



Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand). This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage.

<http://researchspace.auckland.ac.nz/feedback>

General copyright and disclaimer

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library

[Thesis Consent Form](#)

Ecological factors associated with speciation in New Zealand triplefin fishes (Family Tripterygiidae)

by

Maren Wellenreuther

A thesis presented in fulfilment of the requirements for the degree of

Doctor of Philosophy

The School of Biological Sciences

The University of Auckland, 2007

Abstract

Theoretical research has demonstrated that ecological interactions in sympatry or parapatry can generate disruptive selection that in concert with assortative mating can lead to speciation. However, empirical examples are few and restricted to terrestrial and lacustrine systems. New Zealand triplefin fishes (Family Tripterygiidae) are an ideal model system to study speciation in the sea, as they conform to the criteria of an adaptive radiation, being philopatric, speciose and abundant, and having largely sympatric distributions. This thesis investigates two key aspects of the New Zealand triplefin radiation: 1) which ecological traits are under selection?; and 2) which traits are potentially available for the development of assortative mating?

Habitat use was identified as a possible key trait for selection and investigated in detail in this thesis. Habitat use of the majority of New Zealand triplefin species was censused quantitatively throughout most of their latitudinal range and analysed using novel statistical methods. Analyses showed that habitat use was highly divergent between species and thus diversification in habitat may have been a major component in the evolution of this clade. The phylogenetic analysis of habitat characters confirmed that there has been rapid evolution in habitat use among species. Habitat selection at settlement was highly species-specific, indicating that interspecific differences in adult habitat use may be the outcome of active habitat choice established at settlement. These species-specific habitat associations showed no evidence for geographic variation in habitat use. Laboratory trials and field observations of the sister-species pair *Ruanoho decemdigitatus* and *R. whero* showed that competition was linked with body size, with *R. decemdigitatus* being the larger and consequently dominant species. The second part of this thesis investigated which traits may have contributed to prezygotic isolation, and thus to assortative mating. Little evidence was found for divergence in breeding season or male colour patterns. However, divergence in habitat affected breeding habitat choice, as triplefins court and mate in the same territory as that occupied year round. This suggests that assortative mating in New Zealand triplefin species could be the by-product of adaptation to habitat resources. Body size affected mate choice and time at first maturity in the *Ruanoho* sister-species pair, suggesting that size is important in the maintenance of reproductive isolation in these species. Differences in body size may have also lead to assortative mating in other New Zealand triplefin sister-species pairs, as all sister-species pairs differ in maximum body size. The findings of this thesis invoke a strong role for ecologically-based selection in speciation, and support the hypothesis that adaptation to habitat has been a major factor in speciation in this system.

Acknowledgments

This has been an exciting and largely encompassing part of my life for nearly four years. Many people have made this work possible and ensured it happened under the best possible circumstances. I want to express my genuine gratitude to those in both my professional and personal life during this time.

I would like to thank my primary supervisor Kendall Clements for excellent supervision. Thank you for your constructive criticism, enthusiasm, and scientific sharpness. I am also thankful to my co-supervisor Paul Barrett, whose statistical expertise proved invaluable and ensured that I could obtain the best results from this research. This thesis involved a substantial amount of fieldwork, consequently many people helped, either directly or indirectly with this. These people are Zoë Hilton, Damian Moran, Justine Saunders, Jarrod Walker, Kevin Moran, Brady Doak, David Raubenheimer, and Murray Birch. Various parts of this thesis have benefited from readings by, or discussions with Damian Moran, David Raubenheimer, Sean Connell, Russell Gray, Howard Choat, Patrik Nosil, Philip Munday, Mark Hauber and Craig Syms. I would also like to thank Mark Pagel for letting me use his programs, and Alexei Drummond and Quentin Atkinson for helping me to understand phylogenetic comparative methods. I thank the staff of the Leigh Marine Laboratory for their general assistance and for use of their facilities and equipment. Special mention must be made to Brady Doak and Murray Birch, skippers of the R.V. Hawere. From the University of Auckland, School of Biological Sciences, I thank Ian MacDonald for photographing fish under difficult conditions and Vivian Ward for helping with figures. From Portobello Marine Laboratory of the Otago University I thank Paul Meredith and Steve Wing for making my trip to Fiordland possible and enjoyable. Special thanks must also go to the New Zealand Royal Society (Marsden Fund 02-UOA-005 to Kendall Clements), the Tertiary Education Commission (Top Achiever Doctoral Scholarship), and the University of Auckland (University of Auckland Doctoral Scholarship) for financing this research. Utmost thanks go to my husband Damian for his never-ending enthusiasm and emotional support. You always showed interest in my project, offered advice, and discussed new ideas with me, all for which I am extremely grateful. I would also like to thank my New Zealand family Sian, Kevin, Beth, and Scott, for integrating me into your lives. Last of all my thanks must go to my family who have supported me throughout my life. My mother Haide and father Martin deserve special thanks for allowing me to make my own choices and always believing in me from afar. I would definitively not be here otherwise.

