

A MORPHOLOGICAL EXAMINATION OF SYMPATRIC CISCO
FORMS IN FOUR LAKES WITH SPECIFIC REFERENCE TO THE
OCCURRENCE OF SHORTJAW CISCO (*COREGONUS ZENITHICUS*)
IN MANITOBA

BY

LEE MURRAY

A Thesis submitted to
the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

Department of Zoology
University of Manitoba
Winnipeg, Manitoba

© Copyright by Lee Murray, October 2006

THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION

**A MORPHOLOGICAL EXAMINATION OF SYMPATRIC CISCO
FORMS IN FOUR LAKES WITH SPECIFIC REFERENCE TO THE
OCCURRENCE OF SHORTJAW CISCO (*COREGONUS ZENITHICUS*)
IN MANITOBA**

BY

Lee Murray

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree**
OF
MASTER OF SCIENCE

Lee Murray © 2006

Permission has been granted to the Library of the University of Manitoba to lend or sell copies of this thesis/practicum, to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film, and to University Microfilms Inc. to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

ABSTRACT

The shortjaw cisco (*Coregonus zenithicus*) is a widespread species ranging from the Great Lakes region, northwest to Great Slave Lake. Beyond the Great Lakes region, the validity of this species has been questioned due to genetic and morphological variability. Ciscoes were collected from four lakes reported to contain putative *C. zenithicus* (Lake Athapapuskow, George Lake, and Clearwater Lake, MB; and Reindeer Lake, SK). An examination of gillraker count and arrangement, jaw position, body size, and dorsal colouration was used to initially identify cisco forms within each lake. Multivariate analyses including Principal Component Analysis and Discriminant Analysis incorporating additional meristic and morphometric characters were used to examine within-lake and between-lake variation. Sympatric low and high gillraker forms were found within each lake. The low forms were found to conform to populations of *C. zenithicus* reported in the literature and the high forms were found to be consistent with descriptions of *C. artedi*.

ACKNOWLEDGMENTS

First and foremost I would like to thank my supervisor, Dr. J.D. Reist for presenting me with this opportunity, providing guidance and support along the way, and most of all for his patience. I would like to thank my committee members, Dr. K.W. Stewart, Dr. R.A. Bodaly, and Dr. B.A. Ford, for their guidance with the initial design of this study and for their suggestions and comments throughout. Special thanks to Jim Johnson for his assistance in the field and for his guidance throughout the project. Thanks to Thomas Todd and Mark Steinhilber for their valuable discussions about cisco identification and for providing specimens. Thank you to The Royal Ontario Museum of Canada for allowing me to examine museum specimens. Thanks to everyone in the Zoology Department at the University of Manitoba, especially to Madeleine Harris for her invaluable help. I would like to thank all the graduate and undergraduate students along the way that made this an enjoyable experience, especially Dwight Klippenstine. Thanks to North-South Consultants for fish processing assistance and for providing me with an employment opportunity. I would also like to thank Manitoba Conservation and the Saskatchewan Department of Natural Resources for providing the collection permits that allowed this work to be conducted. Finally, I would like to thank my family and my wife, Nicole, for their patience and support. Financial support was provided by Fisheries and Oceans Species At Risk Program, Fisheries and Oceans Canada Arctic Division, University of Manitoba Graduate Studies, Faculty of Science, Department of Zoology, and by the Fish Futures K. W. Stewart Scholarship.

TABLE OF CONTENTS

ABSTRACT.....	I
ACKNOWLEDGMENTS	II
LIST OF FIGURES	VII
LIST OF TABLES.....	XI
LIST OF APPENDICES.....	XIII
1. INTRODUCTION.....	1
The Question	1
Coregoninae Systematics.....	4
Historic Cisco Arrangement	4
Current Arrangement.....	4
Ciscoes.....	6
Validity and Identification of <i>C. zenithicus</i>	10
Is <i>C. zenithicus</i> a distinct and identifiable taxon?.....	10
Is <i>Coregonus zenithicus</i> a valid species?.....	13
Do different forms of <i>C. zenithicus</i> exist throughout its range?.....	19
Species Descriptions.....	20
<i>Coregonus zenithicus</i>	20
<i>Coregonus artedi</i>	27
<i>Coregonus nigripinnis</i>	36
Radiation and Evolution in North America of <i>Coregonus zenithicus</i>	37
Species Concepts and Criteria.....	42

