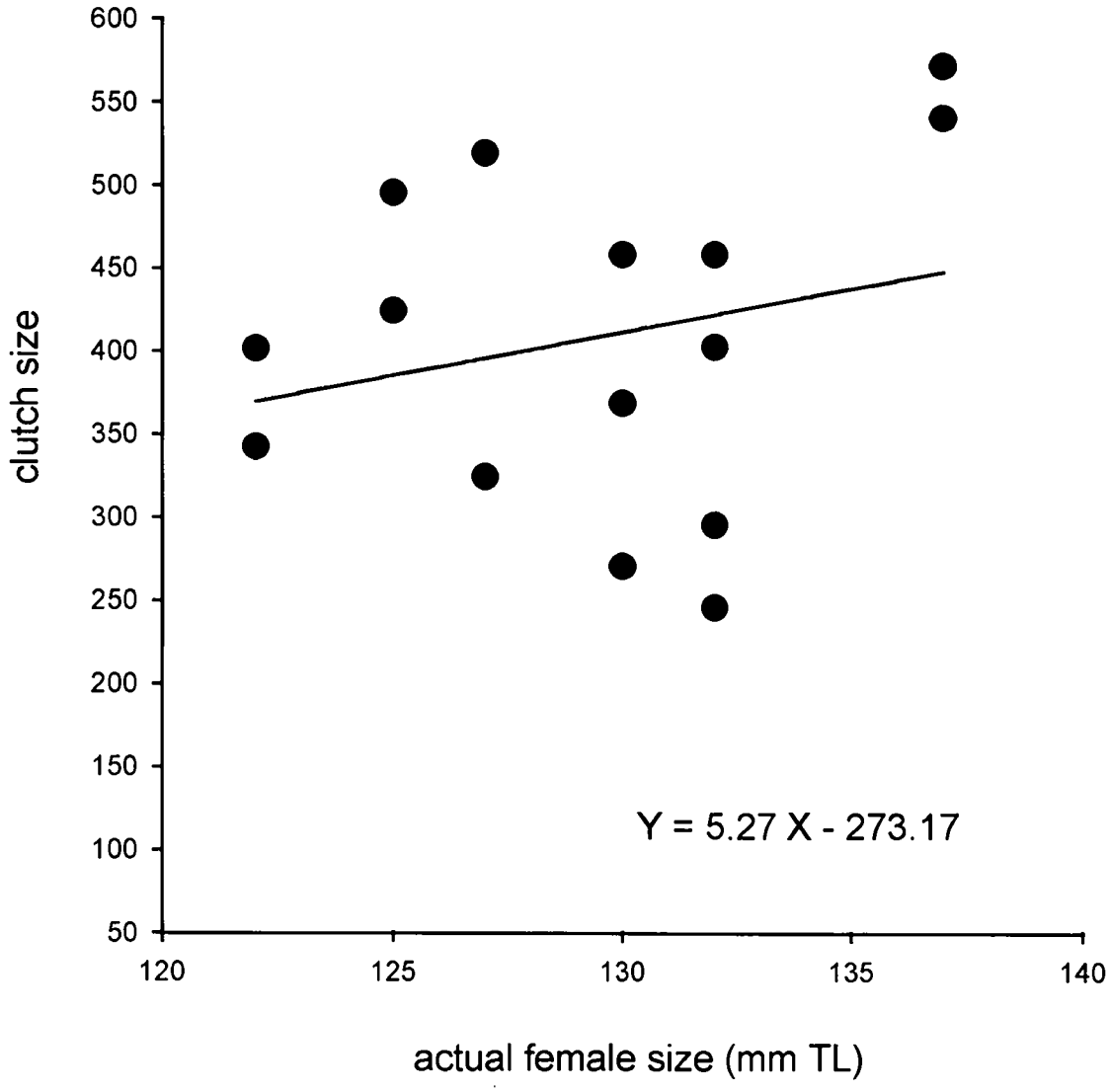

600
550
500
450
400
350
300
250
200
150
100
50
clutch size
120
125
130
135
140
Y = 5.27 X - 273.17
actual female size (mm TL)

Figure 4-2. Calibration of size estimates for *Acanthochromis polyacanthus*.

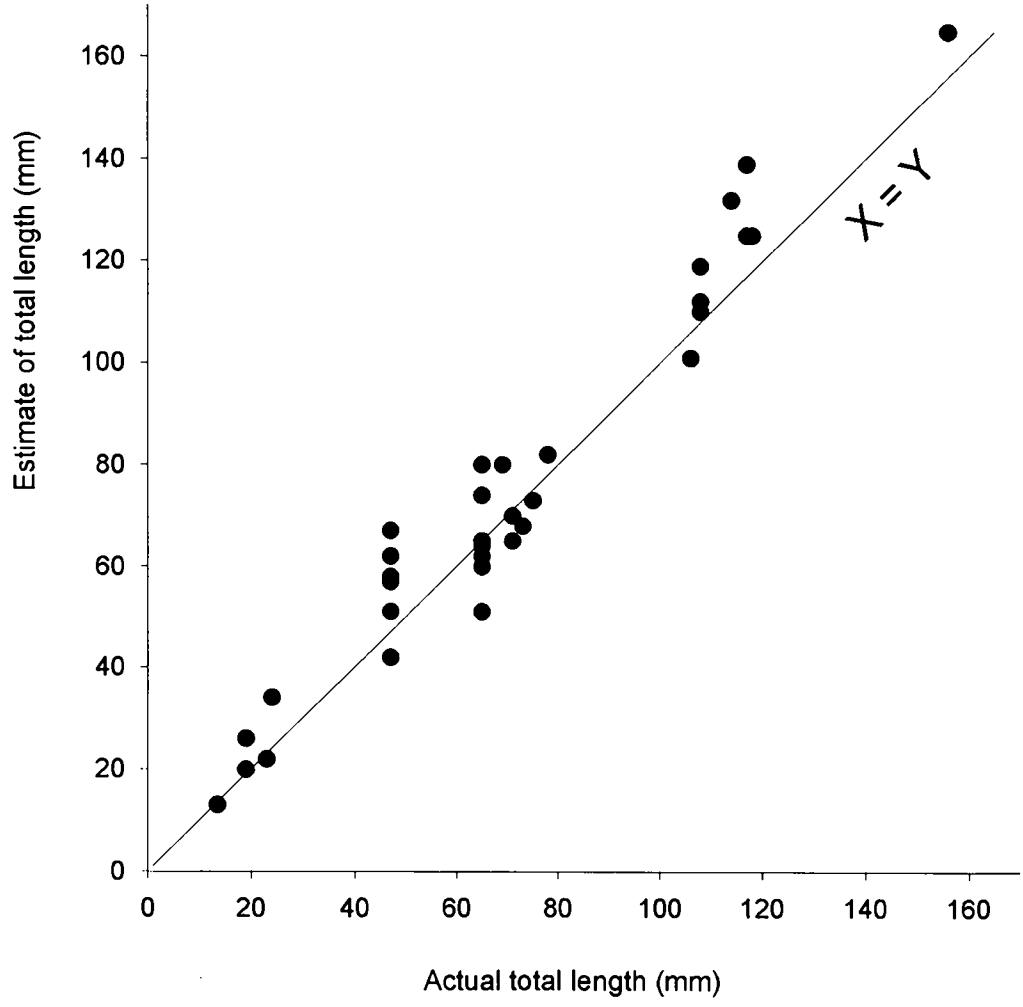

Estimate of total length (mm)
160
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
Actual total length (mm)
X = Y

Figure 4-3. Densities of adult *Acanthochromis* (>90mmTL) in different reef zones around Lizard Island, Great Barrier Reef.

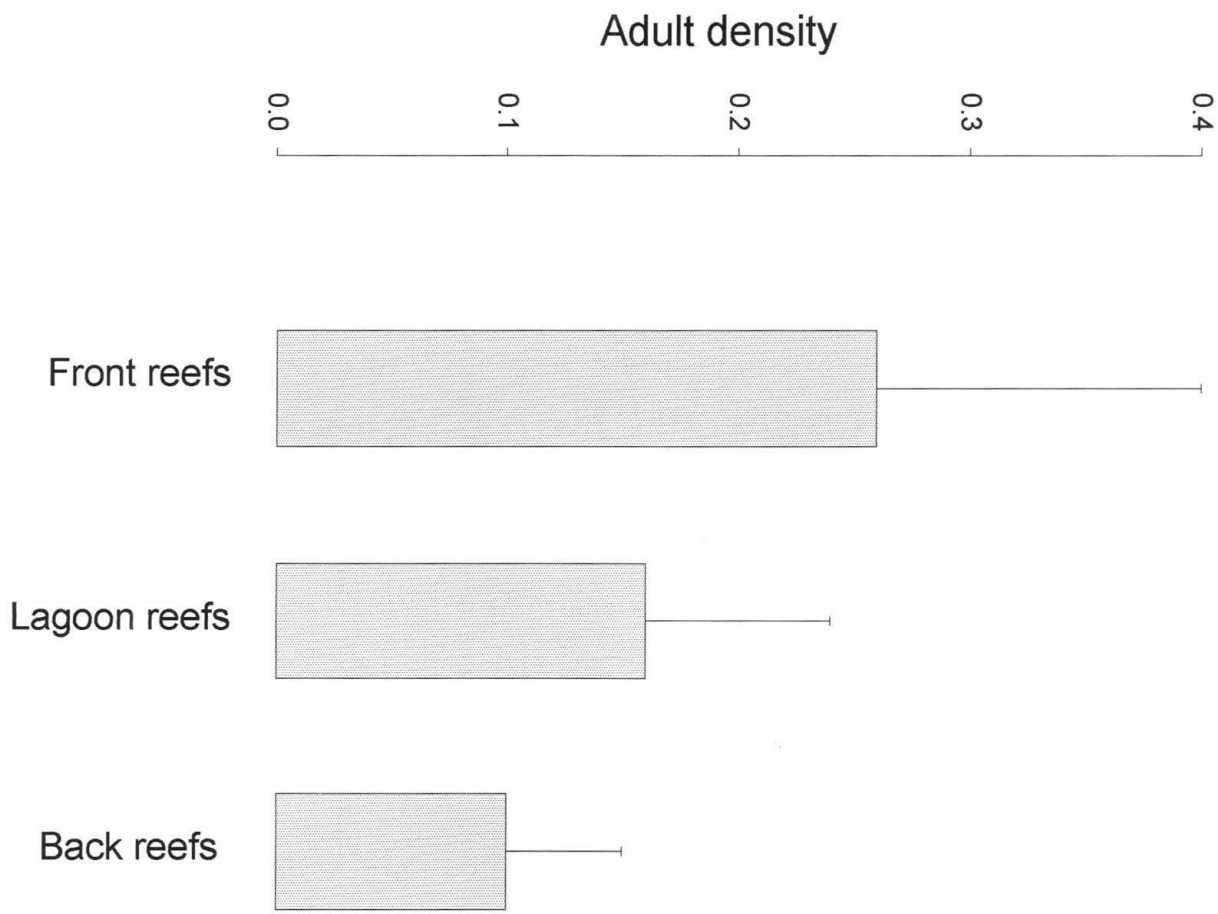

Adult density
0.0
0.1
0.2
0.3
0.4
Front reefs
Lagoon reefs
Back reefs

Figure 4-4. Densities of adult *Acanthochromis* (>90mmTL) estimated in different seasons at Lizard Island, Great Barrier Reef.

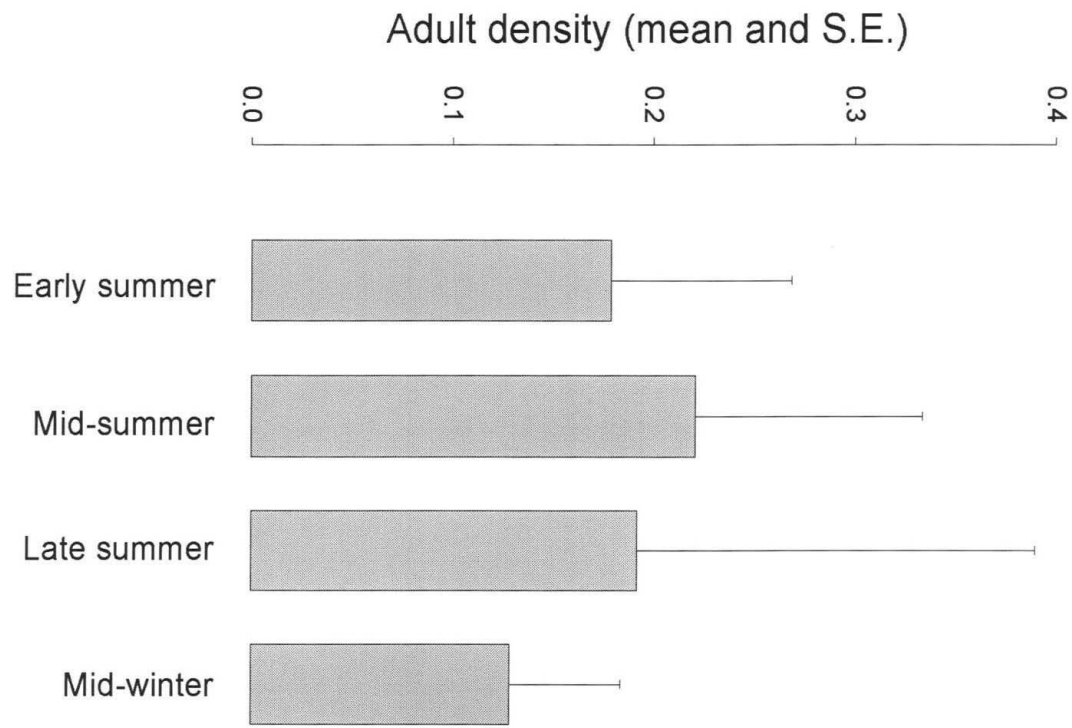

Adult density (mean and S.E.)
0.0
0.1
0.2
0.3
0.4
Early summer
Mid-summer
Late summer
Mid-winter

Figure 4-5. Site-specific densities of adult and subadult *Acanthochromis* around Lizard Island, Great Barrier Reef.

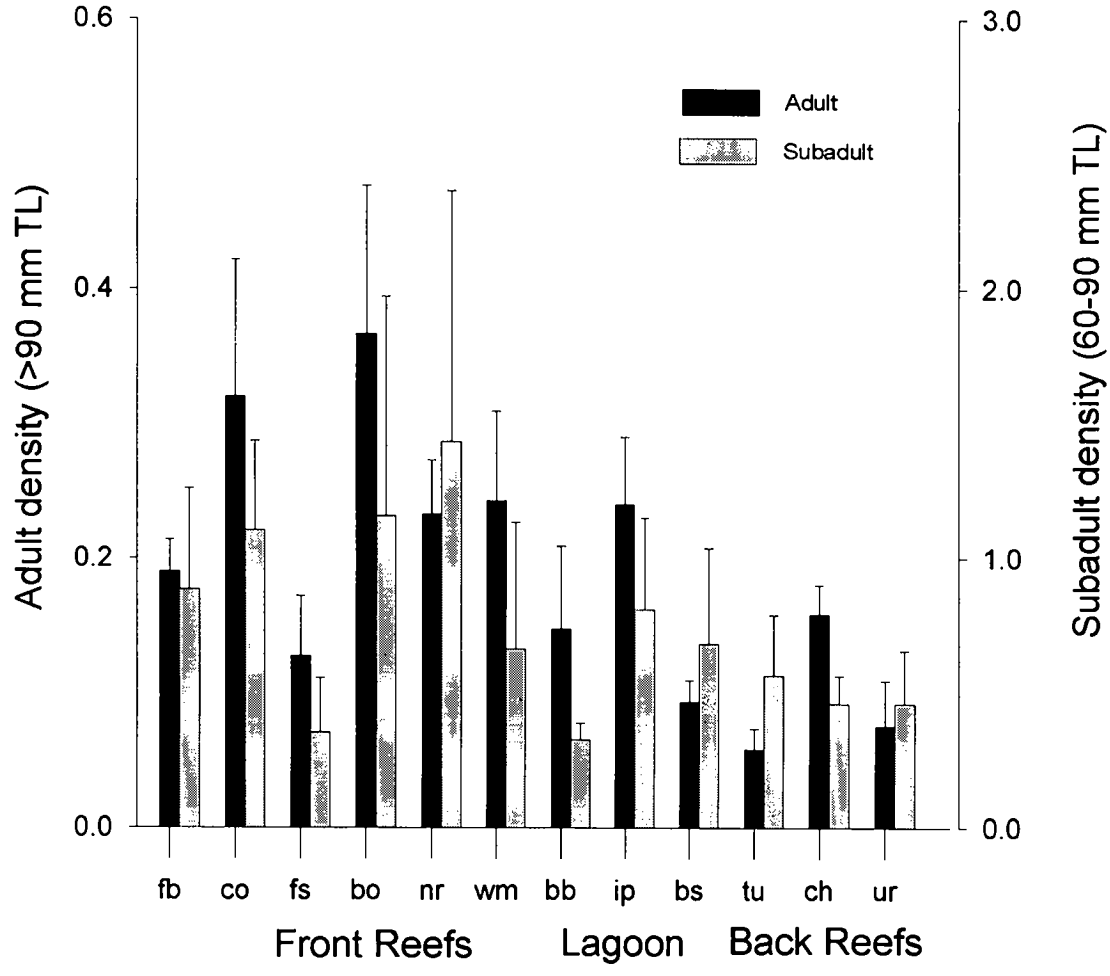

0.6
0.4
0.2
0.0
3.0
2.0
1.0
0.0
Adult
Subadult
Adult density (>90 mm TL)
Subadult density (60-90 mm TL)
fb
co
fs
bo
nr
wm
bb
ip
bs
tu
ch
ur
Front Reefs
Lagoon
Back Reefs

Figure 4-6. Size frequency histograms for *Acanthochromis* adults observed on transects, for each reef zone in each season. Front and Back Reef zones have consistently larger adults.