Table of Contents

ABSTRACT	II
ACKNOWLEDGMENTS.....	III
TABLE OF CONTENTS	IV
LIST OF TABLES.....	VIII
LIST OF FIGURES.....	IX
1 GENERAL INTRODUCTION	- 1 -
1.1 THEORETICAL BACKGROUND.....	- 2 -
1.2 TRIPLEFIN FISHES: AN INTRODUCTION	- 8 -
1.3 OBJECTIVES OF THIS RESEARCH	- 16 -
2 HABITAT USE IN SUBTIDAL TRIPLEFIN FISHES.....	- 18 -
2.1 INTRODUCTION	- 19 -
2.2 MATERIALS AND METHODS.....	- 21 -
2.2.1 <i>Selection of species</i>	- 21 -
2.2.2 <i>Selection of locations and sites</i>	- 22 -
2.2.3 <i>Data collection</i>	- 23 -
2.2.4 <i>Data analysis</i>	- 25 -
2.3 RESULTS.....	- 31 -
2.3.1 <i>Interspecific overlap in habitat use</i>	- 32 -
2.3.2 <i>Similarity between sister-species</i>	- 38 -
2.4 DISCUSSION.....	- 39 -
3 DO TRIPLEFIN FISHES SHOW GEOGRAPHIC VARIATION IN HABITAT USE?	- 45 -
3.1 INTRODUCTION	- 46 -
3.2 MATERIALS AND METHODS.....	- 47 -
3.2.1 <i>Data collection</i>	- 47 -
3.2.2 <i>Data analysis</i>	- 50 -
3.3 RESULTS.....	- 51 -
3.4 DISCUSSION.....	- 56 -
4 EVOLUTION OF HABITAT SPECIALISATION IN TRIPLEFIN FISHES	- 62 -

4.1	INTRODUCTION.....	- 63 -
4.2	MATERIALS AND METHODS.....	- 65 -
4.2.1	<i>Data collection</i>	- 65 -
4.2.2	<i>Data analysis</i>	- 66 -
4.3	RESULTS.....	- 71 -
4.3.1	<i>Habitat specialisation</i>	- 71 -
4.3.2	<i>Evolution of habitat specialisation</i>	- 73 -
4.4	DISCUSSION.....	- 74 -
5	SIMILARITIES IN HABITAT USE BETWEEN TRIPLEFIN RECRUITS AND ADULTS.....	- 79 -
5.1	INTRODUCTION.....	- 80 -
5.2	MATERIALS AND METHODS.....	- 82 -
5.2.1	<i>Data collection</i>	- 82 -
5.2.2	<i>Data analysis</i>	- 84 -
5.3	RESULTS.....	- 86 -
5.3.1	<i>Habitat use of new recruits and adults</i>	- 89 -
5.3.2	<i>Spatial correlations between new recruits and adults</i>	- 94 -
5.4	DISCUSSION.....	- 97 -
6	ECOLOGICAL DIVERSIFICATION OF TWO INTERTIDAL TRIPLEFIN FISHES, <i>B. LESLEYAE</i> AND <i>B. MEDIUS</i>	- 102 -
6.1	INTRODUCTION.....	- 103 -
6.2	MATERIALS AND METHODS.....	- 105 -
6.2.1	<i>Data collection</i>	- 105 -
6.2.2	<i>Data analysis</i>	- 108 -
6.3	RESULTS.....	- 111 -
6.3.1	<i>Spatial patterns</i>	- 111 -
6.3.2	<i>Fish size distribution</i>	- 115 -
6.3.3	<i>Number of individuals in rockpools</i>	- 116 -
6.4	DISCUSSION.....	- 118 -
7	REPRODUCTIVE ISOLATION IN TRIPLEFIN FISHES.....	- 125 -
7.1	INTRODUCTION.....	- 126 -
7.2	MATERIALS AND METHODS.....	- 131 -
7.2.1	<i>Spatial and temporal isolation: data collection and analysis</i>	- 131 -