Study Objectives and Approach.....	46
2. MATERIALS AND METHODS	49
Study Sites.....	49
Lake Athapapuskow	49
Reindeer Lake.....	52
George Lake.....	55
Clearwater Lake.....	58
Specimen Collection.....	61
Biological, Morphometric and Meristic Characters	63
Measurements	63
Counts.....	65
Aging Structure.....	67
Adjustment of Morphometric Data to Account for the Effects of Body Size	67
Statistical Analysis	69
3. RESULTS - COMPARISON OF LAKE ATHAPAPUSKOW CISCOES.....	71
General Biology.....	71
Discrimination of Cisco Forms.....	74
Morphological Confirmation of Differences.....	82
Analysis Including Little Athapapuskow Ciscoes.....	86
Hypothesis Testing of Form Differences.....	89
Summary of Lake Athapapuskow Cisco Forms	95
4. RESULTS - COMPARISON OF REINDEER LAKE CISCOES	97
General Biology.....	97

	Discrimination of Cisco Forms.....	100
	Morphological Confirmation of Differences.....	106
	Hypothesis Testing of Form Differences.....	111
	Summary of Reindeer Lake Cisco Forms.....	116
5.	RESULTS - COMPARISON OF GEORGE LAKE CISCOES.....	118
	General Biology.....	118
	Discrimination of Cisco Forms.....	121
	Morphological Confirmation of Differences.....	129
	Hypothesis Testing of Form Differences.....	134
	Summary of George Lake Cisco Forms.....	138
6.	RESULTS - COMPARISON OF CLEARWATER LAKE CISCOES.....	140
	General Biology.....	140
	Discrimination of Cisco Forms.....	142
	Morphological Examination of Differences.....	146
	Hypothesis Testing of Form Differences.....	154
	Summary of Clearwater Lake Cisco Forms.....	159
7.	RESULTS - EXAMINATION OF BETWEEN-LAKE CISCO VARIATION....	161
	Comparison of Key Characters.....	161
	Multivariate Test of Equality of Cisco Forms.....	167
	Taxonomic Identity of Manitoba Cisco Forms.....	183
8.	DISCUSSION.....	188
	Lake Athapapuskow.....	188
	Reindeer Lake.....	191

George Lake 192
Clearwater Lake..... 194
Comparison of Cisco Forms Between-Lakes 195
Taxonomic Association of Cisco Forms 196
Speculated Origin of Sympatric Cisco Forms 201
9. LITERATURE CITED 207

LIST OF FIGURES

Figure 1.1. Key characters often used to distinguish between <i>Coregonus zenithicus</i> and <i>C. artedi</i>	12
Figure 1.2. Current distribution of putative <i>Coregonus zenithicus</i> in Canada.....	16
Figure 1.3. Recession of the North American glacial ice sheets from the most recent maximum 18 000 years B.P. to 7 000 years B.P. White areas represent glaciers; shaded areas represent land surfaces; black areas represent water bodies (after Pielou 1991).	40
Figure 1.4. Total area covered by glacial Lake Agassiz over its 5 000 year history; approximately 1.5 million km ² . The size of the lake fluctuated over its lifespan, gradually shifting from south to north following the recession of the Laurentide Ice Sheet (after Leverington and Teller 2003).	41
Figure 2.1. Lake Athapapuskow map (Adapted from Day 1983). Numbered dots indicate set number and set information is presented in Appendix 1-1.	51
Figure 2.2. Map of Reindeer Lake (after Dean 1975). Enlarged region shows the focus of sampling effort with sets indicated by numbered dots. Note: set information is presented in Appendix 1-2.	54
Figure 2.3. Bathymetric map of George Lake (adapted from Gibson and Johnson 1969). Note: collection sites are indicated and set information is presented in Appendix 1-3.....	57
Figure 2.4. Bathymetric map of Clearwater Lake (Adapted from Schlick 1978). Numbered dots indicate set numbers; set information is presented in Appendix 1-4. Note: Sets 1 and 2 were conducted in 2000; sets 3 – 6 were conducted in 2002. Note: sets 1 and 3 were made at the same location.	60
Figure 2.5. Morphometric and meristic measurements used in this study (from Vuorinen et al. 1993).....	66
Figure 3.1. Relationship between total gillraker count and standard length for Lake Athapapuskow ciscoes with individuals identified by sex.....	73
Figure 3.2. Plots of standard length versus gillraker number for all Lake Athapapuskow ciscoes showing forms suggested by gillraker counts.....	76
Figure 3.3. Frequency distribution of total gillraker counts for all ciscoes from Lake Athapapuskow. All individuals with counts 35 or less were placed in the low group and 36 or more were placed in the high group with the exception of one individual from Little Athapapuskow with 37 gillrakers which was placed in the low group. The arrow indicates the point of separation between groups.	77
Figure 3.4. Gill arches removed from Lake Athapapuskow ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes and lower panel of high-gillrakered ciscoes from Lake Athapapuskow.	78

