

ResearchOnline@JCU

This file is part of the following reference:

Shand, Julia (1994) *Changes in the visual system of teleost fishes during growth and settlement: an ecological perspective*. PhD thesis, James Cook University.

Access to this file is available from:

<http://eprints.jcu.edu.au/24124/>

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact ResearchOnline@jcu.edu.au and quote <http://eprints.jcu.edu.au/24124/>

**CHANGES IN THE VISUAL SYSTEM OF TELEOST FISHES
DURING GROWTH AND SETTLEMENT: AN ECOLOGICAL
PERSPECTIVE**

Thesis submitted by

JULIA SHAND BSc. (Hons) (Durham)

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

March 1994



Transverse section through the head of a newly-settled fish, the labrid *Stethojulis strigiventer*, standard length 5.7 mm.

Statement on Access to Thesis

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 photographic 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 written acknowledgement for any assistance which I have obtained from it."

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

27th March 1994

ABSTRACT

Nearly all tropical teleost fishes have a pelagic larval phase. Species that settle to a demersal reef-associated mode of life experience dramatic changes in habitat and light environment at this time. In many cases, behaviour associated with feeding, predator avoidance and diel activity also changes. These changes are often rapid, overnight, events. The growth of the eye and extent to which the visual system of larval fishes alters during settlement was investigated in fish with ecologically differing adult lifestyles.

The ocular morphology of 18 species of tropical teleosts caught from a variety of locations across the northern Great Barrier Reef, Australia, was examined prior to and following settlement. Detailed retinal cell counts of 6 species with differing post-settlement lifestyles were carried out on fish covering a range of developmental stages. These were: the reef fish *Stethojulis strigiventer* (Family Labridae), a microcarnivore; *Pomacentrus moluccensis* and *Pomacentrus bankanensis* (Family Pomacentridae), a planktivore and herbivore respectively; *Apogon doederleini* (Family Apogonidae), a nocturnal planktivore; the inter-reef fish *Upeneus tragula* (Family Mullidae), a benthic carnivore; and the inshore planktivore *Ambassis vachelli* (Family Ambassidae). A microspectrophotometric investigation of the visual pigment compliment of *Upeneus tragula* was carried out over the settlement period. In addition microspectrophotometric measurements obtained from the adults of four additional tropical teleosts are presented.

Fish that settled at small and intermediate sizes showed changes in retinal cell densities prior to settlement which appeared to be in anticipation of the post-settlement lifestyle. *Upeneus tragula*, a species that remained pelagic for an extended period was found to maintain adaptations for a pelagic lifestyle in both structural and visual pigment compliment. At settlement the retina of this species under went rapid changes in structure as a double layer of cones in the dorsal retina amalgamated to form a single layer. The loss of long-wavelength sensitivity also occurred at this time.

The theoretical ability of an eye to resolve fine detail improved rapidly as eye size increased. Mechanisms for increasing sensitivity in nocturnal species were found. These included an increase in rod densities and a lowering of Matthiessen's ratio. The ocular features found in the variety of fish examined were considered in relation to the light environment and behaviours of the fish at respective phases of their life history.

ACKNOWLEDGMENTS

This thesis would not have been completed without the help and encouragement of many colleagues and friends. To all, I extend my sincere gratitude. My supervisors Howard Choat, Dave Williams and Chris Alexander have always been ready to give advice and assistance. Bill Muntz, who took on the role of an honorary supervisor, also provided much advice and helpful discussion. Invaluable help with field work and the provision and identification of specimens has been given by Mark McCormick, Mark Meekan, Rob McCauley, Mike Capps, Tony Fowler and Bridgid Kerrigan. Similarly, help with laboratory techniques has been received from Leigh and Heather Winsor, Zollie Florian and the staff of the Marine Biology Department at James Cook University. The setting up of the microspectrophotometer would not have been possible without the skills of Julian Partridge who also advised on analysis of visual pigment data. Additional data analysis has been carried out with considerable assistance from Rob McCauley. Drafts of the thesis have been read by Chris Alexander, Rob McCauley and Julian Partridge. Ann Sharp has always been willing to help with smoothing the way on administrative matters.

Financial assistance was provided by a Commonwealth Scholarship and student grants from the Australian Coral Reef Society and James Cook University.

A very special thanks is owed to Rob McCauley for his friendship, patience and encouragement throughout. Without his continued support my task would have been immeasurably more difficult.

I was first introduced to the world of animal vision by John Lythgoe and it was he who encouraged me to come to Australia and undertake this work. His influence has always been present. Sadly, I am prevented from expressing my gratitude. To his memory I humbly dedicate this thesis.