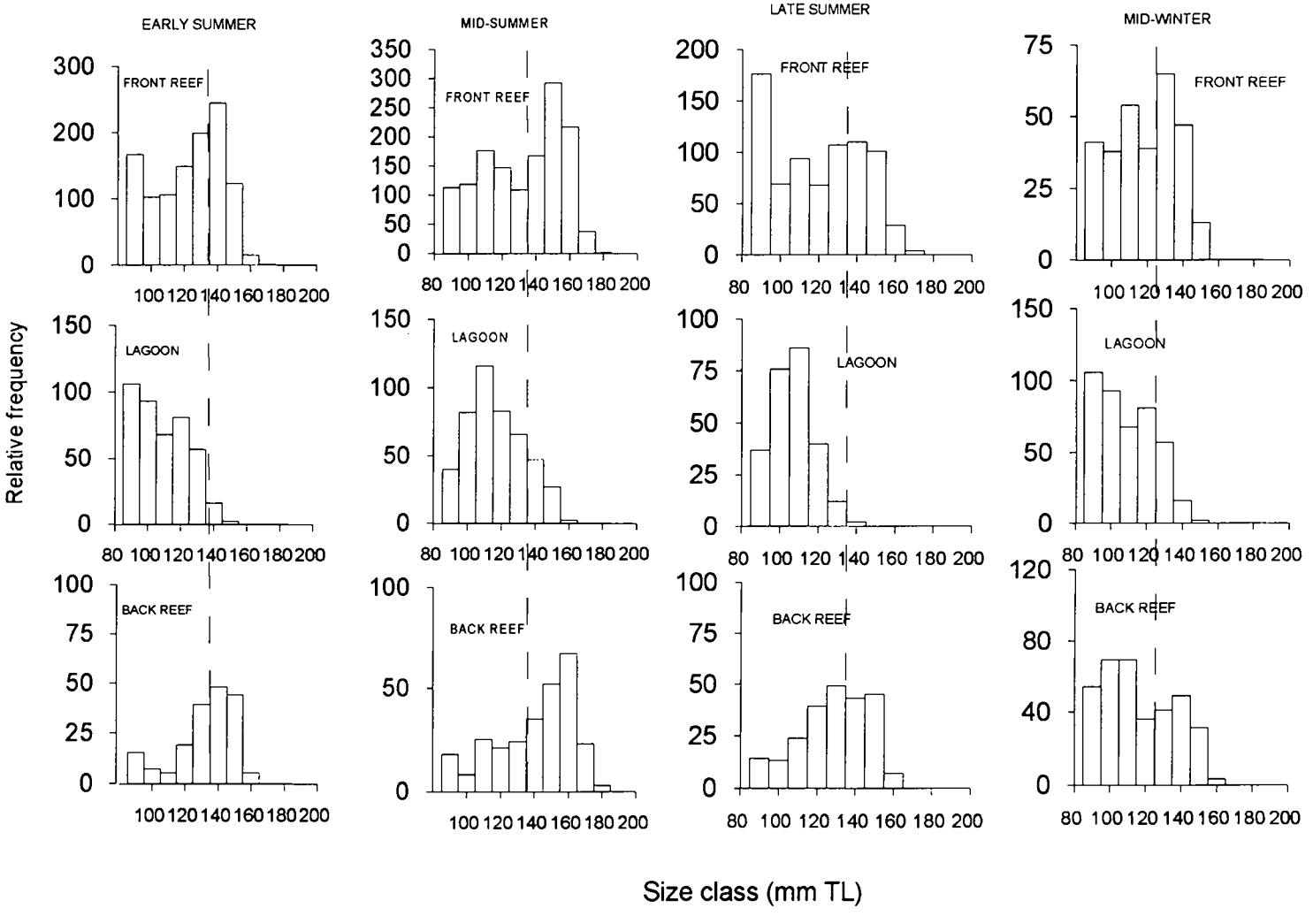

EARLY SUMMER
MID-SUMMER
LATE SUMMER
MID-WINTER
FRONT REEF
LAGOON
BACK REEF
Relative frequency
Size class (mm TL)

Figure 4-7. Number of broods (means and S.E.) observed in reef zones and seasons for each category of brood (New, Older, or Dispersing-age: see text and Table 2-1).

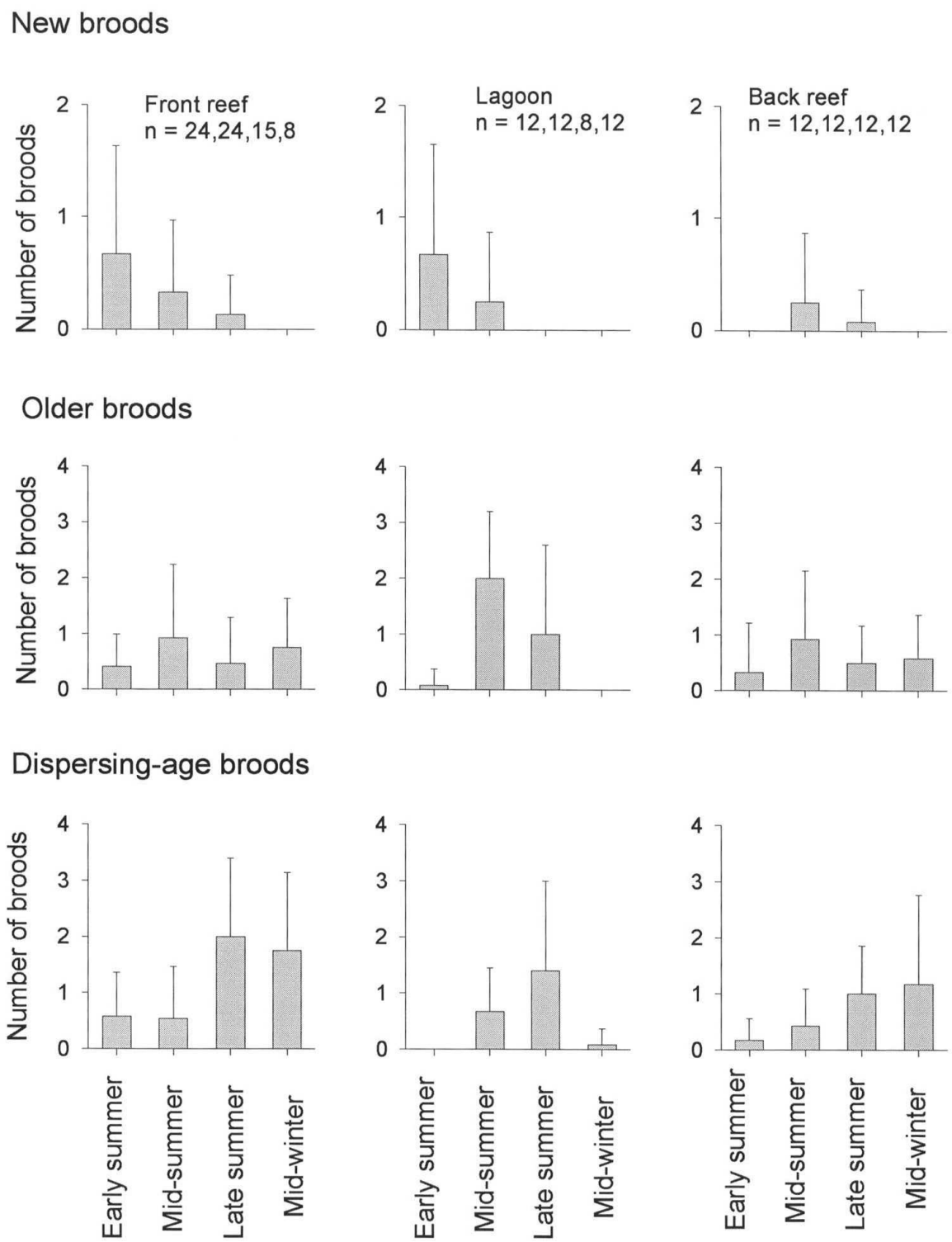

New broods
Front reef
n = 24,24,15,8
Lagoon
n = 12,12,8,12
Back reef
n = 12,12,12,12
Number of broods
Older broods
Dispersing-age broods
Early summer
Mid-summer
Late summer
Mid-winter

Figure 4-8. Number of new *Acanthochromis* broods produced per m^2 seasonally at Lizard Island, Great Barrier Reef.

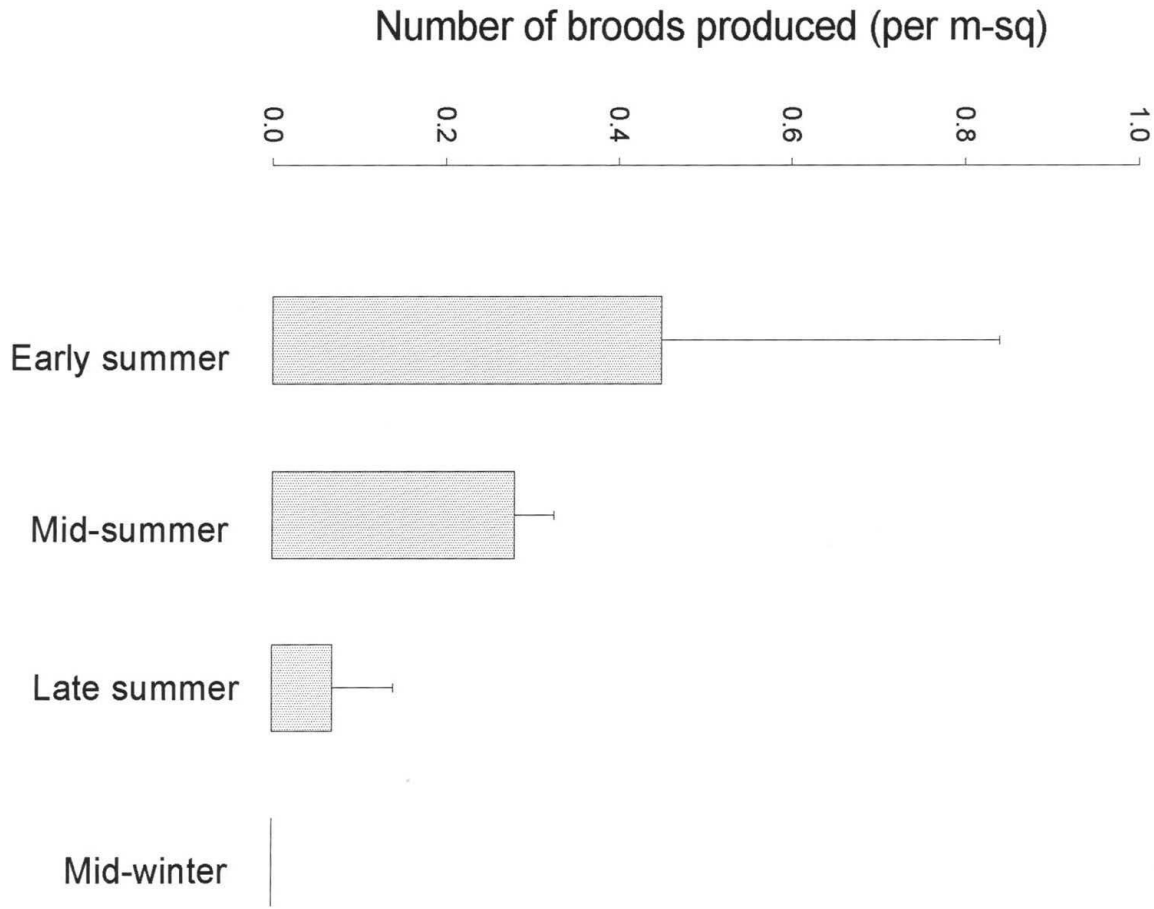

Number of broods produced (per m-sq)
0.0
0.2
0.4
0.6
0.8
1.0
Early summer
Mid-summer
Late summer
Mid-winter

Figure 4-9. Calibration of *Acanthochromis* brood-size estimates.

