

**A multi-scale analysis of population dynamics and sexual size dimorphism in a
widely distributed coral reef fish family (Acanthuridae)**

Thesis submitted by
Elisabeth Danièle Laman Trip
In September 2004

For the research Degree of Master of Science in Marine
Biology within the School of Marine Biology and
Aquaculture at James Cook University

STATEMENT OF ACCESS

I, Elisabeth D. Laman Trip, the author of this thesis, understand that James Cook University 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.

General Abstract

There is a large amount of evidence that the demography and associated life history features of coral reef fish vary across a range of spatial scales. Many Indo-Pacific species are particular in that their geographical distribution extends over ocean basins, and there is increasing evidence that a number of coral reef fish display highly asymptotic growth trajectories. This thesis uses an age-based approach to examine the mechanisms and patterns of variation in the demography and associated life history features over broad geographical scales and in the context of asymptotic growth, exploring the nature of the trade-offs in life history traits associated with variation in growth in coral reef fish. Over 1500 individuals of three Acanthurid species, *Ctenochaetus striatus*, *Acanthurus nigricans* and *Acanthurus leucosternon*, were collected at 14 locations across the Indo-Pacific region. Three critical demographic parameters were examined: mean adult body size, growth rate and longevity, and the relationship between size, age and sex was established using the re-parameterised equation of the Von Bertalanffy Growth Function.

We found a longitudinal trend in life span, with Indian Ocean populations being shorter lived than those of the Pacific region, suggesting the presence of differences in population dynamics and recruitment patterns between ocean basins. In contrast, there was no predictable pattern in growth, which varied primarily across locations indicating a substantial effect on growth of local habitat conditions. There was a clear sex-specific structure in growth within all populations sampled. The mechanism underlying the variation in size among and within populations was a mechanism of fast initial growth, which was consistent across species, geographical scales, and across the sexes. This result indicates that adult body size is determined by the rate of

growth during the early years of post-settlement life of all individuals, regardless of the nature of sexual ontogeny, suggesting the absence of a trade-off between reproductive and somatic growth in both males and females of the study species. The magnitude of the differences in size between the sexes increased in populations where large absolute adult size was favoured, suggesting an allometric relationship between sexual size dimorphism and the rate of growth of the larger sex. The direction of sex-specific size distributions of the study species varied with adult body size of males, providing evidence that female-biased sexual size dimorphism in acanthurid species is the result of selection for small body size in males.

This study illustrates the importance of early post-settlement life history in shaping the demography and life histories in coral reef fish with a highly asymptotic form of growth, and suggests that determinate growth is associated with: 1) a large potential for flexibility in growth, 2) constraints on the nature of the mechanisms underlying variation in size across geographical scales, and between the sexes, and 3) an evolutionary life history trade-off between juvenile survival and lifetime reproductive success overriding the costs of reproductive growth of females.

Acknowledgments

I wish to thank, first and foremost, my supervisor Prof J. Howard Choat, for giving me the opportunity of working on this project, for all that I have learned with him, for his invaluable guidance and help throughout this project.

This study wouldn't have been possible without the help of William Robbins and John Ackerman, who collected most of the samples used in this study, my warmest thanks go to both of them. Part of this study was the result of collaborative work with Dr Ross Robertson and Dr David Wilson, who contributed in funding and collection of samples in the Indian Ocean and American Samoa, and without whom a broad geographical approach in this study could not have been possible.

I wish to thank William Robbins for his friendship, support and advice, for teaching me all about otoliths, and growth in fish. I am very grateful to Graeme Ewing for the idea of using the re-parameterised equation of the Von Bertalanffy Growth Function, and to Rohan Arthur for teaching me the world of macros. Rohan's help was precious in building the macro used for analysis of the data in this study. This project also has greatly benefited from discussions with Rohan Arthur, Monica Gagliano, Michael Berumen, William Robbins, and John Ackerman.

Last but not the least, warmest personal gratitude go to my family and friends, whose support has been invaluable. I wish to thank James Sheppard, Rohan Arthur, William Robbins, and Sula Blake in Australia, and my close family and dearest friend of twenty years, Eva Masson, in France.

This study was supported through CRC Reef Augmentative Grant Program to ED Lamantrip, James Cook University Internal Funding to ED Lamantrip and JH Choat, National Geographic Grant Program to JH Choat and DR Robertson, and through

Queensland Government - Smithsonian Institution (STRI) Collaborative Funding to
JH Choat and DR Robertson.

Table of contents

<i>Statement of access</i>	<i>i</i>
<i>General abstract</i>	<i>ii</i>
<i>Acknowledgments</i>	<i>iv</i>
<i>Table of contents</i>	<i>vi</i>
<i>List of figures and tables</i>	<i>viii</i>
<i>Statement on sources – declaration</i>	<i>xii</i>

General introduction	1
-----------------------------------	----------

Chapter 1. Spatial variation of life history features in a widely distributed coral reef fish across the Indo-Pacific region: the importance of early growth.....6

Synopsis.....	6
1.1. Introduction.....	7
1.2. Material and Methods.....	11
1.3. Results.....	19
1.4. Discussion.....	26

Chapter 2. Demographic analysis of sexual size dimorphism in a widely distributed coral reef fish: fast initial growth as the mechanism underlying large size in males...32

Synopsis.....	32
2.1. Introduction.....	33
2.2. Materials and methods.....	37
2.3. Results.....	42
2.4. Discussion.....	48

Chapter 3. Demographic analysis of female-biased sexual size dimorphism: the mechanisms and evolution of large body size in females in a widely distributed coral reef fish family.....	55
Synopsis.....	55
3.1. Introduction.....	56
3.2. Materials and Methods.....	59
3.3. Results.....	67
3.4. Discussion.....	74
General Conclusions.....	80
References.....	84

List of figures and tables

Chapter 1.