CONTENTS

General Introduction	1
Part I	
Morphology of the teleost eye and changes in retinal structure during growth.	4
Introduction	5
Generalised structure of the teleost eye	5
Generalised structure of the teleost retina	7
Development of the teleost eye	13
Terminology	16
Materials and Methods	18
Study species and collection techniques	18
Morphometrics	26
Preservation, embedding and sectioning techniques	28
Recording retinal structure and estimation of cell densities	29
Visual acuity calculations	31
Results	33
External morphology	33
Retinal structure	41
Development and Growth	46
Visual acuity	63
Discussion	82
External morphology	82
Visual acuity	86
Iridescence and pigmentation of the cornea	89
Retinal morphology during growth and settlement	89

<i>Upeneus tragula</i>	91
Retinal specialisations and ecological correlations	93

Part II

Microspectrophotometry of visual pigments	96
Introduction	97
Materials and Methods	102
Study species	102
Preparation of material	102
The microspectrophotometer	103
Analysis of visual pigment scans	104
Results	107
<i>Upeneus tragula</i>	107
<i>Upeneus moluccensis</i>	115
<i>Ambassis nalua</i>	117
<i>Ambassis vachelli</i>	117
<i>Hemiramphus sp.</i>	121
Discussion	123
<i>Upeneus tragula</i>	123
Mechanisms for visual pigment changes	124
The light environment	126
Short-wavelength sensitivity	128
Rods	131
Correlation with structural changes	132

General Discussion	133
Bibliography	136
Appendix 1. Estimation of shrinkage during histological processing	154
Appendix 2. Sensitivity and resolving power of the vertebrate eye	163
Appendix 3. Changes in retinal structure during development and settlement of the goatfish <i>Upeneus tragula</i>	188
Appendix 4. Metamorphosis of the visual and barbel sensory systems at settlement in the reef fish <i>Upeneus tragula</i> (Family Mullidae)	198
Appendix 5. Microspectrophotometric determinations of rod visual pigments in some adult and larval Australian amphibians	206
Appendix 6. Changes in the spectral absorption of cone visual pigments during the settlement of the goatfish <i>Upeneus tragula</i>: the loss of red sensitivity as a benthic existence begins	212
Appendix 7. The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef.	219

List of Figures

Part I

I.1	Transverse sections through a generalised teleost eye:	6
	A) The whole eye	
	B) Detail of the back wall of the eye	
I.2	Schematic drawing of a radial section through a teleost retina	8
I.3	Schematic drawing of "typical" rods and cones	8
I.4	Schematic drawing of tangential sections through teleost retinæ showing the most common mosaic patterns formed by the arrangement of the cones	11
I.5	Map showing the location of collection sites	21
I.6	Graph showing regression curve used in calculating the correction factor for shrinkage of the eye	27
I.7	Graphs showing changes in eye diameter during growth	34
I.8	Graphs showing changes in lens diameter during growth	35
I.9	Graph showing changes in lens diameter during growth of four pomacentrid species	36
I.10	Graphs showing changes in the ratio of eye to lens diameter during growth	38
I.11	Graphs showing changes in cone density during growth	51
I.12	Graphs showing changes in rod density during growth	53
I.13	Graphs showing changes in the density of cells in the inner nuclear layer during growth	54
I.14	Graphs showing changes in the density of cells in the ganglion cell layer during growth	56
I.15	Graphs showing the changes in the ratio of rods to cones during growth	57
I.16	Graphs showing changes in the ratio of cones to cells in the inner nuclear layer during growth	58
I.17	Graphs showing changes in the ratio of photoreceptors to cells in the inner nuclear layer during growth	60
I.18	Graphs showing changes in the ratios of cones to cells in the ganglion cell layer during growth	61
I.19	Graphs showing changes in the ratio of photoreceptors to cells in the ganglion cell layer	62
I.20	Graphs showing changes in the minimum separable angle calculated for the ventral retina during growth	64
I.21	Graph showing the data for changes in minimum separable angle during growth plotted against lens diameter and fitted with a regression line	65

I.22	Graph showing an extrapolation of the regression line shown in Fig. I.21 and with data from published studies added	66
I.23	Graphs showing changes in cone density in the retina of <i>Upeneus tragula</i> during growth:	71
	A) Dorsal and ventral retina of pre-settlement and wild-settled fish	
	B) Dorsal retina of pre-settlement, partially-settled, aquarium-settled and wild-settled fish	
I.24	Graphs showing changes in the density of bipolar cell nuclei in the retina of <i>Upeneus tragula</i> during growth:	72
	A) Dorsal and ventral retina of pre-settlement and wild-settled fish	
	B) Ventral retina of pre-settlement, partially-settled, aquarium-settled and wild-settled fish	
I.25	Schematic drawing of the eye of <i>Spratelloides delicatulus</i>	80