7.2.2	<i>Hybridisation experiments: data collection and analysis</i>	- 133 -
7.2.3	<i>Male body colouration: data collection and analysis</i>	- 135 -
7.2.4	<i>Male body length: data collection and analysis</i>	- 136 -
7.2.5	<i>Mate choice: data collection and analysis</i>	- 137 -
7.2.6	<i>Courtship behaviour: data collection and analysis</i>	- 139 -
7.3	RESULTS.....	- 139 -
7.3.1	<i>Spatial isolation</i>	- 139 -
7.3.2	<i>Temporal isolation</i>	- 141 -
7.3.3	<i>Hybridisation experiments</i>	- 143 -
7.3.4	<i>Male body colouration</i>	- 145 -
7.3.5	<i>Male body length</i>	- 149 -
7.3.6	<i>Mate choice</i>	- 150 -
7.3.7	<i>Courtship behaviour</i>	- 152 -
7.4	DISCUSSION.....	- 155 -
8	COMPETITION FOR RESOURCES BETWEEN <i>RUANOHO WHERO</i> AND <i>R. DECEMDIGITATUS</i>	- 163 -
8.1	INTRODUCTION	- 164 -
8.2	MATERIALS AND METHODS.....	- 167 -
8.2.1	<i>Data collection: Habitat use in the wild</i>	- 167 -
8.2.2	<i>Data collection: Experimental subjects and competition trials</i>	- 168 -
8.2.3	<i>Data analysis</i>	- 170 -
8.3	RESULTS.....	- 170 -
8.3.1	<i>Habitat use in the wild</i>	- 170 -
8.3.2	<i>Competition trials</i>	- 172 -
8.4	DISCUSSION.....	- 175 -
9	GENERAL DISCUSSION	- 180 -
9.1	SUMMARY OF RESULTS	- 181 -
9.1.1	<i>Which traits are under selection?</i>	- 181 -
9.1.2	<i>Which traits are available for assortative mating?</i>	- 184 -
9.2	SPECIATION IN NEW ZEALAND TRIPLEFIN FISHES	- 186 -
9.3	CONCLUSIONS	- 189 -
10	REFERENCES	- 190 -
I.	APPENDIX (CHAPTER 2)	- 229 -

<i>i</i>	<i>Calculation of the DSE distances</i>	- 229 -
<i>ii</i>	<i>Formula for the d-hat raw stress (for the evaluation of the MDS plot)</i>	- 230 -
II.	APPENDIX (CHAPTER 6)	- 231 -
<i>i</i>	<i>Explanation of the CART methodology and terminology</i>	- 231 -
<i>ii</i>	<i>Determining tree size: pruning</i>	- 233 -
<i>iii</i>	<i>Determining tree size: cross-validation</i>	- 235 -
<i>iv</i>	<i>CART decision block</i>	- 237 -
III.	APPENDIX (CHAPTER 7)	- 238 -
<i>i</i>	<i>Nest microhabitats of nine triplefin species</i>	- 238 -
<i>ii</i>	<i>Pictures of triplefin nests</i>	- 239 -
<i>iii</i>	<i>Details of the homospecific spawning trials</i>	- 242 -
<i>iv</i>	<i>Pictures of the embryo development of <i>R. whereo</i> and <i>R. decemdigitatus</i></i>	- 243 -

List of Tables

TABLE 1: LIST OF NEW ZEALAND TRIPLEFIN SPECIES_____	13
TABLE 2: MICROPOSITION ABBREVIATIONS_____	24
TABLE 3: NUMBER OF HABITAT OBSERVATIONS OF EACH SPECIES AT EACH LOCATION_____	25
TABLE 4: ECOLOGICAL TRAITS USED IN THE COMPARATIVE PHYLOGENETIC ANALYSIS_____	29
TABLE 5: PERCENTAGE MICROPOSITION USE OF 17 TRIPLEFIN SPECIES_____	37
TABLE 6: NUMBER OF TRIPLEFINS USED TO COMPUTE HABITAT SPECIALISATION_____	70
TABLE 7: HABITAT COMPARISONS OF CONSPECIFIC ADULTS AND RECRUITS_____	92
TABLE 8: DISTRIBUTIONAL STATISTICS OF THE ROCKPOOL PREDICTOR VARIABLES_____	110
TABLE 9: CLASSIFICATION INDICES OBTAINED FOR THE FINAL CART TREE_____	112
TABLE 10: LINEAR REGRESSIONS OF HABITAT VARIABLES VERSUS INTERTIDAL HEIGHT_____	114
TABLE 11: SPAWNING PERIODS OF TRIPLEFINS IN NEW ZEALAND_____	141
TABLE 12: RESULTS OF PAIRED T-TESTS OF THE OVERALL MATE CHOICE TEST_____	151
TABLE 13: COURTSHIP DISPLAY OF <i>R. WHERO</i> AND <i>R. DECEMDIGITATUS</i> _____	153
TABLE 14: CATEGORICAL LINEAR MODEL ANALYSIS OF SUBSTRATUM USE_____	173
TABLE 15: DATA TABLE FOR CART EXAMPLE 1_____	231
TABLE 16: DECISION BLOCKS FOR CART EXAMPLE 1_____	233
TABLE 17: DECISION BLOCK CONSTITUTING THE CLASSIFIER FOR THE FINAL TREE_____	237
TABLE 18: TABLE SHOWING NEST MICROHABITAT CHARACTERISTICS_____	238
TABLE 19: TABLE SHOWING THE DETAILS OF THE HOMOSPECIFIC SPAWNING TRIALS_____	242

