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](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 sympathy 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 Sym. 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 Selection of species.................................................................................. - 21 -
       2.2.2 Selection of locations and sites................................................................... - 22 -
       2.2.3 Data collection ....................................................................................... - 23 -
       2.2.4 Data analysis ......................................................................................... - 25 -
   2.3 RESULTS............................................................................................................. - 31 -
       2.3.1 Interspecific overlap in habitat use ............................................................. - 32 -
       2.3.2 Similarity between sister-species............................................................... - 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 Data collection ....................................................................................... - 47 -
       3.2.2 Data analysis ......................................................................................... - 50 -
   3.3 RESULTS............................................................................................................. - 51 -
   3.4 DISCUSSION....................................................................................................... - 56 -

4 EVOLUTION OF HABITAT SPECIALISATION IN TRIPLEFIN FISHES .... - 62 -
Calculation of the DSE distances ................................................................. - 229 -
Formula for the d-hat raw stress (for the evaluation of the MDS plot) ........ - 230 -

II. APPENDIX (CHAPTER 6) .............................................................................. - 231 -
Explanation of the CART methodology and terminology ....................... - 231 -
Determining tree size: pruning ................................................................. - 233 -
Determining tree size: cross-validation .................................................. - 235 -
CART decision block .............................................................................. - 237 -

III. APPENDIX (CHAPTER 7) ............................................................... - 238 -
Nest microhabitats of nine triplefin species ............................................. - 238 -
Pictures of triplefin nests ....................................................................... - 239 -
Details of the homospecific spawning trials ......................................... - 242 -
Pictures of the embryo development of R. whero and R. decemdigitatus .... - 243 -
# List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 1</td>
<td>List of New Zealand triplefin species</td>
<td>13</td>
</tr>
<tr>
<td>Table 2</td>
<td>Microposition abbreviations</td>
<td>24</td>
</tr>
<tr>
<td>Table 3</td>
<td>Number of habitat observations of each species at each location</td>
<td>25</td>
</tr>
<tr>
<td>Table 4</td>
<td>Ecological traits used in the comparative phylogenetic analysis</td>
<td>29</td>
</tr>
<tr>
<td>Table 5</td>
<td>Percentage microposition use of 17 triplefin species</td>
<td>37</td>
</tr>
<tr>
<td>Table 6</td>
<td>Number of triplefins used to compute habitat specialisation</td>
<td>70</td>
</tr>
<tr>
<td>Table 7</td>
<td>Habitat comparisons of conspecific adults and recruits</td>
<td>92</td>
</tr>
<tr>
<td>Table 8</td>
<td>Distributional statistics of the rockpool predictor variables</td>
<td>110</td>
</tr>
<tr>
<td>Table 9</td>
<td>Classification indices obtained for the final CART tree</td>
<td>112</td>
</tr>
<tr>
<td>Table 10</td>
<td>Linear regressions of habitat variables versus intertidal height</td>
<td>114</td>
</tr>
<tr>
<td>Table 11</td>
<td>Spawning periods of triplefins in New Zealand</td>
<td>141</td>
</tr>
<tr>
<td>Table 12</td>
<td>Results of paired t-tests of the overall mate choice test</td>
<td>151</td>
</tr>
<tr>
<td>Table 13</td>
<td>Courtship display of <em>R. whero</em> and <em>R. decemdigitatus</em></td>
<td>153</td>
</tr>
<tr>
<td>Table 14</td>
<td>Categorical linear model analysis of substratum use</td>
<td>173</td>
</tr>
<tr>
<td>Table 15</td>
<td>Data table for CART example 1</td>
<td>231</td>
</tr>
<tr>
<td>Table 16</td>
<td>Decision blocks for CART example 1</td>
<td>233</td>
</tr>
<tr>
<td>Table 17</td>
<td>Decision block constituting the classifier for the final tree</td>
<td>237</td>
</tr>
<tr>
<td>Table 18</td>
<td>Table showing nest microhabitat characteristics</td>
<td>238</td>
</tr>
<tr>
<td>Table 19</td>
<td>Table showing the details of the homospecific spawning trials</td>
<td>242</td>
</tr>
</tbody>
</table>
# 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:** MICROPPOSITION 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 *F. LAPILLUM* RECRUITS ................................ 87  
**FIGURE 21:** DENSITY OF NEW *F. VARium* RECRUITS .................................... 87  
**FIGURE 22:** DENSITY OF NEW *N. SEGMENTATUS* RECRUITS ............................... 88  
**FIGURE 23:** DENSITY OF NEW *O. MARYANNAE* RECRUITS ............................... 88  
**FIGURE 24:** DENSITY OF NEW *R. WHERO* 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:** MICROPPOSITION 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 *B. LESLEYAE* AND *B. MEDIUS* ....................... 108  
**FIGURE 32:** VERTICAL ZONATION OF *B. LESLEYAE* AND *B. MEDIUS* .................. 111
FIGURE 33: RESULTS OF THE CART CROSS-VALIDATION PROCEDURES 113
FIGURE 34: FINAL PRUNED CART TREE 114
FIGURE 35: BODY LENGTH OF B. LESLEYAE AND B. MEDIUS 115
FIGURE 36: LENGTH OF B. LESLEYAE AND B. MEDIUS VERSUS INERTIDAL 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 R. WHERO AND R. DECEMDIGITATUS MALES ______144
FIGURE 44: SIZE OF MATURE R. WHERO AND R. DECEMDIGITATUS ______144
FIGURE 45: MALE BODY COLOURATION OF TRIPLEFINS 146
FIGURE 46: MALE BODY COLOURATION OF TRIPLEFINS 147
FIGURE 47: KARALEPIS STEWARTI UNDER VISIBLE AND UV LIGHT 148
FIGURE 48: RUANOHO DECEMDIGITATUS UNDER VISIBLE AND UV LIGHT 148
FIGURE 49: RUANOHO WHERO UNDER VISIBLE AND UV LIGHT 148
FIGURE 50: MEDIAN BODY LENGTHS OF SPAWNING TRIPLEFIN MALES 149
FIGURE 51: INITIAL FEMALE MATE CHOICE OF R. WHERO AND R. DECEMDIGITATUS ______150
FIGURE 52: PHOTOGRAPH OF R. DECEMDIGITATUS WITH ALL THREE DORSAL FINS ERECT 152
FIGURE 53: PHOTOGRAPH OF R. DECEMDIGITATUS FLICKING THE FIRST DORSAL FIN 152
FIGURE 54: PHOTOGRAPH OF R. DECEMDIGITATUS SHOWING THE LATERAL MOVEMENT 152
FIGURE 55: ETHOGRAM OF THE MALE COURTSHIP DISPLAY IN R. DECEMDIGITATUS 154
FIGURE 56: ETHOGRAM OF THE MALE COURTSHIP DISPLAY IN R. WHERO 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 R. DECEMDIGITATUS AND R. WHERO IN THE WILD 171
FIGURE 60: MICROPPOSITION USE OF R. DECEMDIGITATUS AND R. WHERO IN THE WILD 172
FIGURE 61: PERCENTAGE USE OF SUBSTRATUM TYPES IN THE EXPERIMENTS 173
FIGURE 62: PERCENTAGE USE OF MICROPPOSITION 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 F. LAPILLUM 239
FIGURE 67: NEST OF F. MALCOLMI 239