Part II

II.1	An example of a print-out from a visual pigment sample scan	105
II.2	Histograms of λ_{\max} values and averaged spectral absorbance scans from rods of <i>Upeneus tragula</i> at different stages of development	108
II.3	Mean λ_{\max} values for cone classes in individual <i>Upeneus tragula</i>	110
II.4	Averaged spectral absorbance curves for cone classes at different stages of development in <i>Upeneus tragula</i>	111
II.5	Histograms of λ_{\max} values for cones at different stages of development in <i>Upeneus tragula</i>	112
II.6	Spectral absorbance curve from a single cone in <i>Upeneus tragula</i> prior to and following bleaching	114
II.7	Spectral absorbance curves from a small cone in <i>Upeneus tragula</i>	114
II.8	Histograms of λ_{\max} measurements and averaged spectral absorbance curves from the photoreceptors of <i>Upeneus moluccensis</i>	116
II.9	Histograms of λ_{\max} measurements from individual <i>Ambassis nalua</i>	119
II.10	Averaged spectral absorbance curves for cone classes in <i>Ambassis nalua</i>	119
II.11	Histograms of λ_{\max} measurements and averaged spectral absorbance curves from cones of <i>Ambassis vachelli</i>	120
II.12	Histograms of λ_{\max} measurements and averaged spectral absorbance curves from the photoreceptors of <i>Hemiramphus</i> sp.	122

List of Plates

Frontpiece - Transverse section through the head of a newly-settled fish.	
I.2 Radial sections through teleost retinae:	9
A) Light-adapted	
B) Dark- adapted	
I.3 Radial sections through teleost retinae:	45
A) A nocturnal fish, <i>Apogon doederleini</i>	
B) A diurnal planktivorous fish, <i>Pomacentrus moluccensis</i>	
I.4 Electron micrograph of radial section through the retina of a 20 min hatched <i>Pomacentrus amboinensis</i>	47
I.5 Electron micrographs of retinal photoreceptors of a 2 day hatched <i>Pomacentrus amboinensis</i> retina:	48
A) Cones	
B) Rods	
I.6 Electron micrographs of tangential sections through the retina of 2 day-hatched <i>Pomacentrus amboinensis</i> showing the photoreceptor mosaic:	49
A) At the level of the photoreceptors	
B) At the level of the inner segments	
I.7 Radial sections through the dorsal retina of <i>Upeneus tragula</i> showing the arrangement of cone layers at various stages of development:	68
A) Pre-settlement showing a double layer of cones	
B) Partially-settled showing double layer of cones	
C) 1-day aquarium-settled showing a single layer of cones	
D) Wild-caught settled showing a single layer of cones	
I.8 Tangential sections through the dorsal retinae of <i>Upeneus tragula</i> showing the cone mosaics:	69
A) Pre-settlement	
B) Settled	
I.9 Radial sections through the eye of a Labrid, <i>Stethojulis strigiventer</i> , showing the area centralis:	75
A) The whole eye	
B) Detail of the area centralis	
I.10 Radial sections through the retina of <i>Spratelloides delicatulus</i> :	76
A) The specialised ventral retina	
B) The unspecialised dorsal retina	

- I.11 A series of transverse sections through the eye of *Spratelloides delicatulus* moving from temporal to nasal regions: 78
- A) Temporal retina showing specialised ventral area
 - B) Temporal retina through region of optic nerve
 - C) Temporal retina showing extending unspecialised area
 - D) Mid eye showing specialised area displaced behind unspecialised area
 - E) Nasal retina showing reduced specialised area
 - F) Nasal retina showing unspecialised retina throughout

List of Tables

I.1	List of species investigated with a summary of their size range, location of capture and results obtained.	19
I.2	Ecological notes about the species investigated.	22
I.3	Coefficients for the regression lines fitted to changes in eye diameter during growth.	34
I.4	Coefficients for the regression lines fitted to changes in lens diameter during growth.	35
I.5	Coefficients for the regression lines fitted to changes in lens diameter during growth of four pomacentrid species.	36
I.6	Diameter of the eyes of twelve species at settlement.	37
I.7	Coefficients for the regression lines fitted to the changes in the ratio of eye to lens diameter during growth.	38
I.8	Mean eye to lens ratios for fourteen species of teleosts	40
I.9	Summary of retinal morphology of the species investigated.	42
I.10	Equations and regression coefficients of curves fitted to the changes in cone density during growth.	51
I.11	Equations and regression coefficients of curves fitted to the changes in rod density during growth.	53
I.12	Equations and regression coefficients of curves fitted to the changes in density of cells in the inner nuclear layer during growth.	54
I.13	Equations and regression coefficients of curves fitted to the changes in the density of cells in the ganglion cell layer during growth.	56
I.14	Equations and regression coefficients of curves fitted to the changes in the ratio of rods to cones during growth.	57
I.15	Equations and regression coefficients of curves fitted to the changes in the ratio of cones to cells in the inner nuclear layer during growth.	58

I.16	Equations and regression coefficients of curves fitted to the changes in the ratio of photoreceptors to cells in the inner nuclear layer during growth.	60
I.17	Equations and regression coefficients of curves fitted to the changes in the ratio of cones to cells in the ganglion cell layer during growth.	61
I.18	Equations and regression coefficients of curves fitted to the changes in the ratio of photoreceptors to cells in the ganglion cell layer during growth.	62

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.

Julia Shand

27th March 1994