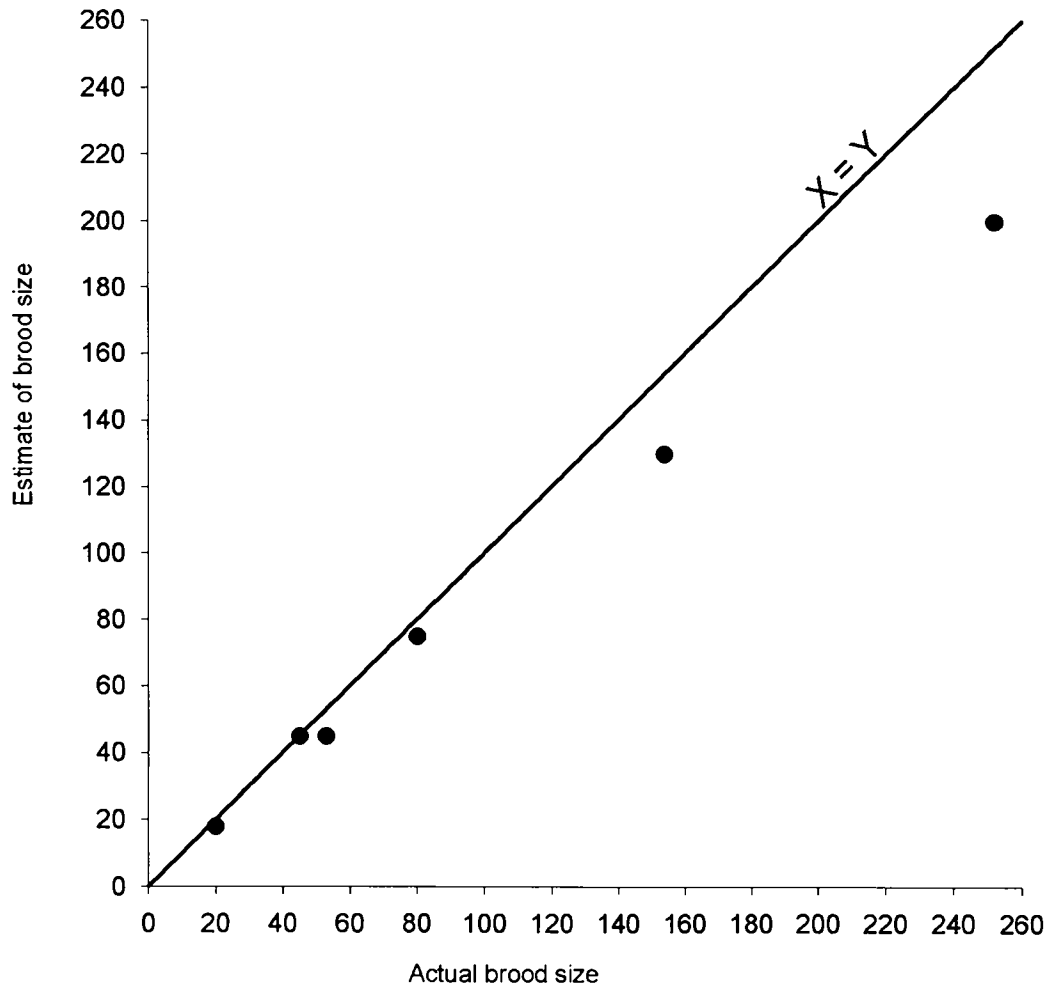
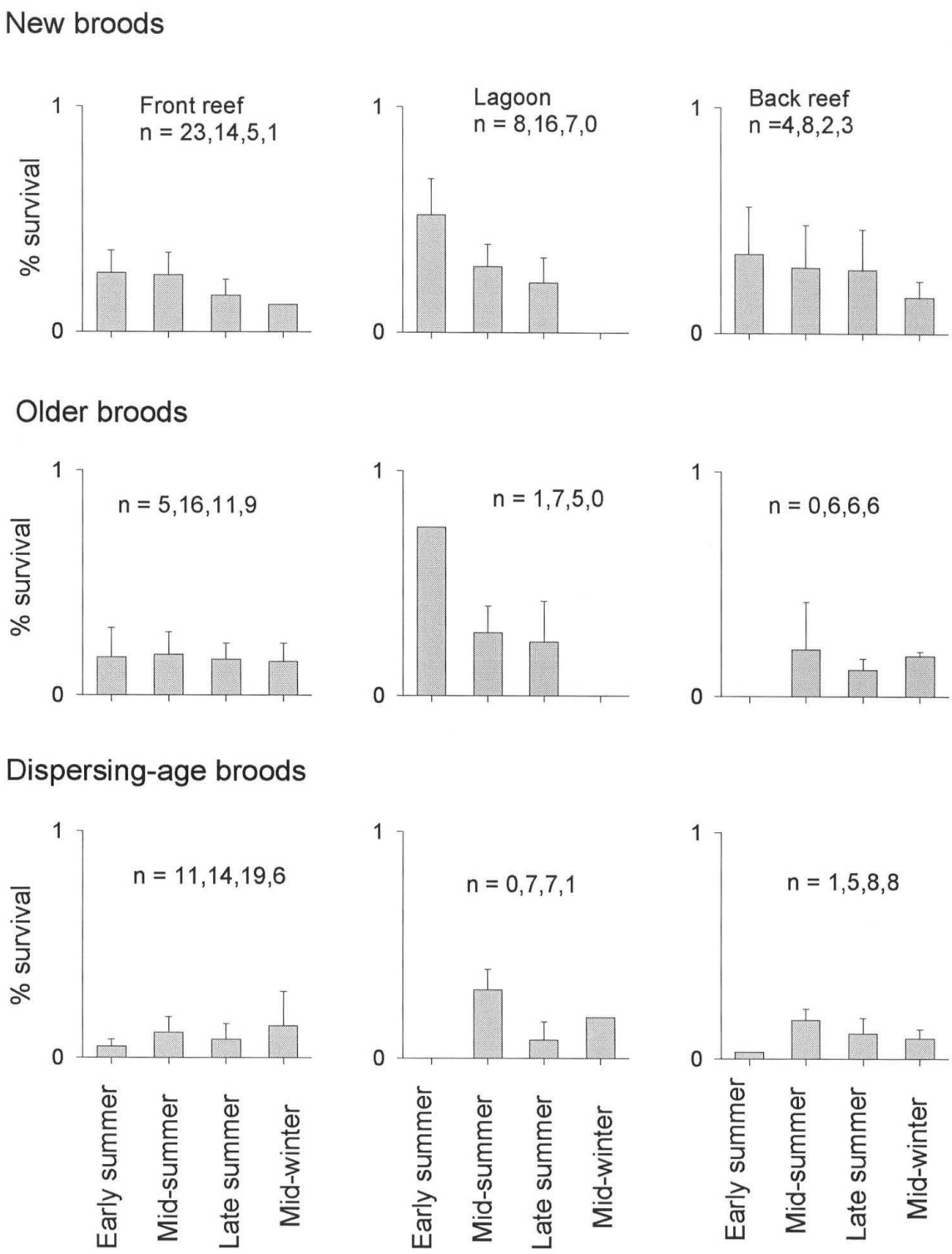

Estimate of brood size
260
240
220
200
180
160
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
180
200
220
240
260
Actual brood size
X = Y

Figure 4-10. Survivorship of *Acanthochromis* broods (means and S.E.) for each reef zone and season.


New broods
Front reef
n = 23,14,5,1
Lagoon
n = 8,16,7,0
Back reef
n =4,8,2,3
% survival
1
0
Older broods
n = 5,16,11,9
n = 1,7,5,0
n = 0,6,6,6
Dispersing-age broods
n = 11,14,19,6
n = 0,7,7,1
n = 1,5,8,8
Early summer
Mid-summer
Late summer
Mid-winter

Chapter Five

Habitat Effects on Growth and Developmental Rates of Juvenile *Acanthochromis*

Introduction

Rates of growth and development are fundamental traits of organisms. In many ways, the absolute limits and the short-term plasticity of these rates determine where early life stages of organisms can survive. While the general growth and developmental trajectory is set by genetics and physiological constraints, habitat differences can significantly affect these rates. For example, these differences might affect overall size- and age-structure and number of sexually-mature individuals in the population, as well as feeding behavior, choice of nesting site, sensory competence-at-age, or vulnerability to predation. On larger scales, consistent environmental differences can set up an "adaptive landscape" in which selection for optimal growth or developmental rates can occur.

Coral reefs exhibit distinct patterns of zonation (Myers, 1989). This zonation is obvious between exposed reefs, or those directly exposed to the wind-driven oceanic currents and waves, and lagoonal reefs, which are typically shallow and more protected from waves and currents. These two reef zones differ in various aspects of their physical, chemical, and biotic environment (Hamner et al, 1988; Gladstone and Westoby, 1988; Eckert, 1986; Leis, 1986; Beukers, 1996).

Growth rates and average sizes of fishes inhabiting lagoonal zones have often been reported to be lower than those in exposed-reef zones (Gladstone and Westoby, 1988; Thresher, 1985). It is unknown whether these differences are due to food limitation. Few studies have reported on the availability of planktonic food to fishes in different reef zones. It can be expected, however, that more oceanic plankton comes in contact with exposed reefs as winds and currents push oceanic waters onto the reefs, whereas oceanic plankton which

reaches protected lagoonal reefs must first pass across reef crest and reef flat habitats. Consequently, plankton levels are likely to be reduced as they pass through this "wall of mouths" into the lagoon (Hamner et al, 1988). If growth rates in lagoonal fish populations are lower due to limited plankton abundance, then increasing plankton (or other food) levels would increase growth rate. In high winds, wave height increases and might drive more oceanic water into lagoons, thereby temporarily increasing plankton levels. Turbulence induced by high winds may also resuspend detritus and organic sediments, releasing nutrients and stimulating in-situ plankton production.

Growth rate and abundance of planktivorous reef fishes have been correlated with current speed, often leading to the suggestion of a causal relationship (Hobson and Chess, 1978; Thresher, 1983). Several experimental studies have shown that growth rates and maturation of coral-reef fishes can be increased by supplemental feeding (Jones, 1986; Forrester, 1990; Eckert, 1985), while others found no effect of supplemental feeding (Robertson, 1981). This suggests that food-limitation may be variable among locations and times. A specific comparison of lagoon and exposed-reef habitats is lacking among these studies. In this study, growth rates of a site-attached reef fish living in lagoonal and exposed reef habitats is examined, and the prediction that strong winds increase growth rates in lagoon fish through increases in available food will be tested.

While growth rates are typically measured using length or weight, this measurement can mask important differences in allocation of energy resources among systems within individuals. For example, environmental differences can result in differential growth or developmental rates among systems, particularly in larval or juvenile stages which are still undergoing differentiation of tissues (Pankhurst, 1992). This difference in growth or developmental rate can have effects on age-specific competence; lowered competence and/or smaller size may increase vulnerability to predation. Therefore, an understanding of the relative allocation of increased

energy to different systems following changes in food availability during early life will further clarify effects of natural environmental variability on the early life histories of reef fishes.

One species of coral-reef fish is particularly well-suited to field studies of early growth and developmental rate responses. *Acanthochromis polyacanthus* occurs commonly in both lagoon and exposed reef zones, and because it broods its young from hatching for several months, sibling juveniles of known age can be repeatedly sampled from the same site (within meters) under varying treatments. This study uses brooded *Acanthochromis* juveniles to assess growth and developmental rates in lagoon and exposed reef habitats on Lizard Island.

Methods

Two experiments were conducted at Lizard Island, Great Barrier Reef. In the first experiment (October 1994) eight recently-hatched (Stage 1: within approximately 10 days of hatch) *Acanthochromis* broods were selected from sites in lagoon and exposed reef zones (Fig. 1-1). Using a small hand-net, a sample of 10 juveniles from each brood was collected for initial measurements. These juveniles were fixed immediately in 10% buffered-seawater formalin. Two replicate broods in each zone were fed ground pieces of two pilchards as a food supplement over a 20-30 min period every second day, for 14 days. As a control for disturbance, the other two broods in each zone were not fed, but visited and mildly disturbed (by a diver remaining close to the brood) for approximately the same period of time. After 14 days, a second collection of 10 individuals was made from each brood and fixed in 10% formalin.

The second experiment was conducted in January 1995 during a period when wind conditions changed from relatively calm (5-10 km/hr) to strong winds (20-30 km/hr) fairly rapidly. Forty-five broods were selected from lagoonal and exposed reef sites around the island (Fig. 1-1). An initial collection of 10 individuals was made from each brood, then each brood was resampled one or more times, over 3-5 day periods. No broods were fed in this experiment.

Daily wind conditions were estimated and recorded on site for the entire period for both experiments, then confirmed with regional weather reports recorded at the closest Bureau of Meteorology weather station (Cooktown). However this weather station is 200 km away from Lizard Island (Fig. 5-1).

Using an ocular micrometer under a dissecting scope, standard length (SL) and eye diameter (ED) of each juvenile collected was measured. Means and standard deviations were calculated for each sample for both measurements. Growth rates were calculated using the equation (Ld-Li)/d , where Ld= the length (either SL or ED) at day d after start, Li= the initial length, d= the number of days since initial collection.

Ossification rates were also estimated from collected specimens and the rates were used as an indicator of developmental rate. Two juveniles were haphazardly subsampled from brood collections made at the beginning and end of the calm-winds period and the strong-winds period, or from fed and unfed treatments in each reef zone. These fish was cleared-and-stained using techniques of Potthoff (1984) and examined for skeletal ossification. A sequence of easily-identifiable skeletal features were chosen in order to calculate the rate of ossification. These include (in approximate order of ossification): cleithrum, anterior portion of notochord, mandible, hypural plates, haemal and neural arches, pectoral base, 1st anal-spine pterygiophore, and all pterygiophores. Ossification rate for each treatment (fed-lagoon, unfed-lagoon, fed-exposed, unfed-exposed, calm-lagoon, strongwinds-lagoon, calm-exposed, strongwinds-exposed) was determined by regressing number of completely ossified features against SL.

For both experiments, growth and developmental rates were analyzed for differences between reef zones and wind-strength or feeding treatments. To test for differences, two-factor ANCOVAs were used with initial size as a covariate and reef-zone and wind-strength or feeding treatment as factors.

Results

The Effects of Supplemental Feeding and Reef Zone on Growth and Developmental Rates

In the October study, the winds were moderate (15-20 km/hr) through most of the experiment, but were variable from 0-30 km/hr. Initial sizes of juveniles ranged from 7.2-12.4 mm SL.

Among the size range of fish measured in the feeding experiment, initial SL had no effect on SL-growth rate (p=0.38, R=0.130) (Fig.5-2), and ANCOVA indicated no significant two-way or three-way interactions with growth. Therefore, growth rates were pooled for comparisons of feeding and zone factors. Growth rates for SL in this experiment ranged from .35 to .47 mm/day over the 14-day period. No significant differences in SL-growth rate were found among fed or unfed treatments, or between zones (Table 5-1a). Variance was higher in fed treatments than in unfed treatments in both zones (Exposed: $F_{1,3}$ = 46.89, p<0.02; Lagoon: $F_{1,3}$ = 8.96, p<0.10; Fig. 5-3). Because feeding did not appear to have any consistent effect beyond increasing variance, the analysis was rerun after pooling fed and unfed treatments. Zone differences were still not detectable at statistically significant levels (ANOVA $F_{1,6}$=2.38; p=0.17).

For measurements of ED-growth rate, initial SL had no statistically significant effect, although it explained >46% of the variance (p=0.062; R=0.467; Fig. 5-4). ANCOVA indicated no significant interactions with SL and therefore ED-growth rates were pooled and tested in a 2-factor ANOVA. No significant differences were found among fed or unfed treatments, or between zones (Table 5-1b; Fig. 5-5). ANOVA still did not detect differences among zones following pooling fed and unfed treatments (R=0.52; p=0.35).

Ossification rates were given by slopes of the regression of initial SL vs. ossification stage. Initial SL had a significant effect on the stage of ossification (Fig. 5-6). No significant

differences were detected between zones or feeding treatments (Table 5-1c). When feeding treatments were pooled, ANCOVA still did not detect significant differences among zones (Fig. 5-6).

The Effects of Wind Strength and Reef Zone on Growth and Developmental Rates

In the January study, winds were initially calm (5-10 km/hr) from 25 Dec to 2 Jan, then increased but were variable over the next few days, followed by 6 days of strong southeast winds (20- 35 km/hr) (Fig. 5-2). Initial length of fish in this study ranged from 5.0 to 15.8 mm SL.

Significant interactions between initial length and other factors were found, thus initial SL was kept as a covariate in the ANCOVA with zone and wind as factors (Table 5-2a). There was a significant effect of wind, and significant interactions between SL and wind, between wind and zone, and (borderline) between SL, wind, and zone (Table 5-2a). Several trends are suggested by plots of these data (Fig. 5-7): (1) over the size range of the juveniles examined, growth rates were highly variable and no strong overall effect of initial SL is apparent (among treatments, some slightly increase in SL-growth rate as initial size increases, and others decrease in SL-growth rate as initial size increases); (2) exposed-reef juveniles grew similarly in calm and strong winds; (3) lagoon juveniles in strong winds had generally higher growth rates than the other treatments, and (4) lagoon juveniles in calm winds had generally lower growth rates than the other treatments. Means and standard errors for wind/zone combinations are given in Fig. 5-8.

In the analysis of ED-growth rate, a significant interaction between initial SL and wind was found, therefore ANCOVA was used for further analysis between factors with initial SL as a covariate. The overall model indicated significant differences in ED-growth rate among treatments. A significant effect of wind was found, as well as a significant interaction between SL and wind (Table 5-2b). Trends in the data suggest that (1) again, there is no consistent

effect of initial SL on ED-growth rate; (2) lagoon juveniles in calm and strong winds had similar slopes, indicating a decreasing ED-growth rate with increasing SL; and (3) lagoon juveniles in calm conditions had a lower intercept than lagoon juveniles in strong winds, suggesting an overall lower ED-growth rate in these juveniles (Fig. 5-9). Ossification rates were analyzed using ANCOVA on stage data for juveniles at the beginning and end of the sample period, with SL as covariate and wind and zone as factors. Analysis of covariance detected a significant effect of SL, but no other significant differences in ossification rates were found among treatments (Table 5-2; Fig. 5-10).