List of Figures

FIGURE 1: SAMPLING LOCATIONS AROUND NEW ZEALAND	21
FIGURE 2: PHYLOGRAM OF 17 TRIPLEFIN SPECIES	31
FIGURE 3: RELATIVE DENSITIES OF TRIPLEFIN SPECIES AT SEVEN LOCATIONS	32
FIGURE 4: MEAN USE OF DEPTH AND EXPOSURE	33
FIGURE 5: PERCENT USE OF SUBSTRATUM TYPES	34
FIGURE 6: 3-DIMENSIONAL MDS SOLUTION OF TRIPLEFIN HABITAT USE	35
FIGURE 7: MICROPOSITION USE OF TRIPLEFIN SPECIES	36
FIGURE 8: SAMPLING LOCATIONS AROUND NEW ZEALAND	48
FIGURE 9: ABIOTIC HABITAT COMPOSITION AT DIFFERENT LOCATIONS	51
FIGURE 10: BIOTIC HABITAT COMPOSITION AT DIFFERENT LOCATIONS	52
FIGURE 11: CANONICAL DISCRIMINANT ANALYSIS OF HABITAT TYPES AT LOCATIONS	53
FIGURE 12: PARTIAL CANONICAL CORRELATION OF FISH AND HABITAT VARIABLES	54
FIGURE 13: PARTIAL CANONICAL DISCRIMINANT ANALYSIS OF TRIPLEFINS AT LOCATIONS	55
FIGURE 14: MAP OF SITES SURVEYED AT THE HAURAKI GULF	66
FIGURE 15: PHYLOGENY OF 15 TRIPLEFIN SPECIES	69
FIGURE 16: HABITAT SPECIALISATION IN DEPTH AND EXPOSURE	71
FIGURE 17: HABITAT SPECIALISATION IN SUBSTRATUM TYPES	72
FIGURE 18: COMBINED SPECIALISATION INDEX	73
FIGURE 19: MAP OF STUDY SITES IN THE INNER AND OUTER HAURAKI GULF	82
FIGURE 20: DENSITY OF NEW <i>F. LAPILLUM</i> RECRUITS	87
FIGURE 21: DENSITY OF NEW <i>F. VARIUM</i> RECRUITS	87
FIGURE 22: DENSITY OF NEW <i>N. SEGMENTATUS</i> RECRUITS	88
FIGURE 23: DENSITY OF NEW <i>O. MARYANNAE</i> RECRUITS	88
FIGURE 24: DENSITY OF NEW <i>R. WHERO</i> RECRUITS	89
FIGURE 25: SUBSTRATUM USE OF TRIPLEFIN ADULTS AND RECRUITS	90
FIGURE 26: USE OF DEPTH AND EXPOSURE BY TRIPLEFIN ADULTS AND RECRUITS	90
FIGURE 27: MICROPOSITION USE BY TRIPLEFIN ADULTS AND RECRUITS	91
FIGURE 28: SPECIALISATION INDEX OF TRIPLEFIN ADULTS AND RECRUITS	95
FIGURE 29: RECRUIT VERSUS ADULT DENSITY	96
FIGURE 30: ROCKPOOL STUDY SITES	106
FIGURE 31: PHOTOGRAPHS OF <i>B. LESLEYAE</i> AND <i>B. MEDIUS</i>	108
FIGURE 32: VERTICAL ZONATION OF <i>B. LESLEYAE</i> AND <i>B. MEDIUS</i>	111