Figure 3.5.	General appearance of Lake Athapapuskow ciscoes. The Fish in upper panel had a standard length of 187 mm and 30 gillrakers and is representative of the low form. The fish in lower panel had a standard length of 99 mm and 39 gillrakers and is representative of the high form. Note: previously frozen specimens.	79
Figure 3.6.	Total gillraker count distributions for all Lake Athapapuskow collection sites. Arrows indicate separation between groups for sets 2 and 3 based on key characters. Each panel indicates set number, date, depth, and number of fish captured (see also Appendix 2-2).....	80
Figure 3.7.	PCA plots for ciscoes from Big Athapapuskow based upon meristic and morphometric characters adjusted by ratios. Variable loadings are described in the text. Form was assigned <i>a posteriori</i> using key character criteria outlined in the text.	83
Figure 3.8.	Plot of scores from PCA of all ciscoes from Lake Athapapuskow using meristic characters (not including gillraker counts) and morphometric characters adjusted by common within-group residuals.....	87
Figure 3.9.	Plot of the functions calculated by a Discriminant Analysis of all Lake Athapapuskow cisco forms. All morphometric characters were adjusted by common-within-group residuals.....	94
Figure 4.1.	Relationship between total gillraker count and standard length for Reindeer Lake ciscoes with individuals identified by sex.....	99
Figure 4.2.	Frequency distribution of total gillraker counts for all ciscoes from Reindeer Lake. All individuals with counts of 32 or less were tentatively placed in the low group, those with 33 to 38 were placed in the mid group, and those with 39 or more were placed in the high group.....	102
Figure 4.3.	Relationship between total gillraker count and standard length for the initial groups. Hypothesized groups were based on gillraker count distributions (see text).	103
Figure 4.4.	General appearance of Reindeer Lake ciscoes. The fish in the upper panel is representative of the low form and had a standard length of 196 mm and 25 gillrakers. The fish in the middle panel is representative of the mid form and had a standard length of 158 mm and 33 gillrakers. The fish in the lower panel is representative of the high form and had a standard length of 154 mm and 37 gillrakers. (Note: previously frozen specimens).....	104
Figure 4.5.	Gill arches removed from Reindeer Lake ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes, middle panel of mid-gillrakered ciscoes, and lower panel of high-gillrakered ciscoes from Reindeer Lake.	105
Figure 4.6.	Plot of PCA scores for Reindeer Lake ciscoes using meristic and morphometric characters adjusted by ratios. Boundaries show forms suggested by the results of this analysis.....	108
Figure 4.7.	Discriminant function plots for Reindeer Lake ciscoes. Individuals identified by exploratory PCA are shown in the upper panel and new groups predicted by Discriminant Analysis are shown in the lower panel.	115