Discussion

Currents around the Lizard Island region of the Great Barrier Reef are primarily wind-driven and respond rapidly to changes in wind patterns (Frith et al., 1986). Increasing the current, and thus the water mass that passes over a reef, must increase the amount of plankton available to planktivores. Furthermore, increasing winds may increase plankton levels through resuspension of sediments; higher levels of nutrients made available in this way could increase localized plankton production. The important question, however, is whether this increase in plankton is biologically significant to reef populations. This study found that changes in growth rates in juvenile *Acanthochromis* correlated with rapidly changing wind conditions. Although this experiment did not control for potential effects of other temporal influences, for example lunar effects, the results suggest that lagoonal juveniles may be able to rapidly increase their somatic growth rate after a short period of high winds. Further, lagoonal juveniles in calm conditions tended to grow more slowly than exposed-reef juveniles, suggesting that food-limitation may occur in this situation. These results support the idea that, if bursts of plankton are carried into the lagoon by increases in wind-driven waves and currents, *in situ* growth rates of planktivorous juvenile fishes can change.

The October feeding study attempted to experimentally increase food levels in lagoon and exposed-reef zones. These experiments could not support the hypothesis of food limitation as the cause of lower growth rates in the lagoon; differences between zones and feeding treatments were not able to be detected in this experiment. For future studies, increased sample sizes and methods which could provide more frequent feeding with less disturbance would increase the ability to detect any growth rate differences and potentially reduce experimental error in the results.

In the January experiment, when winds were strong, growth was significantly greater in lagoon fish, suggesting they may be able to compensate for previous energetic deprivation by growing particularly quickly. Eye growth also increased during strong winds, though variability within treatments was higher and no zone effects were found. The somatic growth rate seemed to be more responsive in general, while eye growth and ossification rate were more constant. Previous studies suggest that somatic growth and eye growth (and development) may be dissociated during ontogeny (Pankhurst, 1992). The cause and effects of these different patterns of growth and development within an individual could have implications for understanding and predicting habitat or population-level patterns, and the direction of selection. Further studies are needed.

Table 5-1. Results of ANOVA for SL-growth rates, ED-growth rates, and ossification rates for treatments in the October 1994 feeding experiment.

A) SL-growth rate

source	df	SS	F	p
Food	1	0.0021	3.05	0.1559
Zone	1	0.00026	0.8	0.5720
Food*Zone	1	0.0023	3.31	0.1428
Error	4	0.0028		

B) ED-growth rate

source	df	SS	F	p
Food	1	0.000012	2.43	0.1941
Zone	1	0.0000012	0.24	0.6511
Food*Zone	1	0.0000099	1.96	0.2338
Error	4	0.0000202		

C) Ossification rate

source	df	SS	F	p
SL	1	136.62	25.52	0.0010 *
Zone	1	3.57	0.67	0.4539
SL*Zone	1	6.85	1.28	0.2908
Food	1	9.65	1.80	0.1758
SL*Food	1	1.50	0.28	0.6106
Food*Zone	1	12.29	2.30	0.1682
SL*Zone*Food	1	8.81	1.65	0.2354
Error	8			

Table 5-2. Results of ANCOVA for SL-growth rates, ED-growth rates and ossification rates for *Acanthochromis* juveniles in the January 1995 experiment.

A) SL-growth rate

source	df	SS	F	p
SL	1	0.028	2.82	0.1048
Wind	1	0.109	11.09	0.0026 *
SL*Wind	1	0.106	10.79	0.0029 *
Zone	1	0.007	0.68	0.4177
SL*Zone	1	0.0048	0.49	0.4898
Wind*Zone	1	0.046	4.73	0.0390 *
SL*Wind*Zone	2	0.041	4.16	0.0516
Error	26	0.255		

B) ED-growth rate

source	df	SS	F	p
SL	1	0.00004	.28	0.6021
Wind	1	0.00068	4.7	0.0395 *
SL*Wind	1	0.00067	4.63	0.0409 *
Zone	1	0.00004	0.27	0.6056
SL*Zone	1	0.00006	0.41	0.5259
Wind*Zone	1	0.00021	1.47	0.2367
SL*Wind*Zone	1	0.000148	1.02	0.3210
Error	26	0.00376		

C) Ossification rate

source	df	SS	F	p
SL	1	42.93	52.23	0.0001 *
Wind	1	0.328	0.40	0.1761
SL*Wind	1	1.364	1.66	0.2186
Zone	1	0.328	0.40	0.5376
SL*Zone	1	0.327	0.40	0.5382
Wind*Zone	1	0.380	0.46	0.5079
SL*Wind*Zone	1	0.174	0.21	0.6526
Error	14	11.51		

Figure 5-1. Wind conditions in the Lizard Island region during the study period.

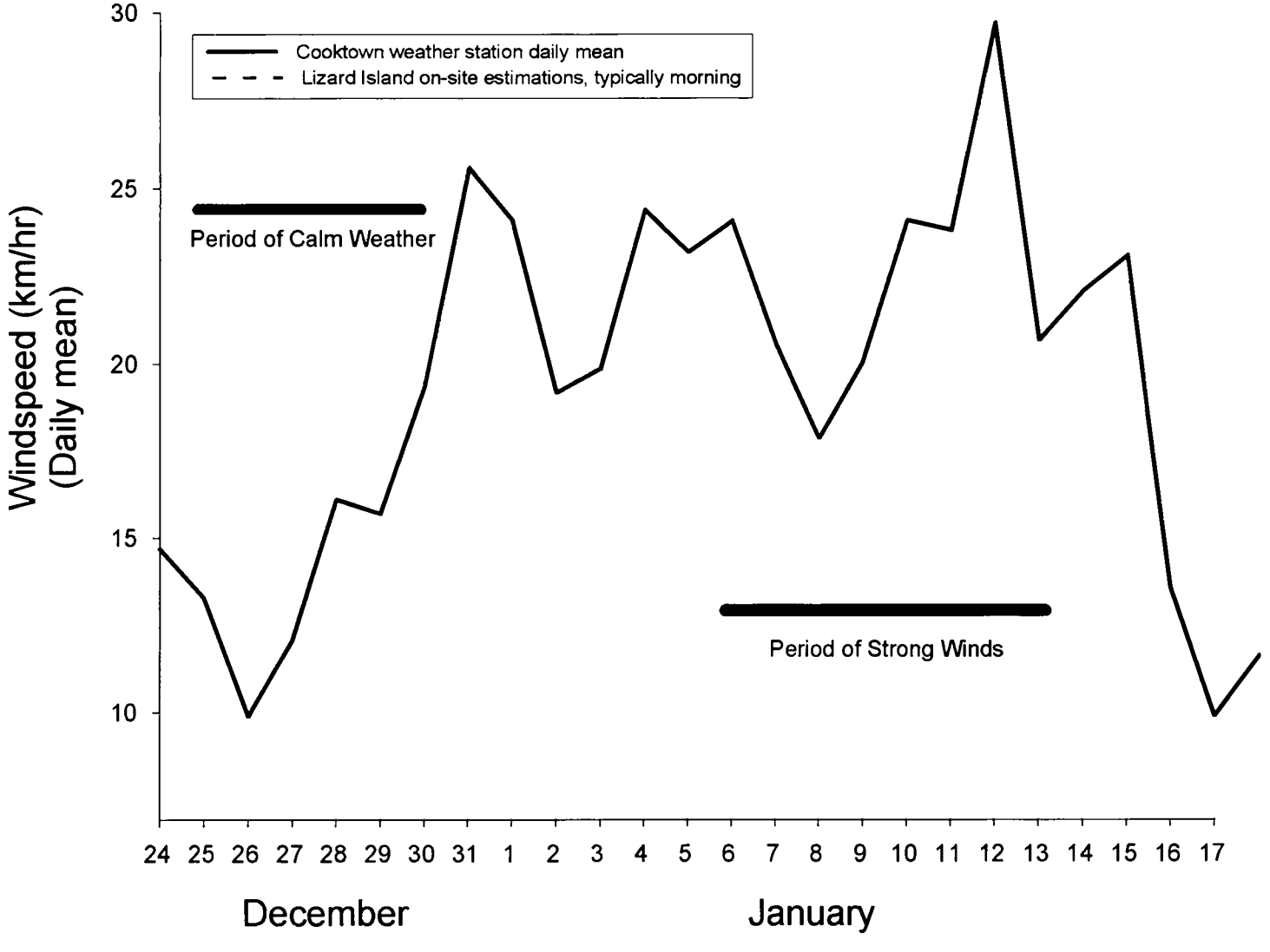

Cooktown weather station daily mean
Lizard Island on-site estimations, typically morning
Period of Calm Weather
Period of Strong Winds
Windspeed (km/hr)
(Daily mean)
30
25
20
15
10
24 25 26 27 28 29 30 31 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
December
January

Figure 5-2. Growth rates (mm/day) in standard length (SL) for juvenile *Acanthochromis*, plotted against initial size, for each treatment in the October experiment. Growth rates were determined by differences between means of juveniles sampled at the beginning and ending of the treatment period, divided by the number of days.

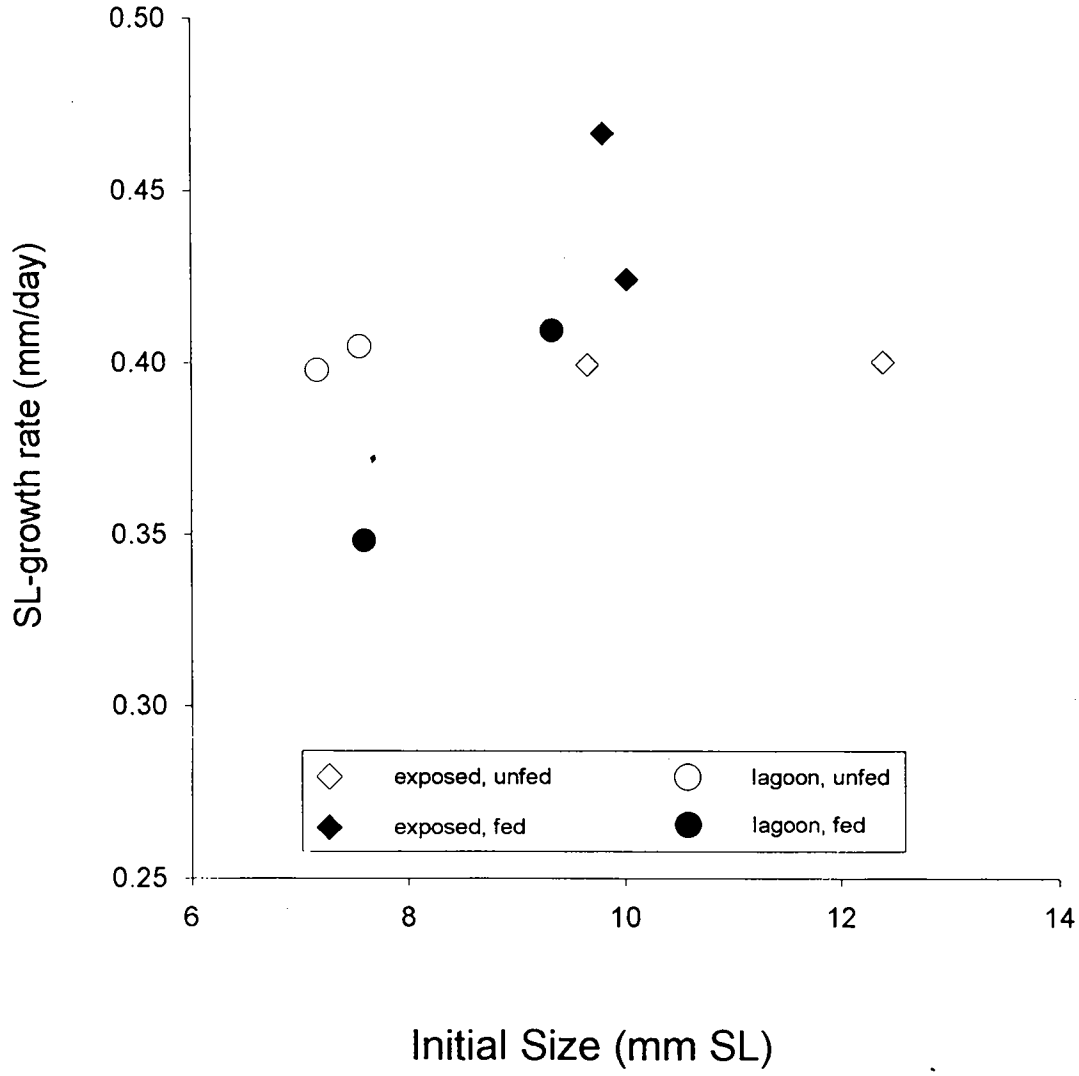

0.50
0.45
0.40
0.35
0.30
0.25
SL-growth rate (mm/day)
6
8
10
12
14
Initial Size (mm SL)
exposed, unfed
lagoon, unfed
exposed, fed
lagoon, fed

Figure 5-3. Standard length (SL) growth rates (mm/day) for *Acanthochromis* juveniles in each feeding treatment in each reef-zone during the October 1994 experiment.

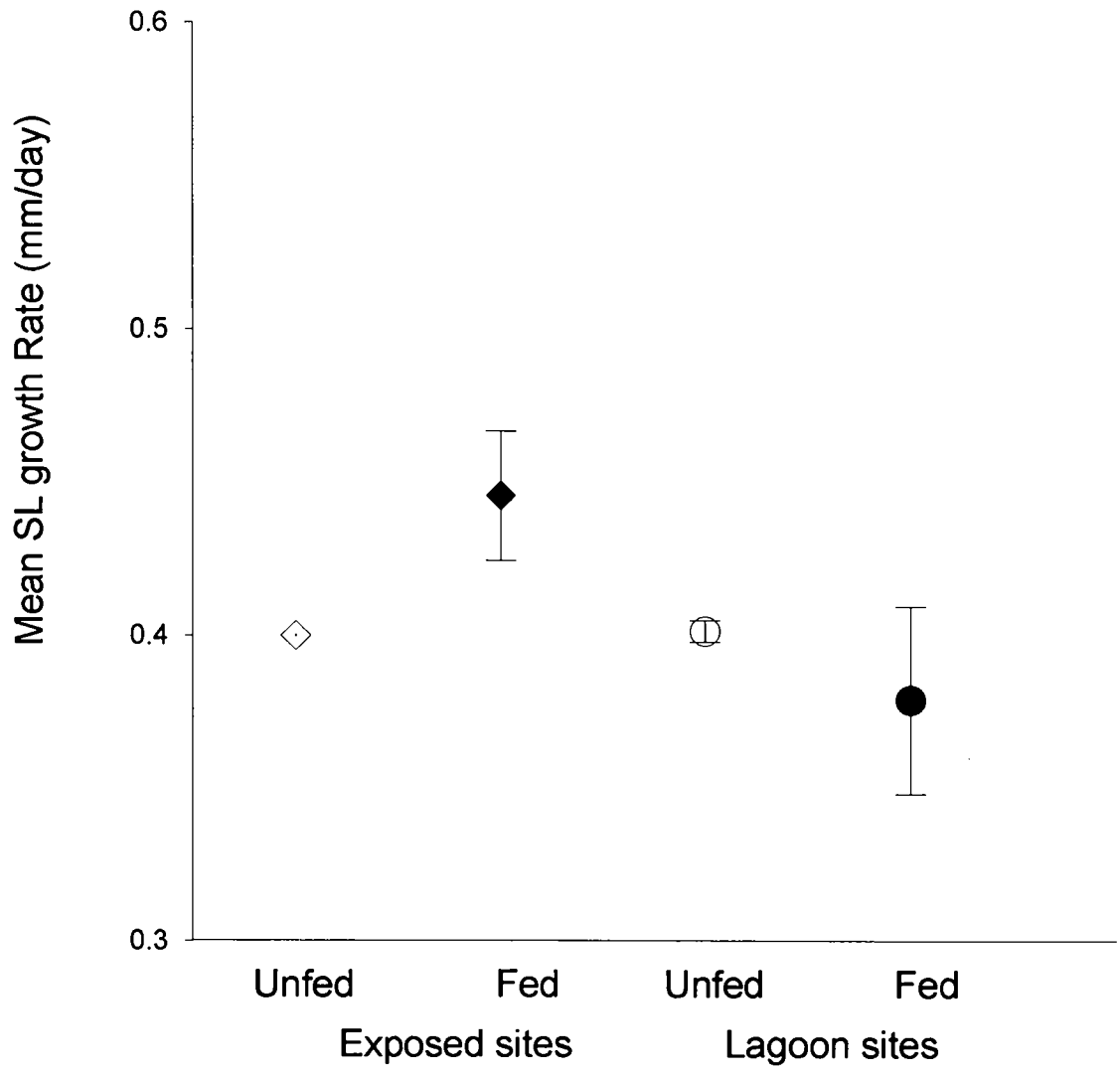

Mean SL growth Rate (mm/day)
0.6
0.5
0.4
0.3
Unfed
Fed
Unfed
Fed
Exposed sites
Lagoon sites

Figure 5-4. Growth rates (mm/day) in eye diameter (ED) for juvenile *Acanthochromis*, plotted against initial size, for each treatment in the October experiment. Growth rates were determined by differences between means of juveniles sampled at the beginning and ending of the treatment period, divided by the number of days.