FIGURE 33: RESULTS OF THE CART CROSS-VALIDATION PROCEDURES	113
FIGURE 34: FINAL PRUNED CART TREE	114
FIGURE 35: BODY LENGTH OF <i>B. LESLEYAE</i> AND <i>B. MEDIUS</i>	115
FIGURE 36: LENGTH OF <i>B. LESLEYAE</i> AND <i>B. MEDIUS</i> VERSUS INTERTIDAL HEIGHT	116
FIGURE 37: MEAN NUMBER OF INDIVIDUALS PER ROCKPOOL	117
FIGURE 38: OTHER SPECIES FOUND IN ROCKPOOLS	117
FIGURE 39: MAP OF STUDY SITES IN THE INNER AND OUTER HAURAKI GULF	131
FIGURE 40: MATE CHOICE APPARATUS	138
FIGURE 41: CANONICAL DISCRIMINANT ANALYSIS OF NESTING SITES VERSUS SPECIES	140
FIGURE 42: GEOGRAPHIC VARIATION IN NESTS	142
FIGURE 43: SIZE OF REPRODUCTIVE <i>R. WHERO</i> AND <i>R. DECEMDIGITATUS</i> MALES	144
FIGURE 44: SIZE OF MATURE <i>R. WHERO</i> AND <i>R. DECEMDIGITATUS</i>	144
FIGURE 45: MALE BODY COLOURATION OF TRIPLEFINS	146
FIGURE 46: MALE BODY COLOURATION OF TRIPLEFINS	147
FIGURE 47: <i>KARALEPIS STEWARTI</i> UNDER VISIBLE AND UV LIGHT	148
FIGURE 48: <i>RUANOHO DECEMDIGITATUS</i> UNDER VISIBLE AND UV LIGHT	148
FIGURE 49: <i>RUANOHO WHERO</i> UNDER VISIBLE AND UV LIGHT	148
FIGURE 50: MEDIAN BODY LENGTHS OF SPAWNING TRIPLEFIN MALES	149
FIGURE 51: INITIAL FEMALE MATE CHOICE OF <i>R. WHERO</i> AND <i>R. DECEMDIGITATUS</i>	150
FIGURE 52: PHOTOGRAPH OF <i>R. DECEMDIGITATUS</i> WITH ALL THREE DORSAL FINS ERECT	152
FIGURE 53: PHOTOGRAPH OF <i>R. DECEMDIGITATUS</i> FLICKING THE FIRST DORSAL FIN	152
FIGURE 54: PHOTOGRAPH OF <i>R. DECEMDIGITATUS</i> SHOWING THE LATERAL MOVEMENT	152
FIGURE 55: ETHOGRAM OF THE MALE COURTSHIP DISPLAY IN <i>R. DECEMDIGITATUS</i>	154
FIGURE 56: ETHOGRAM OF THE MALE COURTSHIP DISPLAY IN <i>R. WHERO</i>	154
FIGURE 57: MAP OF STUDY AND COLLECTION SITES	167
FIGURE 58: LENGTH OF SPECIMENS USED FOR THE COMPETITION TRIALS	169
FIGURE 59: DEPTH AND EXPOSURE OF <i>R. DECEMDIGITATUS</i> AND <i>R. WHERO</i> IN THE WILD	171
FIGURE 60: MICROPOSITION USE OF <i>R. DECEMDIGITATUS</i> AND <i>R. WHERO</i> IN THE WILD	172
FIGURE 61: PERCENTAGE USE OF SUBSTRATUM TYPES IN THE EXPERIMENTS	173
FIGURE 62: PERCENTAGE USE OF MICROPOSITION TYPES IN THE EXPERIMENTS	174
FIGURE 63: EXAMPLE OF A CART ANALYSIS	232
FIGURE 64: EXAMPLE 2 OF A CART ANALYSIS	234
FIGURE 65: EXAMPLE OF PRUNING A CART TREE	236
FIGURE 66: NEST OF <i>F. LAPILLUM</i>	239
FIGURE 67: NEST OF <i>F. MALCOLMI</i>	239

FIGURE 68: NEST OF <i>F. VARIUM</i>	240
FIGURE 69: NEST OF <i>G. NIGRIPENNE</i>	240
FIGURE 70: NEST OF <i>G. CAPITO</i>	241
FIGURE 71: NEST OF <i>O. MARYANNAE</i>	241
FIGURE 72: NEST OF <i>R. WHERO</i>	242
FIGURE 73: EGGS OF <i>R. DECEMDIGITATUS</i> AND <i>R. WHERO</i>	243