Figure 5.1. Relationship between total gillraker count and standard length for George Lake ciscoes with sex identified.....	120
Figure 5.2. Frequency distribution of total gillraker counts for all ciscoes from George Lake. All individuals with counts of 38 or less were placed in the low form along with one individual with 39 gillrakers. All but one individual with 39 or more were placed in the high form.....	123
Figure 5.3. Relationship between gillraker count and standard length for George Lake ciscoes with individuals identified by initial forms.....	124
Figure 5.4. Gill arches removed from George Lake ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes and lower panel of high-gillrakered ciscoes from George Lake.....	125
Figure 5.5. General appearance of George Lake ciscoes. The upper panel shows a member of the low form and had a standard length of 160 mm and 32 gillrakers. The lower panel shows a member of the high form had a standard length of 102 mm and 41 gillrakers. (Note: previously frozen specimens).....	126
Figure 5.6. Plot of PCA scores for George Lake ciscoes using meristic characters and morphometric characters adjusted by ratios. Forms were assigned <i>a posteriori</i> as outlined in the text. Boundaries indicate Forms suggested by this PCA.	131
Figure 6.1. Relationship between standard length and gillraker count for Clearwater Lake with individuals identified by sex.	141
Figure 6.2. Frequency distribution of total gillraker counts for all ciscoes from Clearwater Lake.	143
Figure 6.3. Gill arches excised from Clearwater Lake ciscoes. Upper panel shows typical gillraker structure of cisco with lower gillraker count and lower panel of cisco with higher gillraker count.	144
Figure 6.4. General appearance of Clearwater Lake ciscoes. The cisco in upper panel had a standard length of 113 mm and 36 gillrakers and was representative of the low form. The cisco in lower panel had a standard length of 91 mm and 42 gillrakers and was representative of the high form. (Note: previously frozen specimens).....	145
Figure 6.5. Plot scores on components 1 and 2 from PCA of ciscoes from Clearwater Lake using meristic characters including premaxillary angle. Two potential forms are suggested by the combined separation on components 1 and 2.	147
Figure 6.6. Plots of scores for the first two Principal Components using morphometric characters adjusted by common-within-group residuals (upper panel). Lower panel displays scores from Component 2 with total gillraker count. Forms were designated <i>a posteriori</i>	152
Figure 6.7. Frequency plot of discriminant scores from DA of Clearwater Lake ciscoes using morphometric characters adjusted by common-within-group residuals.....	157

Figure 7.1. Plot of scores from PCA of all cisco forms using meristic characters and morphometric characters adjusted by ratios. Forms were designated <i>a posteriori</i>	170
Figure 7.2. Plot of scores from PCA of Manitoba cisco forms using morphometric characters adjusted by common-within-group residuals. Upper panel shows components one and two, lower panel one and three.	174
Figure 7.3. Games-Howell pairwise comparison results following an ANOVA for between-lake comparison of 26 characters (6 meristic and 20 morphometric adjusted by common within-group residuals). Values indicate the total number of mean differences found to be statistically significantly between cisco forms across all lakes ($p < 0.05$).	177
Figure 7.4. Plot of function coefficient scores from Discriminant Analysis using premaxillary angle and morphometric characters adjusted by common-within-group residuals. Forms were identified based on predicted group membership values suggested by the DA results.	182
Figure 7.5. Plot of component scores for PCA of meristic and morphometric characters adjusted by ratios. Individual Lake Nipigon and Lake Superior known <i>Coregonus zenithicus</i> specimens are indicated by solid and shaded squares respectively. Ellipses include the majority of Manitoba ciscoes into their respective forms.	187

LIST OF TABLES

Table 1.1.	Taxonomic summary of North American ciscoes, compiled from Koelz (1929), Hubbs and Lagler (1964), McPhail and Lindsey (1970), Clarke (1973), Scott and Crossman (1973), Todd and Smith (1992), Steinhilber (2000).....	9
Table 1.2.	Key characteristics of <i>Coregonus artedi</i> and <i>C. zenithicus</i>	11
Table 1.3.	Reported occurrences of <i>Coregonus zenithicus</i> in North America	17
Table 1.4.	Examples of the prolific identification of <i>Coregonus artedi</i> subspecies in the past (from Hubbs and Lagler 1964).....	35
Table 3.1.	Descriptive statistics for the low and high gillraker forms collected from Lake Athapapuskow. All variables are represented by raw, untransformed values..	81
Table 3.2.	Character loadings and variance explained by PCA on Big Athapapuskow ciscoes using meristic and morphometric characters adjusted by ratios.....	84
Table 3.3.	Character loadings and eigenvalues from PCA of all Lake Athapapuskow ciscoes using meristic and morphometric characters adjusted by common-within-group residuals.	88
Table 3.4.	ANOVA probability values between cisco forms from Lake Athapapuskow and Levene's test for homogeneity of variance. Values in bold indicates significance at $P<0.05$	90
Table 3.5.	Discriminant Analysis results for all Lake Athapapuskow cisco forms. Analysis 1 with Little Athapapuskow and Big Athapapuskow low forms combined and analysis 2 with them treated separately.	93
Table 4.1.	Character loadings and variance explained for PCA of Reindeer Lake ciscoes using meristic and morphometric characters adjusted by ratios.....	109
Table 4.2.	ANOVA probability values between Reindeer Lake cisco forms and Levene's test of homogeneity of variance. Values in bold indicate significance at $P<0.01$	112
Table 4.3.	Discriminant Analysis results for Reindeer Lake ciscoes using meristic characters and morphometric characters adjusted by residuals.....	114
Table 5.1.	Descriptive statistics for George Lake ciscoes placed in the low-gillraker form.	127
Table 5.2.	Descriptive statistics for George Lake ciscoes placed in the high-gillraker form.	128
Table 5.3.	Character loadings and variance explained for PCA of George Lake ciscoes using meristic characters and morphometric characters adjusted by ratios.	132
Table 5.4.	ANOVA test probability values between George Lake cisco forms and Levene's test of homogeneity of variance. Values in bold indicate significance at $P<0.05$	135