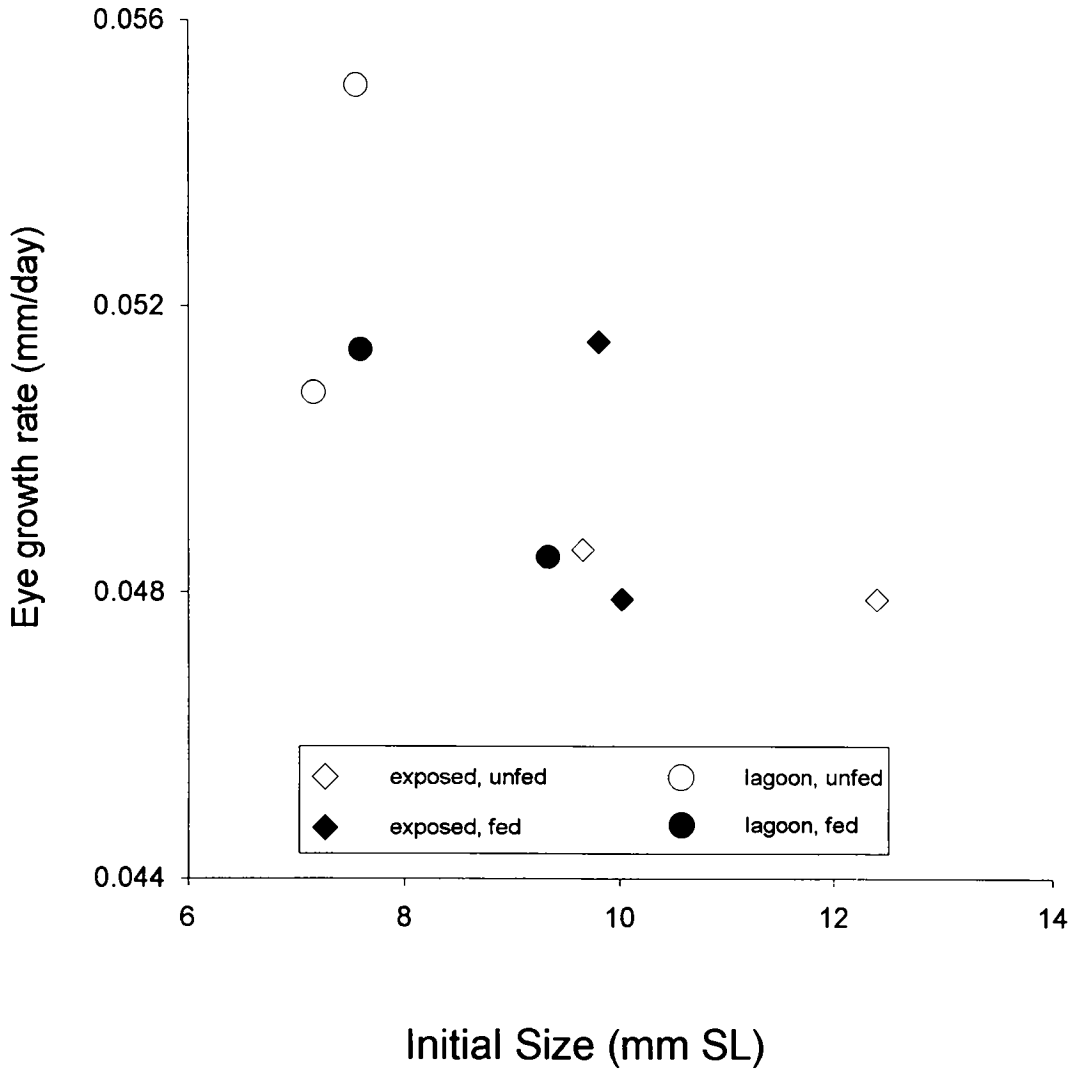

0.056
0.052
0.048
0.044
Eye growth rate (mm/day)
6
8
10
12
14
Initial Size (mm SL)
exposed, unfed
lagoon, unfed
exposed, fed
lagoon, fed

Figure 5-5. Eye-diameter (ED) growth rates (mm/day) for *Acanthochromis* juveniles in each feeding treatment in each reef zone during October 1994 experiment.

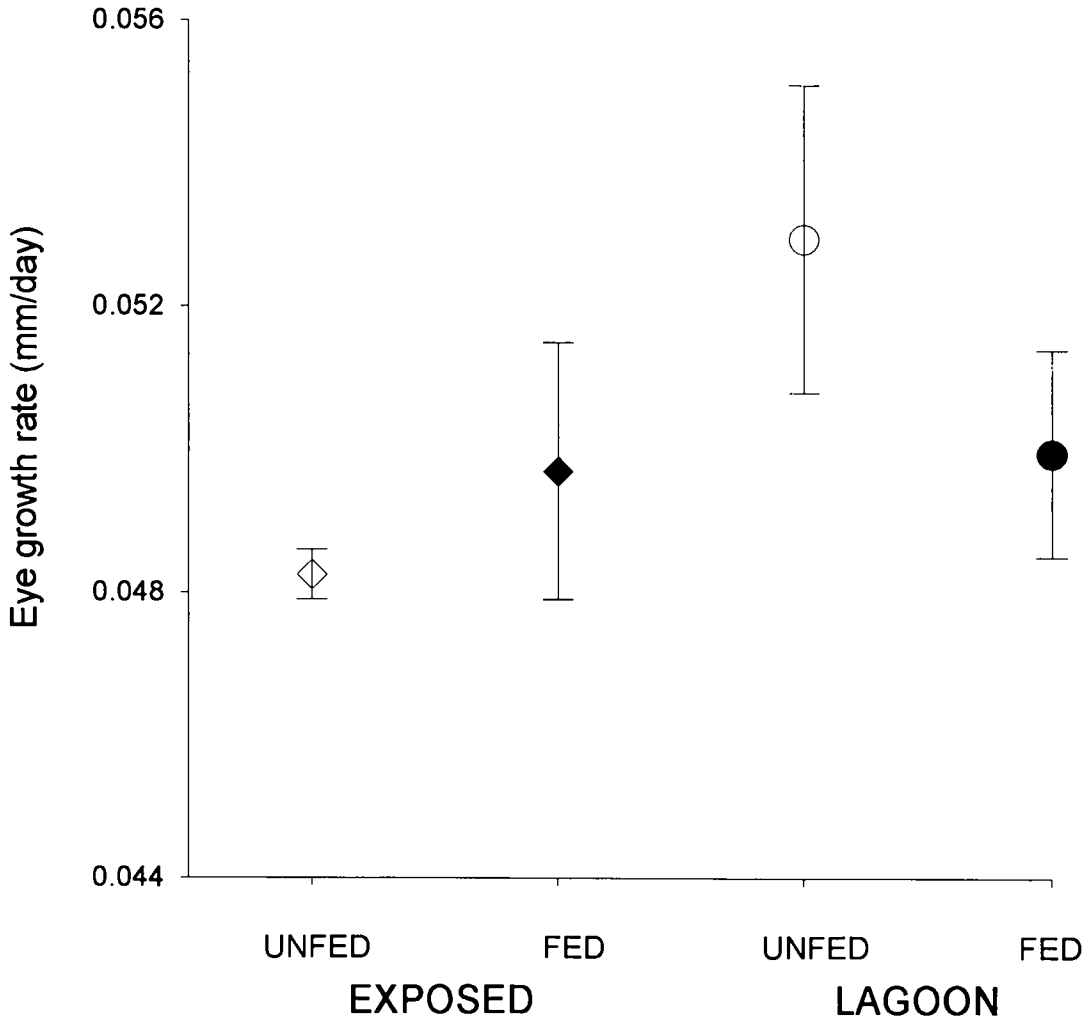

0.056
0.052
0.048
0.044
Eye growth rate (mm/day)
UNFED
FED
UNFED
FED
EXPOSED
LAGOON

Figure 5-6. Ossification rates for *Acanthochromis* juveniles in each treatment during the October 1994 experiment. Y-axis is ossification stage (number of ossified skeletal features) and X-axis is standard length (mm).

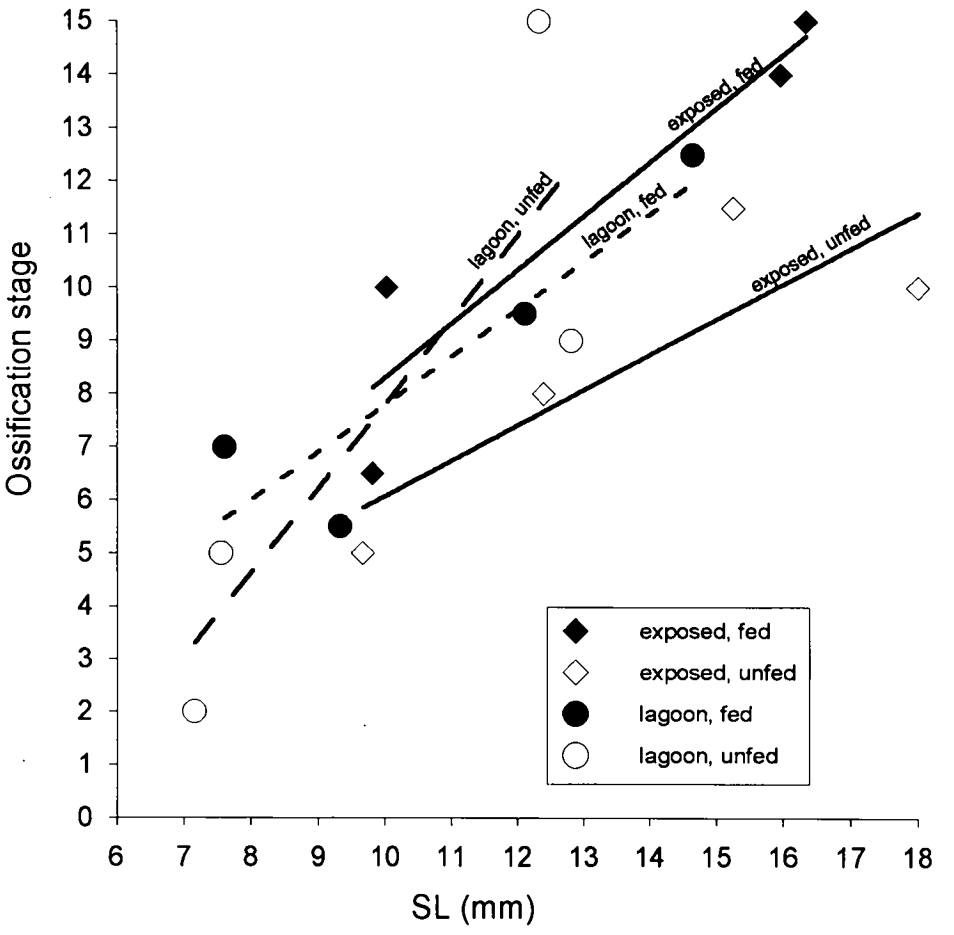

Ossification stage
SL (mm)
exposed, fed
lagoon, unfed
lagoon, fed
exposed, unfed
exposed, fed
exposed, unfed
lagoon, fed
lagoon, unfed

Figure 5-7. Growth rates (mm/day) in standard length (SL) for juvenile *Acanthochromis*, plotted against initial size, for each treatment (wind, reef zone) in the January experiment. Growth rates were determined by differences between means of juveniles sampled at beginning and ending of treatment period, divided by number of days.

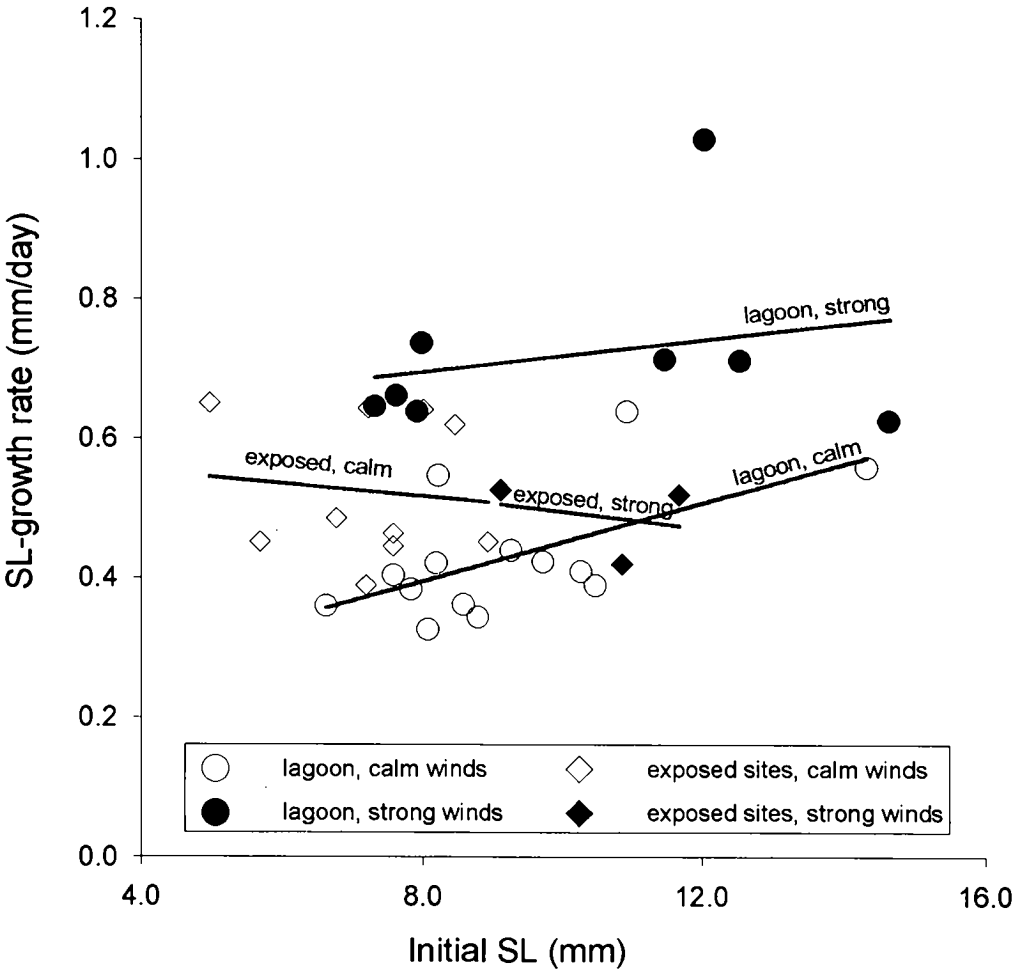

1.2
1.0
0.8
0.6
0.4
0.2
0.0
SL-growth rate (mm/day)
4.0
8.0
12.0
16.0
Initial SL (mm)
lagoon, strong
exposed, calm
exposed, strong
lagoon, calm
lagoon, calm winds
lagoon, strong winds
exposed sites, calm winds
exposed sites, strong winds

Figure 5-8. Mean SL-growth rates of *Acanthochromis* juveniles in each treatment during the January 1995 experiment.