<u>Figure 1</u> : Diagram illustrating the hypotheses explaining the alternative mechanisms underlying variation in growth when growth is asymptotic.....	p10
<u>Figure 2</u> : Map illustrating the 14 sampling locations of <i>Ctenochaetus striatus</i> across the Indo-Pacific region.....	p12
<u>Figure 3</u> : Size-at-age relationships for <i>Ctenochaetus striatus</i> across the Indo-Pacific region.....	p20
<u>Figure 4</u> : Ordination of the variables $L(1)$ for initial size, $L(5)$ for adult size and mean T_{max} for longevity exploring the demography of <i>Ctenochaetus striatus</i> across the Indo-Pacific region using principal component analysis (PCA).....	p21
<u>Table 1</u> : Results of analyses of variance testing variation in initial body size, adult body size, and mean longevity in <i>Ctenochaetus striatus</i> across the Indo-Pacific region. Two geographical scales were examined: 1) between ocean basins, and 2) among locations.....	p22
<u>Figure 5</u> : Patterns of spatial variation in initial size $L(1)$, adult size $L(5)$ and longevity $mean T_{max}$ across the Indo-Pacific region. Comparison of mean estimates and variance components are presented.....	p23
<u>Figure 6</u> : Latitudinal variation in initial size $L(1)$, adult size $L(5)$ and longevity $mean T_{max}$ in the West Pacific region.....	p24
<u>Table 2</u> : Results of regression analysis examining latitudinal variation in initial body size, adult body size and mean longevity in <i>Ctenochaetus striatus</i> within the West Pacific region.....	p25

Figure 7: Relationship between mean initial size and mean adult size of *Ctenochaetus striatus* across populations sampled in the Indo-Pacific region, illustrating the mechanism underlying spatial variation in size in the study species.....p26

Chapter 2.

Figure 1: Diagram illustrating the hypotheses for the mechanism underlying sexual size dimorphism in the case where males achieve a larger adult size than females for a species with an asymptotic growth trajectory.....p36

Figure 2: Map illustrating the 9 sampling locations of *Ctenochaetus striatus* across the Indo-Pacific region.....p38

Figure 3: Sex-specific growth trajectories of *Ctenochaetus striatus* across the Indo-Pacific region.....p43

Table 1: Results of analysis of variance comparing adult size and initial size of males and females in *Ctenochaetus striatus* across populations sampled in the Indo-Pacific region.....p44

Figure 4: Mean initial body size and adult body size of males and females of *Ctenochaetus striatus* across the Indo-Pacific region.....p45

Table 2: Results of Homogeneity-of-slopes Model testing for significant differences in mean growth rate between males and females of *Ctenochaetus striatus* across the Indo-Pacific region.....p46

Figure 5: Relationship between initial size and adult size of males and females in *Ctenochaetus striatus* across the Indo-Pacific region, illustrating sex-specific growth rates in the case of male-biased sexual size dimorphism.....p47

Figure 6: Regression plot showing the influence of male and female adult size on the magnitude of sexual size dimorphism in *Ctenochaetus striatus* across the Indo-Pacific region.....p48

Chapter 3.

Figure 1: Map illustrating the sampling locations of the sister species *Acanthurus nigricans* in the Pacific Ocean, and *Acanthurus leucosternon* in the western Indian Ocean.....p61

Figure 2: Sex-specific growth trajectories of sister species *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region.....p68

Table 1: Results of nested analysis of variance comparing adult size and initial size of males and females of *Acanthurus nigricans* and *A. leucosternon* across the Indo-Pacific region.....p69

Figure 3: Mean initial size and adult body size of males and females of *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region.....p70

Table 2: Results of Homogeneity-of-slopes Model testing for significant differences in mean growth rate between males and females of the sister species *Acanthurus nigricans* and *A. leucosternon* across the Indo-Pacific region.....p70

Figure 4: Relationship between mean initial size and adult size of males and females in *Acanthurus nigricans* and *Acanthurus leucosternon* across populations sampled in the Indo-Pacific region, illustrating sex-specific growth rates in species with female-biased sexual size dimorphism.....p71

Figure 5: Regression plot showing the influence of male and female adult body size on the magnitude of sexual size dimorphism in species with female-biased sexual size dimorphism.....p72

Table 3: Analysis of variance of mean adult size of males and females on the direction of sexual size dimorphism in three Acanthurid species across the Indo-Pacific region: *Ctenochaetus striatus* where males grow larger than females, and *Acanthurus nigricans* and *A. leucosternon* where females grow larger than males.....p73

Table 4: Pair-wise comparison of group means using Tuckey’s Test. Direction of sexual size dimorphism was significantly affected by sex in ANOVA (table 3). Here we examine the nature of this difference, in order to identify the groups that differed significantly.....p73

Figure 6: Variation in mean adult size of males and females in species with opposite patterns of sexual size dimorphism within the coral reef fish family Acanthuridae..p74

STATEMENT ON 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 is given.