Table 5.5.	Discriminant Analysis results for George Lake cisco forms.....	137
Table 6.1.	Character loadings and variance explained by a PCA of Clearwater Lake ciscoes based upon meristic characters and premaxillary angle.	148
Table 6.2.	Character loadings and variance explained by PCA of Clearwater Lake ciscoes for morphometric characters adjusted with common-within-group residuals.	153
Table 6.3.	ANOVA probability values between Clearwater Lake cisco forms and Levene's test of homogeneity of variance. Values in bold indicates significance at $P < 0.05$	155
Table 6.4.	Discriminant Analysis results for Clearwater Lake cisco forms using morphometric characters adjusted by common-within-groups residuals.....	158
Table 7.1.	Comparison of key character values for cisco forms identified in this study including known <i>C. zenithicus</i> specimens from Lake Superior and Lake Nipigon.	165
Table 7.2.	Comparison of character values for cisco forms identified in this study including known <i>C. zenithicus</i> specimens from Lake Superior and Lake Nipigon.	166
Table 7.3.	Character loadings and variance explained by PCA on all cisco forms using meristic and morphometric characters adjusted by ratios.....	169
Table 7.4.	Character loadings and variance explained by PCA on all cisco forms using morphometric characters adjusted by common-within-group residuals.....	173
Table 7.5.	Coefficients for Discriminant Analysis of all cisco forms using premaxillary angle and morphometric characters adjusted by common-within-group residuals.	180
Table 7.6.	Classification results from Discriminant Analysis of all cisco forms using premaxillary angle and morphometric characters adjusted by common-within-group residuals.	181
Table 7.7.	Range of values for gillraker count reported by various sources for <i>Coregonus zenithicus</i> and <i>C. artedi</i> populations throughout North America.	185
Table 7.8.	Character loadings and variance explained by PCA on all cisco forms using meristic characters and morphometric characters adjusted by ratios.	186

LIST OF APPENDICES

Appendix 1-1 .	Physical characteristics of Lake Athapapuskow (after Day 1983)....	216
Appendix 1-2.	Physical characteristics of Reindeer Lake (after Dean 1975).....	217
Appendix 1-3.	Physical characteristics of George Lake (data from Gibson and Johnson 1969).	218
Appendix 1-4.	Physical parameters of Clearwater Lake (after Schlick 1978).	219
Appendix 2-1.	Collection information for sets from Lake Athapapuskow, 2000.	220
Appendix 2-2.	Collection information for sets from Reindeer Lake, 2001.....	221
Appendix 2-3.	Collection information for sets from George Lake.....	222
Appendix 2-4.	Collection information for sets from Clearwater Lake.....	223
Appendix 3-1.	Descriptive statistics for the combined cisco catch from Big Athapapuskow. All variables are represented by raw, untransformed values.....	224
Appendix 3-2.	Standard length frequency distribution for all ciscoes from both basins of Lake Athapapuskow.....	226
Appendix 3-3.	Standard length versus weight for ciscoes from Lake Athapapuskow collection sites. Set number, date, depth, and number of number of fish captured and included in the legend.....	227
Appendix 3-4.	Age frequency distribution for Lake Athapapuskow.....	228
Appendix 3-5.	Relationship between total gillraker count and standard length for all ciscoes collected from Lake Athapapuskow with individuals identified to maturity state.	229
Appendix 3-6.	Size-at-age for Lake Athapapuskow cisco forms.	230
Appendix 3-7.	Plot of components 1 and 2 of PCA for ciscoes from Big Athapapuskow based upon meristic variables. Form was assigned <i>a posteriori</i> using key character criteria outlined in the text.....	231
Appendix 3-8.	Character loadings and variance explained by PCA of Big Athapapuskow ciscoes based upon meristic variables and premaxillary angle.	232
Appendix 3-9.	PCA plots for ciscoes from Big Athapapuskow based upon morphometric characters adjusted by ratios. Form was assigned <i>a posteriori</i> using key character criteria outlined in the text.	233
Appendix 3-10.	Character loadings and variance explained for PCA of Big Athapapuskow morphometric characters adjusted by ratios.	234
Appendix 3-11.	Plot of scores from PCA of Big Athapapuskow cisco using morphometric characters adjusted by common within-groups residuals.	235