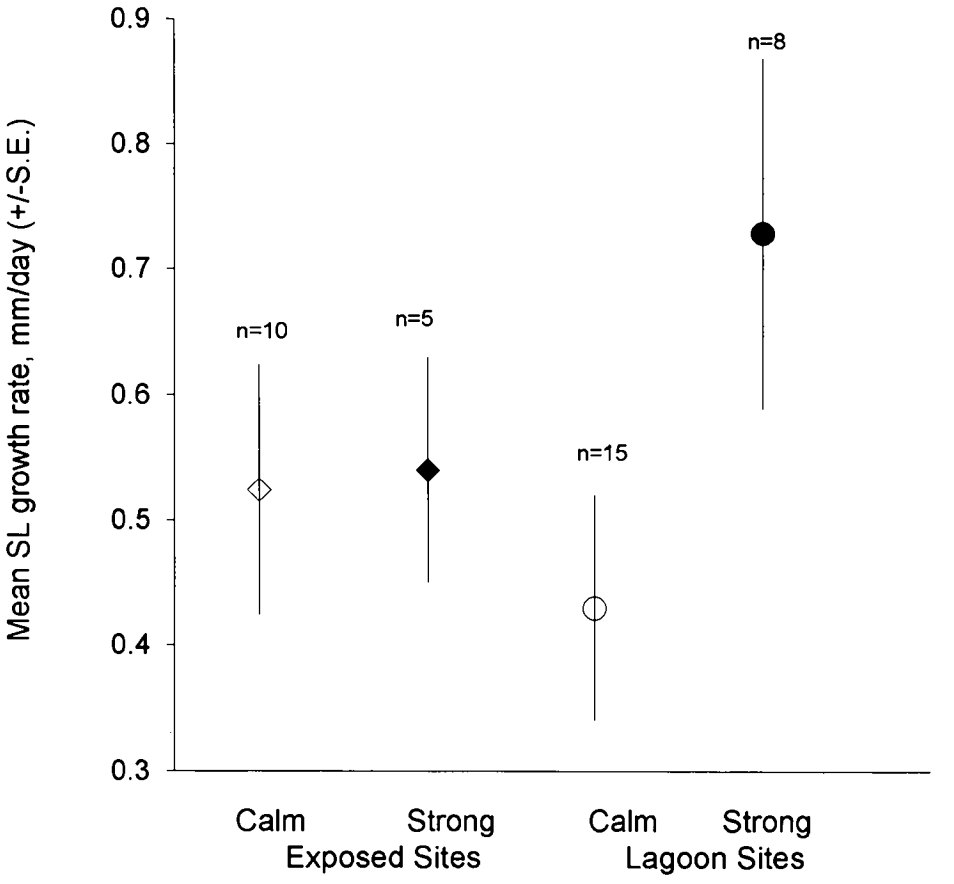

Mean SL growth rate, mm/day (+/-S.E.)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
n=10
n=5
n=15
n=8
Calm
Strong
Calm
Strong
Exposed Sites
Lagoon Sites

Figure 5-9. ED-growth rates of *Acanthochromis* juveniles plotted against initial SL in each treatment (wind, reef zone) during the January 1995 experiment.

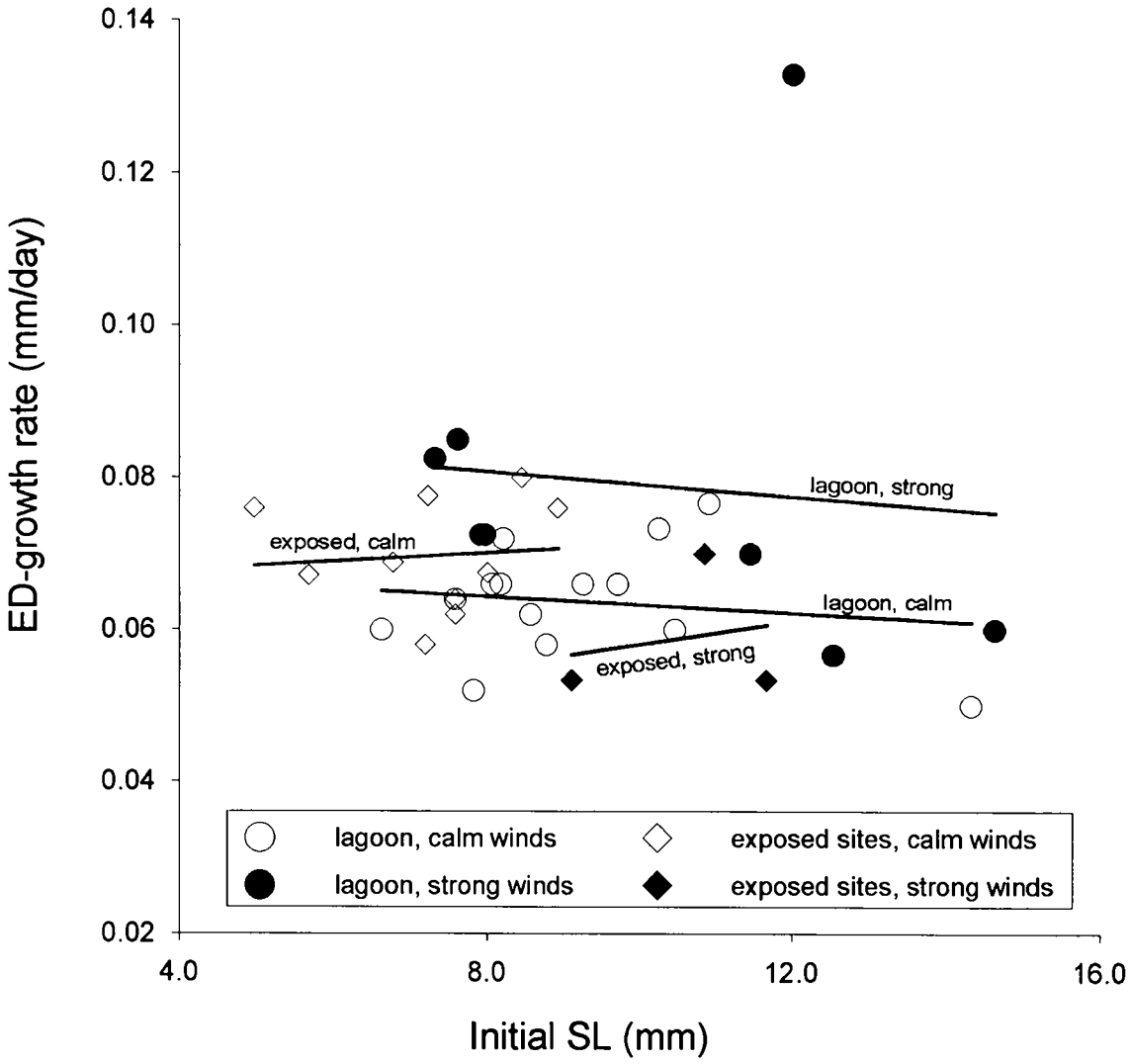
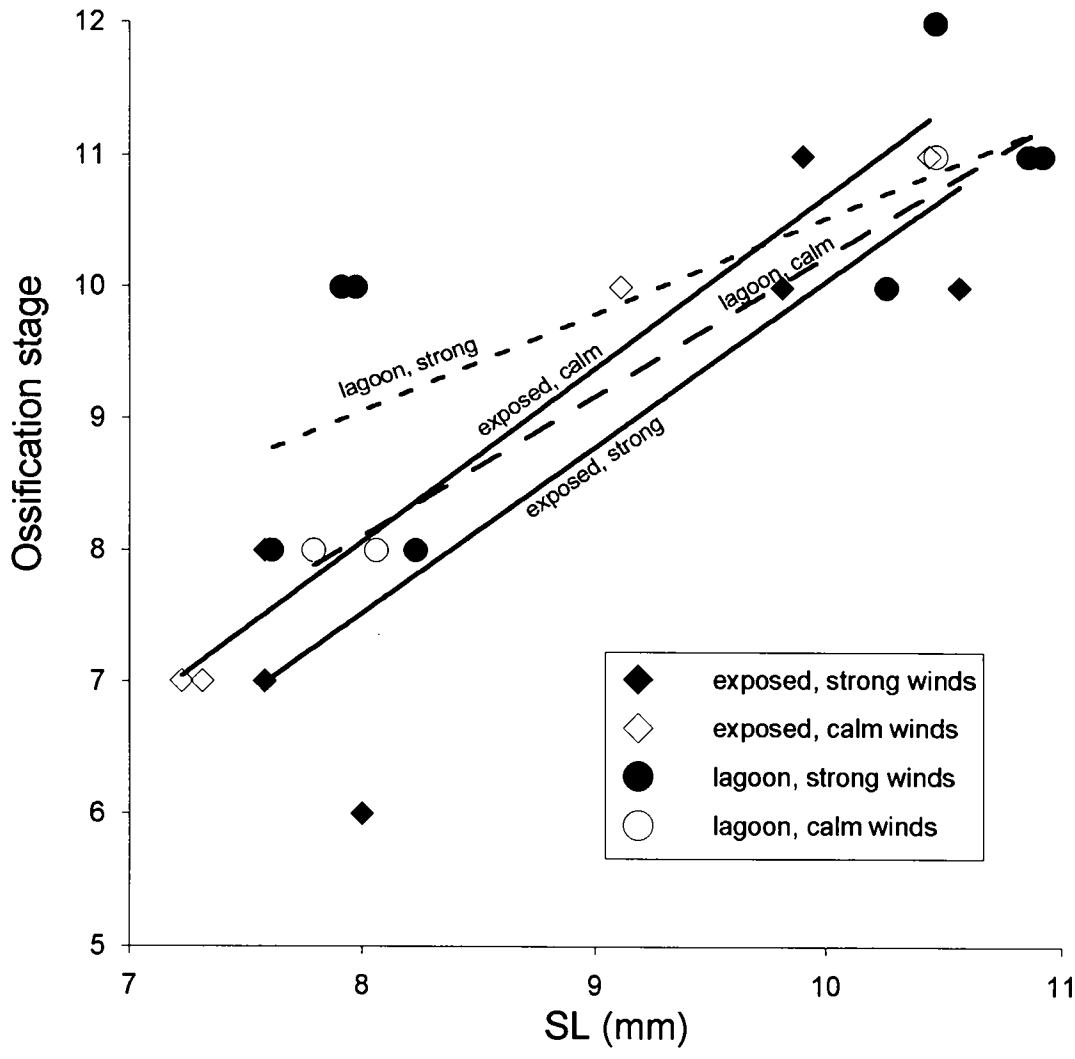

0.14
0.12
0.10
0.08
0.06
0.04
0.02
ED-growth rate (mm/day)
4.0
8.0
12.0
16.0
Initial SL (mm)
lagoon, strong
exposed, calm
lagoon, calm
exposed, strong
lagoon, calm winds
lagoon, strong winds
exposed sites, calm winds
exposed sites, strong winds

Figure 5-10. Ossification rate of Acanthochromis juveniles in each treatment during the January 1995 experiment. Y-axis is ossification stage (number of ossified skeletal features) and X-axis is standard length (mm).


Ossification stage
SL (mm)
12
11
10
9
8
7
6
5
7
8
9
10
11
lagoon, strong
exposed, calm
lagoon, calm
exposed, strong
exposed, strong winds
exposed, calm winds
lagoon, strong winds
lagoon, calm winds

Chapter Six

General Discussion

The studies presented in this thesis attempt to advance our understanding of some of the influences of the coral-reef environment on the life cycle and demographic parameters of the damselfish *Acanthochromis polyacanthus*. In this chapter, the results from these studies are summarized and discussed in the context of current thoughts about the ecology and evolution of coral-reef fishes and other taxa with complex life histories.

The *Acanthochromis* Life History

Acanthochromis is unique among the 300+ species of coral reef damselfishes, and very unusual among all marine teleost fishes, in that the pelagic larval stage has been eliminated from its life cycle. Along with this rare life-history, *Acanthochromis* has many highly divergent species-specific traits, mainly concentrated in the early life stages. These can be summarized briefly. Relative to other damselfishes, the egg stage of *Acanthochromis* lasts much longer, the eggs are much larger, and the young are consequently much larger and more developed at hatching (Ch. 2). The hatching time-of-day is also unusual: *Acanthochromis* offspring hatch during the morning or midday rather than at dusk hatching as do all other damselfishes (Ch.2). Parental care is extended far beyond that of confamilial species. Parental behaviors include guarding against predators and conspecific intrusions, and herding the juveniles, which has the function of maintaining brood integrity. Parents probably use olfactory cues to identify their young (Ch. 3). Specialized juvenile behaviors include, most notably, "glancing" off the sides of the parents and ingesting mucus, a behavior which does not likely contribute much nutrition to the juveniles (Ch. 3). Brooding lasts for months, a long time when compared with either its

damselfish relatives or the freshwater cichlid species which exhibit similar brooding behaviors (Ch. 2, 3; Noakes, 1979; Thresher, 1985; Nakazono, 1993). The "fledging" of *Acanthochromis* juveniles from the brooding site occurs at a size and age which is much greater than the size and age of the settlers of its damselfish relatives (Ch. 2, 4; Robertson, 1973, Thresher, 1983) . Although dispersal from the immediate nesting area is clearly initiated by the parents aggressively chasing their offspring, dispersal from the surrounding area was observed to be slow and gradual along the contiguous reefs of Lizard Island (Ch. 2). Several months elapsed between fledging and sexual maturity (Ch. 2). During this subadult stage, *Acanthochromis* appear to aggregate and/or move along the reef singly (Ch. 2). At approximately 9 months of age, *Acanthochromis* form pairs, with the male courting the female in a similar manner to that described for other pomacentrids (Ch. 2; Thresher, 1984). Mates of similar size and appearance are selected (Ch. 2; Planes and Doherty, submitted a, b). Eggs are spawned in prepared nests relatively deep in caves in the reef (Robertson, 1973; Thresher, 1983).

Whether or not the *Acanthochromis* life-history is a relict of the life-histories of ancestors or a relatively recent and highly-derived one, it is significant that there are no intermediate forms, such as species that brood their larvae for only a few days. This implies that *Acanthochromis* is the sole survivor of a life-history style from which other forms are now extinct. The comparative studies of this thesis have helped to clarify some of the environmental and ancestral influences which maintain and probably produced this atypical life history. For example, many of these characteristics described above suggest that predation was important as a selective factor acting on the survival of early life stages on the reef.

Predation as a Driving Force in the Evolution of Coral-Reef Fish Life Histories

Of the three hypotheses for the prevalence of pelagic larvae in early life histories of coral-reef fishes (see Ch. 1), the anti-predation hypothesis is most supported by the characteristics of *Acanthochromis*. Many of the unique traits of *Acanthochromis* clearly function to reduce mortality due to predation. For example, nesting deep in caves may serve as a deterrent to predation, at least by mobile fish predators. The large and relatively competent hatchlings suggest an advantage either to producing large eggs or having a long embryonic developmental period. Although there is large variation in sizes at settlement among reef fishes, most reef fish settle roughly between 8 and 25 mm (from "largest presettlement specimens observed" in each reef-fish family, *in* Leis and Rennis, 1983). While the upper size limit at which settlement occurs is quite variable (up to 200 mm SL), there appears to be a more-defined lower size limit for settlement of about 5 mm SL. A newly-hatched *Acanthochromis* is slightly over 5 mm SL, suggesting it may be at the minimum possible size for a reef-dwelling fish. Size refuges from predation have been suggested for numerous systems, including tropical fishes and invertebrates (Pepin et al, 1992; Anderson, 1988). Parental care is likely to be important in the case of *Acanthochromis* for allowing such small and relatively undeveloped settlers to survive on the reef.