Appendix 3-12. Character loadings and variance explained by PCA of Big Athapapuskow ciscoes with morphometric characters adjusted by common within-group residuals.	236
Appendix 4-1. Descriptive statistics for all ciscoes from Reindeer Lake. All variables are represented by raw, untransformed values.	237
Appendix 4-2. Standard length frequency distribution for all ciscoes from Reindeer Lake.	238
Appendix 4-3. Standard length versus weight for ciscoes from Reindeer Lake. Set number, date, depth, and number of number of fish captured and included in the legend.	239
Appendix 4-4. Age frequency distribution for ciscoes from Reindeer Lake.....	240
Appendix 4-5. Relationship between total gillraker count and standard length for all ciscoes from Reindeer Lake with individuals identified to maturity state.....	241
Appendix 4-6. Total gillraker count distributions for all Reindeer Lake collection sites. Arrows indicate hypothesized boundaries for the forms. Set 4 is not shown because it consisted of only one individual.....	242
Appendix 4-7. Descriptive statistics for the Reindeer Lake low gillraker form. All characters are represented by raw, untransformed values.....	243
Appendix 4-8. Descriptive statistics for the Reindeer Lake mid gillraker form. All characters are represented by raw, untransformed values.....	244
Appendix 4-9. Descriptive statistics for the Reindeer Lake high gillraker form. All characters are represented by raw, untransformed values.....	245
Appendix 4-10. Size-at-age plots for Reindeer Lake cisco groups.	246
Appendix 4-11. Plot of PCA scores on components 1 and 2 for Reindeer Lake ciscoes using meristic characters and premaxillary angle.	247
Appendix 4-12. Character loadings and variance explained from PCA of ciscoes from Reindeer Lake using meristic characters and premaxillary angle.....	248
Appendix 4-13. Plot of PCA scores for ciscoes from Reindeer Lake using morphometric characters adjusted by ratios. Form was assigned <i>a posteriori</i> using criteria outlined in text.	249
Appendix 4-14. Character loadings and variance explained by PCA of Reindeer Lake ciscoes using morphometric characters adjusted by ratios.....	250
Appendix 4-15. PCA plot for Reindeer Lake ciscoes using morphometric characters adjusted to common within-group residual values. Groups were identified <i>a posteriori</i>	251
Appendix 4-16. Character loadings and variance explained by PCA for Reindeer Lake ciscoes using morphometric characters adjusted by common within-group residuals.	252

Appendix 5-1. Descriptive statistics for the combined cisco catch from George Lake. All characters are represented by raw, untransformed data.	253
Appendix 5-2. Standard length frequency distribution for all ciscoes collected from George Lake.	254
Appendix 5-3. Standard length versus weight for ciscoes collected from George Lake in 2000 and 2001.	255
Appendix 5-4. Age frequency distribution for George Lake ciscoes.	256
Appendix 5-5. Relationship between total gillraker count and standard length for all ciscoes from George Lake with maturity identified.	257
Appendix 5-6. Size-at-age plots for George Lake cisco forms.	258
Appendix 5-7. Plot of PCA scores on components 1 and 2 for ciscoes collected from George Lake using meristic characters including premaxillary angle. Forms were identified <i>a posteriori</i> as outlined in text.	259
Appendix 5-8. Character loadings and variance explained from PCA of George Lake ciscoes using meristic characters and premaxillary angle.	260
Appendix 5-9. PCA plot for ciscoes collected from George Lake using morphometric characters adjusted by ratios. Groups were identified <i>a posteriori</i> following PCA using meristic characters. Boundaries indicate groups suggested by this PCA.	261
Appendix 5-10. Character loadings and variance explained by PCA of George Lake ciscoes using morphometric characters adjusted by ratios.	262
Appendix 5-11. Plot of PCA scores for George Lake ciscoes using morphometric characters adjusted by common-within-group residuals. Forms were assigned <i>a posteriori</i> as outlined in the text. Boundaries show forms suggested by this PCA.	263
Appendix 5-12. Character loadings and variance explained for PCA of George Lake ciscoes using morphometric characters adjusted with common-within-group residuals.	264
Appendix 5-13. Frequency distribution of discriminant scores from DA of George Lake cisco forms.	265
Appendix 6-1. Descriptive statistics for the combined cisco catch from Clearwater Lake. All variables are represented by raw, untransformed values.	266
Appendix 6-2. Standard length frequency distribution for all ciscoes from Clearwater Lake.	267
Appendix 6-3. Standard length versus weight for ciscoes from Clearwater Lake. Capture information is indicated in the legend including set number, date, depth of set, and number of ciscoes collected.	268
Appendix 6-4. Age frequency distribution for Clearwater Lake ciscoes.	269
Appendix 6-5. Relationship between total gillraker count and standard length for all ciscoes from Clearwater Lake with individuals identified by maturity state.	270

Appendix 6-6. Total gillraker count frequency distributions for all Clearwater Lake collection sites. Set number, date, depth, and number of ciscoes collected are indicated above each graph. 271

Appendix 6-7. Plot of scores for components 1 and 2 from PCA using morphometric characters adjusted by ratios. Upper panel displays results without forms identified, lower panel displays groups suggested by meristic PCA designated *a posteriori*. . 272

Appendix 6-8. Character loadings and variance explained for PCA of Clearwater Lake morphometric characters adjusted by ratios..... 273

Appendix 7-1. Results from an ANOVA between all cisco forms including Levene's test of homogeneity of variance. Most characters were found to be significantly different ($P<0.05$). 274

Appendix 7-2. Pairwise comparison of mean differences between meristic and morphometric characters adjusted by common-within-group residuals for all cisco forms. Values in bold indicate significant differences ($P<0.05$). The Games-Howell test assuming inequality of variance was used to adjust the significance level for the pairwise tests. See Figure 2.5 and text for character abbreviations. 275

1. INTRODUCTION

The Question

The occurrence of multiple sympatric forms of ciscoes in Manitoba lakes has been examined several times in the past (Dymond 1943, Keleher 1950, Clarke 1969, Clarke 1973). The outcome of these studies is that two species of ciscoes are currently considered present in Manitoba, *Coregonus artedi* LeSueur 1818, cisco, and *C. zenithicus* (Jordan and Evermann 1909), shortjaw cisco. Recent genetic studies have suggested that sympatric populations of *C. artedi* and *C. zenithicus* found outside of the Great Lakes region may be more closely related to each other than to conspecific populations in other lakes suggesting a sympatric origin of these forms (Turgeon and Bernatchez 2003). Morphological variability between the Great Lakes *C. zenithicus* populations and those found within inland lakes suggests they may represent two distinct taxa, divergent genetic lineages, or phenotypes of a common morphotype (i.e., allopatric origin of forms) (Todd and Steinhilber 2002, Todd 2003). The main objective of this study was to examine morphological variation within and between various cisco populations for evidence supporting the presence of these taxa. This group provides the basis for exciting research with respect to taxonomic differentiation, definition of species limits, and resolution of identification problems in northern fishes.

Due to the geological history of the area, the fish fauna of northern North American freshwater lakes represents recently evolved clades and colonizing populations. Salmonids tend to display the greatest amount of taxonomically unrecognized diversity of all northern freshwater fishes. These fish provide many examples of different

morphological forms repeatedly occurring within and among lakes (Koelz 1929, Dymond 1943, Lindsey et al. 1970, Clarke 1973, Smith and Todd 1984, Bodaly et al. 1992, Bernatchez et al. 1996, Pigeon et al. 1997, Steinhilber et al. 2002, Turgeon and Bernatchez 2003). The origin of these sympatric morphs is of utmost importance to how we view adaptive radiation and speciation in northern freshwater fishes and provides an opportunity for studying evolutionary mechanisms and the role of ecological factors (Smith and Skúlason 1996, Gislason et al. 1999). The evolutionary processes responsible for the taxonomic landscape we see today are difficult to determine; however, the products of these processes are available for us to study. Products of evolutionary processes exist in the differing forms of taxa at varying levels of differentiation. The sympatrically occurring cisco forms found in many northern lakes, often of uncertain taxonomic status, are an example.