The clear necessity of parental care in *Acanthochromis* further supports the idea that predation is an important selective force in early life histories. *Acanthochromis* juveniles without parents are eaten by predators very quickly (Nakazono, 1993; pers. obs.). The intensity and complexity of parental care and parent/juvenile interactions are also indicative of an environment with high predation (Clutton-Brock, 1991). Parents guard and tend juveniles until they are quite old. In fact, they are much older and larger at the termination of parental care than settlers of other damselfishes. However, guarding of

Acanthochromis juveniles is most intense during stages 1 and 2 (Ch. 3), and a stage-2 juvenile is roughly equivalent to the size and age of a settler of other damselfish species (approx. 12mm SL; 30 days old). Furthermore, parental care increases in reef zones where predators are more abundant (Ch. 3), and mortality rates are greater in these same areas (Ch. 4). Differences in these vital rates suggest that predation significantly influences population dynamics and could be a strong selective pressure causing microevolutionary change in reef fish populations.

The overall conclusion derived from the many unique (among damselfishes) predator-avoidance strategies of *Acanthochromis* must therefore support the anti-predation hypothesis for the maintenance of a pelagic larval stage in coral reef fishes. Furthermore, other characteristics of the species show evidence *against* the dispersal hypothesis. *Acanthochromis* demonstrates that the lack of a dispersive pelagic larval stage does not necessarily fatally restrict a species' geographic range and doom the species to a quick extinction. While it is now clear that gene flow is much lower between *Acanthochromis* populations than between populations of other damselfish species (Doherty et al, 1995; Planes, 1995), gene flow appears to be high enough for *Acanthochromis* to occur over a fairly wide geographic range. This range contains many reefs separated by 100s of kilometers and relatively deep water. The mode of dispersal over such barriers is unknown, but the scale and interval of dispersal may be significant. To achieve a widespread distribution, dispersal may not have to occur in every clutch, but it may be enough that juveniles occasionally move across large areas of open water. Occasionally, *Acanthochromis* juveniles have been captured in midwater light-trap samples typically used for attracting pelagic presettlement larvae of reef fishes (P. Doherty, Australian Institute of Marine Science, pers. comm.).

Demographic Responses

Other variations in demographic parameters were found between reef zones, seasons, and as an interaction between wind-strength and reef zone. These variations among local environments provide a measure of the environmental pressures and their demographic correlates.

Acanthochromis produced more broods early in the spawning season (Oct-Jan). In these same seasons, survival (brood size of later-stage juveniles) was greater. If this pattern is shown to be consistent through time, it suggests that seasonal variation in spawning could be influenced by differential reproductive success. In contrast, *Acanthochromis* produced more broods in reef zones in which juvenile survival was lower. On the exposed reef-zone of Lizard Island, juvenile mortality rate was higher, and parental care effort was more intense. This zone is also where predators of *Acanthochromis* juveniles are in higher densities (Beukers, 1996; B. Stewart and C. Syms, unpubl. data). Thus, the choice of nesting site (at least at the spatial scale of reef zone) does not seem to be influenced by juvenile survival rate. Other factors varied between zones and may provide explanation for this unusual result. Growth rate was typically greater in exposed reef-zones, and adult size was generally greater. Exposed zones typically have more available plankton than leeward (e.g. lagoonal) areas (Hamner et al., 1988). Thus the advantage of growing faster in exposed zones (and possibly reaching reproductive maturity faster) may offset the greater average mortality rate in these areas.

These patterns of demographic response indicate some of the trade-offs and environmental variables which affect the ecology of *Acanthochromis*. The mechanisms for changes in populations, and eventual evolution at higher taxonomic levels, begin with shifts in existing traits and parameter values. These subtle shifts in physiology, e.g. delay in production of a hormone signal, or increasing the rate of differentiation of an organ, may

be produced by environmental variation, be selectively advantageous, and become more frequent under certain conditions. Such microevolutionary changes may become fixed in populations as the processes which promote speciation occur (e.g. restricted gene flow and isolation). It seems logical that small changes in morphology and life-history are not as likely to be eliminated from populations as are large ones. One sees the evidence of this in nature: closely-related species usually have similar life-histories. Major differences in life history traits seem to occur only in exceptional circumstances. Is *Acanthochromis* an exception?

History and Heterochrony: a Potent Combination For Major Shifts in Life-History Traits

Many of the unusual traits of *Acanthochromis* appear to be extensions of traits already existing in the pomacentrid family rather than novel structures and behaviors. Some of the traits that do not occur in the pomacentrids are shared uniquely with the Cichlidae, a freshwater family which seems likely, by current systematic analysis, to share a fairly close phylogenetic link with pomacentrids (Kaufman and Liem, 1982; Stiassny and Jensen, 1991). These historic links suggest that the pomacentrid family may have been more likely than other lineages to develop a life-history such as that of *Acanthochromis'*. The only way to test such an hypothesis is through the comparative method, which is to examine independent lineages and correlate the conditions under which a similar life-history has appeared (Harvey and Pagel, 1991).

The translation from genotype to phenotype is made through developmental processes. The control and sequence of developmental processes is, like any other trait, both inherited and subject to change in response to ecological pressures. Many of the major differences in the *Acanthochromis* life-history are related to the early developing stages, and appear to be extensions or modifications of traits already present in some of their relatives. All pomacentrids and most cichlids lay demersal eggs and protect them;

Acanthochromis extends this protection into the juvenile stage. Compared with other pomacentrids, the egg-stage is extended and the size of the eggs is enlarged. The number of vertebrae and dorsal-fin spines are increased. All these traits suggest that the same sequences of morphological and behavioral development are used, but they are extended through time or in magnitude.

Changes in developmental sequences are called heterochrony, of which there are several types (change in onset, rate, or termination). Heterochrony is a broad concept which can be useful in explaining patterns of development, growth, allometry, scaling, and functional adaptation (Hall, 1992). Invoking a specific type of heterochrony is only possible when one knows the condition of the ancestor relative to the descendent (Hall, 1992). The lack of knowledge of the phylogeny of the Pomacentridae makes it impossible to determine which direction the change has occurred in the family. One possibility for the evolutionary mechanism for the traits observed in *Acanthochromis* relative to other damselfishes is "hypermorphy", or the extending of characteristics beyond that of the ancestor (McKinney and McNamara, 1991).

Hypermorphy, increased parental care, and increased offspring size are all typically associated with unpredictable environments and with high mortality rates (Endler, 1994; Clutton-Brock, 1991; McKinney and McNamara, 1991; Gould, 1977). By most accounts, coral reefs fit this description well on scales relevant to fishes (Doherty 1980, 1994; Eckert, 1987). Thus, the extensions of characteristics seen in the *Acanthochromis* life history (increased parental care, larger eggs, increased meristics) are what might be expected according to the general environment-phenotype correlation found in other systems.

Predation-directed heterochronies therefore seem likely to affect the evolution of life histories (and other phenotypic traits): they are the most commonly described developmental heterochronies in the literature (review in McKinney and McNamara, 1991;

Bell, 1988). Other studies of early life history traits suggest that heterochronic changes in one trait can affect the direction of changes in others.

In this study, I found evidence of a trade-off between growth rates and developmental rates, and an interaction of these rates with the durations of early life history stages of damselfishes. Other studies of fishes and amphibians with complex life histories also have reported this relationship. Because growth rate and developmental rate can be affected by environmental conditions, and these rates affect timing of stage transitions, predictions may be possible about the responses of these traits within the system.

Trade-offs and the Prediction of the Timing of Stage Transitions

The Werner (1986) model predicts that in complex life cycles, the time spent in a particular stage will evolve to minimize risk in that stage: the mortality/growth ratio is minimized. The model presented in Ch. 6 is based on these ideas and is clearly testable at each link. For example, one could make predictions for the timing of *Acanthochromis* life-history transitions (hatch/settlement) in other environments. In a reef environment with lower predation pressure, the M/G ratio would theoretically decrease. As a consequence (assuming equal growth rates), one might expect hatching to occur earlier. This prediction can be tested on the genetically-distinct population at One Tree Island, southern Great Barrier Reef, where recent studies suggest that a regional difference in predation rates exists (Caley, 1995). In this way, correlations of environmental differences and fixed population-level differences are possible with this species.

Further studies in testing the relationships in the model presented in this thesis are needed, through both field studies of population characteristics and controlled laboratory experiments examining correlated responses of traits. As comparative data become more available, these tests will be possible and will undoubtedly lead to a greater understanding of ecological and evolutionary changes in early life histories.

References

Alcalay, O. M. and P. C. Sikkel, 1994. Diel periodicity of hatching of demersal eggs in the temperate damselfish, *Hypsypops rubicundus*. Bull. Mar. Sci. 54(2): 565-569.

Aldenhoven, J. M., 1986. Local variation in mortality rates and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Aust. J. Mar. Freshwater Res. 37: 353-360.

Alford, R. A., 1996. Tadpole Ecology: Resource Use, Competition, and Predation. Ch. 9 in Biology of Anuran Larvae. Ed. R. Altig and R. W. McDiarmid. University of Chicago Press.

Alford, R. A. and R. N. Harris, 1988. Effects of larval growth history on anuran metamorphosis. Am. Nat. 131(1): 91-106.

Allen, G. R. 1975. Damselfishes of the South Seas. T.F.H. Publications, London

Anderson, J. T., 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northw. Atl. Fish. Sci. 8: 55-66.

Arvedlund, M. and L. E. Nielsen, 1996. Do the anemonefish *Amphiprion ocellaris* (Pisces: Pomacentridae) imprint themselves to their host sea anemone *Heteractis magnifica* (Anthozoa: Actinidae)? Ethology 102:

Barlow, G. W., 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. Env. Biol. Fish. 6: 65-85.

Bell, M. A., 1988. Stickleback fishes: Bridging the gap between population biology and paleobiology, TREE 3: 320-325.

Berven, K. A. and D. E. Gill, 1983. Interpreting geographic variation in life-history traits. Amer. Zool. 23: 85-97.

Berven, K. A., D. E. Gill, and S. J. Smith-Gill, 1986. Countergradient selection in the green frog, *Rana clamitans*. Evolution 33(2): 609-623.

Beukers, J.S., 1996. The Relative Roles of Recruitment and Postrecruitment in the Population Regulation of a Coral Reef Damselfish. Ph.D. thesis. James Cook University of North Queensland, Australia.

Bolin, R. L., 1930. Embryonic development of the labrod fish *Oxyjulis californicus*. Copeia 1930(4): 122.

Booth, D. J., 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. Ecology 76(1): 91-106.

Breder, C.M., Jr. and D. E. Rosen, 1966. Modes of reproduction in fishes. The Natural History Press, Garden City, New York.

Brockelman, W. Y.,1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50: 632-644.

Caley, M.J. 1995a. Reef-fish community structure and dynamics: an interaction between local and larger scale processes. Marine Ecology Progress Series, in press.

Caley, M. J., 1995b. Community dynamics of tropical reef fishes: local patterns between latitudes. Marine Ecology Progress Series, in press.

Chambers, R. C. and W. C. Leggett, 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J. Fish. Aquat. Sci. 44: 1936-1947.

Chambers, R. C., W. C. Leggett, and J. A. Brown, 1988. Variation in and among early

life history traits of laboratory-reared winter flounder *Pseudopleuronectes americanus*. Marine Ecology Progress Series 47: 1-15.

Christy, J. H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: A hypothesis. Science 199: 453-455.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton, N.J.

Colin, P.L., 1982. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). Fish. Bull. 80: 853-862.

Colin, P. L. and L. J. Bell, 1991. Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ. Biol. Fishes 31: 229-260.

Cogger, H. G., 1994. Reptiles and Amphibians of Australia. 5th ed. Ed. Peter Hutton. Reed Books, NSW.

Connell, S. 1994. Ph.D. dissertation, University of Sydney, Sydney, Australia.

Davis, M. W. and B. L. Olla, 1995. Formation and maintenance of aggregations in walleye pollock, *Theragra chalcogramma*, larvae under laboratory conditions: role of visual and chemical stimuli. Environ. Biol. Fishes. 44: 385-392.

Delsman, H. C., 1930. Fish eggs and larvae from the Java Sea. 16. *Amphiprion percula* c.v. Treubia Vol. XII (3-4): 367-370.

Doherty, P.J., 1980. Biological and physical constraints on t he populations of two sympatric territorial damselfishes on the southern Great Barrier Reef. Ph.D. dissertation, University of Sydney, Sydney, Australia.

Doherty, P.J., 1983. Diel, lunar and seasonal rhythms in the reproduction of two tropical damselfishes: *Pomacentrus flavicauda* and *P. wardi*. Mar. Biol. 75:215-224.

Doherty, P.J., 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. Bull. Mar. Sci. 41: 411-422.

Doherty, P.J., 1991. Spatial and Temporal Patterns in Recruitment. Ch. 10 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

Doherty, P. J., D. McB. Williams, and P. F. Sale, 1985. The adaptive significance of larval dispersal in coral reef fishes. Environ. Biol. Fishes. 12: 81-90.

Doherty, P. J. and T. Fowler, 1994. An empirical test of recruitment limitation in a coral reef fish. Science 263: 935-939.

Doherty, P. J., P. Mather, and S. Planes, 1994. *Acanthochromis polyacanthus*, a fish lacking larval dispersal, has genetically differentiated populations at local and regional scales on the Great Barrier Reef. Marine Biology 121: 11-21.

Eckert, G. J., 1984. Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Group, Great Barrier Reef. Mar. Biol. 78: 123-127.

Eckert, G. J., 1987. Estimates of adult and juvenile mortality for labrid fishes at One Tree Island, Great Barrier Reef. Mar. Biol. 95: 167-171.

Endler, J. A., 1994. Multiple-trait coevolution and environmental gradients in guppies. TREE 10(1): 22-29.

Fahay, M., 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest. Atl. Fish. Sci. 4.

Fitzpatrick, S., 1992. Pomacentrid intrafamilial relationships: a cladistic approach. Honour's thesis, James Cook University of North Queensland, Australia.

Forrester, G. E., 1990. Factors influencing the juvenile demography of a coral reef fish population. Ecology 71: 1666-1681.

Forsman, A. and R. Shine, in press. Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. Funct. Ecol.

Fricke, H. W., 1974. Oko-ethologie des momogamen Anemonenfisches *Amphiprion bicinctus* (Freiwasseruntersuchung aus dem Roten Meer). Z. Tierpsychol. 36: 429-512.

Frith, C. A., J. M. Leis, and B. Goldman, 1986. Currents in the Lizard Island region of the Great Barrier Reef Lagoon and their relevance to potential movements of larvae. Coral Reefs 5: 81-92.

Fryer, G. and T. D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution. Oliver and Boyd, Edinburgh.

Fuiman, L. A., 1983. Growth gradients in fish larvae. J. Fish Biol. 23: 117-123.

Fuiman, L. A. and D. Higgs, in press. Ontogeny, Growth, and the Recruitment Process. *In*: R.C. Chambers and E.A. Trippel, eds. Early life history and recruitment in fish populations. Chapman and Hall.

Fujita, S., 1957. On the egg development and prelarval stage of a damselfish, *Chromis notatus* (Temminck et Schlegel). Journal? Vol. XII. Fisheries Laboratory, Kyushu University.

Gladstone, W. and M. Westoby, 1988. Growth and reproduction in *Canthigaster valentini* (Pisces: Tetraodontidae): a comparison of a toxic reef fish with other reef fishes. Env. Biol. Fish. 21(3): 207-221.

Griffith, H., 1990. Miniaturization and elongation in *Eumeces* (Sauria: Scincidae). Copeia 1990(3): 751-758.

Gould, S. J., 1977. Ontogeny and Phylogeny. The Belknap Press of Harvard University Press, Cambridge, MA.

Hall, B. K., 1992. Evolutionary Developmental Biology. Chapman and Hall, London.

Hamner, W. M., M. S. Jones, J. H. Carleton, I.R. Hauri, and D. M. Williams, 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull. Mar. Sci. 42: 459-479.

Harvey, P. H. and M. Pagel, 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Hixon, M. 1991. Predation as a Process Structuring Coral Reef Fish Communities. Ch. 17 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

Hobson, E. S. and J. R. Chess, 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull. 76: 133-153.

Houde, E. D., 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2: 17-29.

Houde, E. D., 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES J. of Mar. Sci. 51: 91-97.

Hunter, J. R., 1972. Swimming and feeding behavior of larval anchovy Engraulis mordax. Fish. Bull. 70(3): 821-838.

Huntingford, F. A. and P. Torricelli, 1991. Behavioural Ecology of Fishes. Ettore Majorana International Life Sciences Series vol. 11. Harwood Academic Publishers, Switzerland.

Huntingford, F. A. and P. J. Wright, 1991. The development of adaptive variation in predator avoidance in freshwater fishes. *In* Behavioural Ecology of Fishes. Ettore Majorana International Life Sciences Series vol. 11. Harwood Academic Publishers, Switzerland.

James, N.P.E. and M. N. Bruton, 1992. Alternative life-history traits with reproduction in *Oreochromis mossambicus* (Pisces: Cichlidae) in small water bodies of the eastern Cape, South Africa. Env. Biol. Fish. 34: 379-392.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3:65-84.

Jones, G. P., 1986. Food availability affects growth in a coral reef fish. Oecologia 70: 136-139.

Jones, G. P., 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. Ch. 11 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

Jones, G. P., D.J. Ferrell, and P. F. Sale, 1991. Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. Ch. 7 in The Ecology of Coral Reef Fishes. Ed. P. Sale. Academic Press, Inc.

Kaufman, L. and K. F. Liem, 1982. Fishes of the suborder Labroidei (Pisces, Perciformes): phylogeny, ecology, and evolutionary significance. Breviora. Museum of Comparative Zoology, Harvard University 472: 1-19.

Kaufman, L., J. Ebersole, J. Beets, and C. C. McIvor, 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environ. Biol. Fishes 34: 109-118.

Kawasa, H., N. Mochioka, and A. Nakazono, 1993. Otolith increment formation and planktonic larval duration of a temperate damselfish *Chromis notatus notatus*. Jap. J. Ich. 40(3): 377-380.

Keenleyside, M. H. A., 1991. Cichlid fishes: Behaviour, ecology, and evolution. Chapman and Hall, London.

Kerrigan, B. A., 1995. Temporal patterns in size and condition at settlement in two tropical reef fishes (Pomacentridae: *Pomacentrus amboinensis* and *P. nagasakiensis*). Marine Ecology Progress Series.

Kingsford, M. J., 1985. The demersal eggs and planktonic larvae of *Chromis dispilis* (Teleostei: Pomacentridae) in northeastern New Zealand coastal waters. New Zealand J. Mar. and Freshw. Res. 19: 429-438.

Kingsford, M. J., 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 11: 193-198.

Kotrschal, K., H. Adam, R. Brandstatter, H. Junger, M. Zaunreiter, and A. Goldschmid, 1990. Larval size constraints determine directional ontogenetic shifts in the visual system of teleosts. Z. zool. Syst. Evolut.-forsch. 28: 166-182.

Lamon, M. S. and J. A. Ward, 1983. Measurements of reproductive effort from successive reproductive cycles for the Asian cichlid *Etroplus maculatus. In* Predators and prey in fishes. Ed. D. Noakes et al. Dr W. Junk Publ., Netherlands.

Leips, J. and J. Travis, 1994. Metamorphic responses to changing food levels in two species of hylid frogs. Ecology 75(5): 1345-1356.

Leis, J. M., 1986. Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Marine Biology 90: 505-516.

Leis, J. M. 1991. The Pelagic stage of Reef Fishes: The Larval Biology of Coral Reef Fishes. Ch. 8 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

Leis, J. M. and D. Rennis, 1983. The Larvae of Indo-Pacific Coral Reef Fishes. New South Wales University Press, Sydney, Australia, and Univ. of Hawaii Press, Honolulu, Hawaii.

Magurran, A. E., B. H. Seghers, G. R. Carvalho, and P. W. Shaw, 1994. Evolution of adaptive variation in antipredator behaviour. *In* Behavioural Ecology of Fishes. Ettore Majorana International Life Sciences Series vol. 11. Harwood Academic Publishers, Switzerland.

McCormick, M. I., 1993. Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula* (Mullidae). Environ. Biol. Fish. 37: 269-282.

McFarland, W. N., 1991. The visual world of coral reef fishes. Ch. 2 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

McGehee, M. A., 1995. Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. Environ. Biol. of Fishes 44: 393-401.

McKinney, M. L. and K. J. McNamara, 1991. Heterochrony: The evolution of ontogeny. Plenum Press, New York.

Miyagawa, K., 1989. Experimental analysis of the symbiosis between anemonefish and sea anemones. Ethology 80:19-46.

Moyer, J. T. and L. J. Bell, 1976. Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. Japan J. Ichthyol. 23: 23-32.

Murdoch, J., 1995. Variation in early life histories of damselfishes on the Great Barrier Reef. Master's thesis, James Cook University, Australia.

Myers, R. F., 1989. Micronesian Reef Fishes. Publ. Coral Reef Graphics, Guam.

Nakazono, A. 1993. One-parent removal experiment in the brood-caring damselfish *Acanthochromis polyacanthus*, with preliminary data on reproductive biology. Aust. J. Mar. Freshwater Res. 44: 699-707.

Noakes, D.L.G. 1979. Parent-touching behavior by young fishes: Incidence, function, and causation. Env. Biol. Fish. 4: 389-400.

Noakes, D.L.G. and G.W. Barlow, 1973. Ontogeny of parent-contacting in young *Cichlasoma citrinellum* (Pisces, Cichlidae). Behavior XLVI: 222-255.

Pankhurst, N. W., 1992. Ocular morphology of the sweep *Scorpis lineolatus* and the spotty *Notolabrus celidotus* (Pisces: Teleostei) grown in low intensity light. Brain, Behavior, and Evolution 39: 116-123.

Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48: 503-518.

Pepin, P., T.H. Shears, and Y. de Lafontaine, 1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). Marine Ecology Progress Series 81: 1-12.

Pitt, K. A., 1994. The larval stage of coral reef fish: Larval duration, growth, and factors influencing larval supply. Honour's thesis, James Cook University of North Queensland, Australia.

Planes, S. and P. J. Doherty. Hybrid zones in *Acanthochromis polyacanthus*: A marine fish lacking pelagic larvae. I. Strong tension after secondary contact in the central Great Barrier Reef. Submitted to Evolution.

Planes, S. and P. J. Doherty. Hybrid zones in *Acanthochromis polyacanthus*: A marine fish lacking pelagic larvae. II. Founder effects dominate local populations in the northern Great Barrier Reef. Submitted to Evolution.

Potthoff, T., 1984. Clearing and Staining Techniques. In Ontogeny and Systematics of Fishes. Special Publication Number 1. American Society of Ichthyologists and Herpetologists.

Potthoff, T., S. Kelly, V. Saksena, M. Moe, and F. Young, 1987. Description of larval and juvenile yellowtail damselfish, *Microspathodon chrysurus*, Pomacentridae, and their osteological development. Bull. Mar. Sci. 40: 330-375.

Powers, M. K. and P. A. Raymond, 1990. Development of the visual system. Ch. 12 in

The Visual System of Fish. Eds. R. Douglas and M. Djamgoz. Chapman and Hall. pp. 419-437.

Quertermus, C. J. and J. A. Ward, 1969. Development and significance of two motor patterns used in contacting parents by young Orange Chromides (*Etroplus maculatus*). Anim. Behav. 17: 624-635.

Randall et al, 1985. Cybium 9 (4): 411-413.

Randall, J. E., G. R. Allen, and R. C. Steene, 1990. Fishes of the Great Barrier Reef and Coral Sea. Crawford House Press, Bathurst.

Radtke, R. 198?. Life history characteristics of the Hawaiian damselfish *Abudefduf abdominalis*, defined from otoliths. Proc. Int. Coral Reef Symp. (Tahiti).

Re, P., 1980. The eggs and newly-hatched larvae of *Abudefduf luridus* (Cuvier 1830) (Pisces: Pomacentridae) from the Azores. Publ. do Meuseu e Laboratorio Zoologico e Antropologico. 2. Serie. Vol. VII no. 8.

Re, P., and J. Gomez, 1982. The eggs, newly-hatched larvae and juveniles of the Azorian *Chromis* (Pisces: Pomacentridae). Boletim da Sociedade Portuguesa de Ciencias Naturais. Lisboa. XXI: 9-18.

Reist, J. D., 1983. Behavioral variation in pelvic phenotypes of brook stickleback, *Culaea inconstans*, in response to predation by northern pike, *Esox lucius*. In Predators and prey in fishes. Ed. D. Noakes et al. Dr W. Junk Publ., Netherlands.

Robertson, D.R. 1973. Field observations on the reproductive behavior of a pomacentrid fish, *Acanthochromis polyacanthus*. Z. Tierpsychologie. 32: 319-324.

Robertson, D.R. 1991. The Role of Adult Biology in the Timing of Spawning of Tropical Reef Fishes. Ch. 13 in The Ecology of Coral Reef Fishes. P. Sale, ed.

Robertson, D. R., D. G. Green, B. C. Victor, 1988. Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. Ecology 69 (2): 370-381.

Rothschild, B. J., 1986. Dynamics of Marine Fish Populations. Harvard University Press.

Sargent, R. C., P. D. Taylor, and M. R. Gross, 1987. Parental care and the evolution of egg size in fishes. Am. Nat. 129: 32-46.

Seiro, H. and S. Imai, 1973. Breeding and early development of a pomacentrid, *Pomacentrus nagasakiensis* Tanaka in the Aquarium. Mem. Fac. Fish., Kagoshima Univ. 22(1): 95-106.

Shand, J., submitted. Ontogenetic changes in retinal structure and visual acuity: a comparative study of coral-reef teleosts with differing post-settlement lifestyles. Environ. Biol. Fish.

Shapiro, D. Y., Hensley, D.A., and Appeldoorn, R.S., 1988. Pelagic spawning and egg transport in coral-reef fishes: A skeptical overview. Env. Biol. Fish. 22:3-14.

Shaw, E. S., 1955. The embryology of the Sergeant Major, *Abudefduf saxatilis* . Copeia 1955(2): 85-89.

Shaw, R.G. and T. Mitchell-Olds, 1993. ANOVA for unbalanced data: An overview. Ecology 74(6): 1638-1645.

Shine, R., 1978. Propagule size and parental care: the "safe harbor" hypothesis. J. Theoret. Biol. 75: 417-424.

Smith, C. S. and S. D. Fretwell, 1974. The optimal balance between size and number of offspring. Am. Nat. 108: 499-506.

Smith-Gill, S. J. and K. A. Berven, 1979. Predicting amphibian metamorphosis. Am. Nat. 113(4): 563-585.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press. Oxford, U.K..

Stiassny, M. L. J. and J. S. Jensen, 1991. Labroid intrarelationships revisited: morphological complexity, key innovations and the study of comparative diversity. Bull. Mus. Comp. Zool. 151: 269-319.

Sundararaj, B., 1916. Notes on the freshwater fishes of Madras. Rec. Ind. Mus. 12: 282-286. [Cited in Noakes, 1979.]

Sutterlin, A. M., 1975. Chemical attraction of some marine fish in their natural habitat. J. Fish. Res. Board Canada. 32: 729-738.

Suzuki, K., S. Hioki, and M. Kashihara, 1985. Life history of the damselfish *Pomacentrus coelestis* in Suruga Bay, Japan. J. Fac. Mar. Sci. Technol., Tokai Univ. 21: 99-114.

Suzuki, K., S. Hioki, and M. Kurita, 1985. Life history of the damselfish *Chromis notatus* in Suruga Bay, Japan. J. Fac. Mar. Sci. Technol., Tokai Univ. 21: 115-127.

Sweatman, H. P. A., 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. Mar. Biol. 75:225-229.

Sweatman, H. P. A., 1985. The influence of some species of coral reef fishes on larval recruitment. Ecol. Monogr. 55: 469-485.

Sweatman, H. P. A., 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J. Exp. Mar. Biol. Ecol. 124: 163-174.

Tanaka, Y. and T. Mori, 1989. Reproductive behavior, egg and larval development of the staghorn damsel *Amblyglyphidodon curacao* in the aquarium. Bull. Inst. Oceanic Res. and Devel. Tokai U. 10: 3-12.

Thorrold, S. R. and M. J. Milicich, 1990. Marine Biology 105:375-384.

Thresher, R. E., 1983. Habitat effects on reproductive success in the coral reef fish, *Acanthochromis polyacanthus*. Ecology 64:1184-1199.

Thresher, R. E., 1983. Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. Marine Ecology Progress Series 10: 137-145.

Thresher, R. E., 1984. Reproduction in Reef Fishes. TFH Publ., Neptune City, New Jersey.

Thresher, R. 1985. Distribution, abundance and reproductive success in the coral reef fish *Acanthochromis polyacanthus*. Ecology 66: 1139-1150.

Thresher, R. E., 1985. Brood-directed parental aggression and early brood loss in the coral reef fish, Acanthochromis polyacanthus (Pomacentridae). Anim. Behav. 33: 897-907.

Thresher, R. E., 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. Ch. 15 in The Ecology of Coral Reef Fishes. ed. P. Sale. Academic Press, Inc.

Thresher, R. E., P. L. Colin, and L. J. Bell, 1989. Planktonic duration, distribution, and population structure of western and central Pacific damselfishes (Pomacentridae). Copeia 1989(2): 420-434.

Townshend, T. J., and R. J. Wootton, 1984. Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum*. J. Fish Biol. 23: 91-104.

Travis, J., 1983. Variation in development patterns of larval anurans in temporary ponds. I. Persistent variation within a *Hyla gratiosa* population. Evolution 37: 496-512.

Tulley, J. J. and F. A. Huntingford, 1987. Parental care and the development of adaptive variation in anti-predator responses in sticklebacks. Anim. Behav. 35(5): 1571-1573.

Tzioumis, V. 1995. Ph.D. dissertation. University of Sydney, Sydney, Australia.

Tzioumis, V. and M. J. Kingsford, 1995. Periodicity of spawning of two temperate damselfishes: Parma microlepis and Chromis dispilis. Bull. Mar. Sci. 57(3): 596-609.

Victor, B. C., 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can. J. Fish Aquat. Sci. 43: 1208-1213.

Ward, J. A. and G. W. Barlow. 1967. The maturation and regulation on glancing off the parents by young orange chromides (*Etropus maculatus*: Pisces--Cichlidae). Behaviour 29: 1-56.

Ward, J. A. and G. W. Barlow, 1966. The maturation and regulation of glancing off the parents by young Orange Chromides (*Etroplus maculatus*: Pisces - Cichlidae). Behaviour XXIX: 1-56.

Warner, R. R.,1995. Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, Thalassoma bifasciatum. Env. Biol. Fish. 44: 337-345.

Wellington, G. M. and B. C. Victor, 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101: 557-567.

Werner, E., 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am. Nat. 128 (3): 319-341.

Wilbur, H. M. and J. P. Collins, 1973. Ecological aspects of amphibian metamorphosis. Science 182: 1305-1314.

Williams, D., 1991. Patterns and Processes in the Distribution of Coral Reef Fishes. Ch. 16 in The Ecology of Fishes on Coral Reefs. Ed. P. Sale. Academic Press, Inc.

Winsor, L., 1984. Manual of Basic Zoological Microtechniques for Light Microscopy. Townsville: James Cook University. ISBN 0.86443.091.4.

Wisendon, B. D. and M.H.A. Keenleyside, 1995. Brood size and the economy of brood defence: examining Lack's hypothesis in a biparental cichlid fish. Env. Biol. Fish. 43: 145-151.

Zar, J. H., 1984. Biostatistical Analysis. 2nd Edition. Prentice-Hall, Inc. Englewood Cliffs, N.J.

Zoran, M. J. and J. A. Ward, 1983. Parental egg care behavior and fanning activity for the orange chromide, *Etroplus maculatus*. In Predators and prey in fishes. Ed. D. Noakes et al. Dr W. Junk Publ., Netherlands.