Several questions exist regarding these cisco forms. Most notably did these forms have a sympatric or allopatric origin?, if and how did they arise multiple times?, and what taxonomic level do these forms represent? The first two questions are inherently linked by the evolutionary processes that created them, either through allopatry, sympatry, or a combination of the two. The third question is a human perception problem in how we recognize taxa and define species limits. Applying species boundaries to this group of fishes has been problematic to researchers for decades due to the phenotypic variability displayed across North America.

The extreme morphological and ecological variation displayed by North American ciscoes has plagued attempts by α -taxonomists to consistently identify diagnostic characters. Only a few identification keys exist for this group and they often fail to separate forms when several locations are considered. These keys have relied heavily on gillraker counts, which usually separate forms within a single lake, however, when applied to multiple lakes their effectiveness for distinguishing between forms is reduced due to overlapping values. Some phenetic studies based on morphology have resulted in polytomies that phylogenetic studies using molecular markers have failed to corroborate (Bodaly et al. 1991, Bernatchez et al. 1991, Lockwood 1993, Sajdak and Phillips 1997, Reed et al. 1998). This lack of agreement between morphology and genetics has made it difficult to identify the appropriate conservation units for the cisco group (Turgeon and Bernatchez 2003).

A reasonable approach to examining species boundaries in a plastic group like the ciscoes (where cross fertilization studies are not practical for examining reproductive isolation) is to use multivariate phenetic analyses. These methods incorporate a large number of morphological variables simultaneously, reducing them into phenetic space so the patterns of variation can be more easily examined. Similarities and differences displayed by the analysis of the morphological data can then be used to make inferences about underlying genetic relationships.

Coregoninae Systematics

Historic Cisco Arrangement

Ciscoes have been considered separate from the whitefishes in the past on the basis of their many long gillrakers, antrose premaxillae, and maxillae ending beneath the pupil compared to few, short gillrakers, retrose premaxillae, and maxillae ending anterior to the pupil (Clarke 1973). Whitefish were placed in the genus *Coregonus* by Linnaeus (1758). In 1818 Le Sueur first described North American ciscoes and he classified them with the whitefish in the genus *Coregonus*. From 1850 to 1911 North American ciscoes were considered to be worthy of their own generic status and were placed in the genus *Argyrosomus*. In 1911 *Leucichthys* replaced *Argyrosomus* because the latter was already in use for a sciaenid. The name *Leucichthys* was first used in 1874 by Dybowski for a group of Coregoninae with terminal mouths. Ciscoes and whitefish are currently grouped together in the genus *Coregonus*. To further complicate the situation, some species of cisco sometimes have retrose premaxillae, a whitefish character, while some Eurasian whitefish have many long gillrakers similar to ciscoes (Clarke 1973). Norden's (1961) study of salmonid phylogeny based on osteology supports the grouping of the whitefishes and ciscoes together in the same genus based on a lack of osteological differences.

Current Arrangement

Ciscoes are members of the family Salmonidae, which includes the trout, salmon, and graylings. Along with whitefish and the inconnu, ciscoes comprise the subfamily Coregoninae, which differ from trout and salmon by having larger scales and toothless maxillae (Scott and Crossman 1973, Clarke 1973, Nelson 1994). Coregonines are

present throughout the northern hemisphere with many endemic species present in either North America or Eurasia. They occur predominantly in freshwater; however, many species are anadromous (Nelson 1994). There are three currently recognized genera within the subfamily: *Prosopium*, the round whitefishes; *Stenodus*, the inconnu; and *Coregonus*, the lake whitefishes and ciscoes (Scott and Crossman 1973, Nelson 1994). The taxonomic relationships between the three genera, which currently include 32 recognized species and an unknown number of subspecies and races, remain tentative (Nelson 1994).

Prosopium is believed to be the most basal genus within the Coregoninae. This group is distinguishable from others in the Coregoninae by a single nostril flap, a basiobranchial plate on the floor of the branchial chamber, and parr marks on their young (Scott and Crossman 1973). The morphological and genetic evidence suggests *Prosopium* to be relatively distantly related to *Coregonus* and *Stenodus* (Bernatchez et al. 1991, Smith and Todd 1992, Lockwood 1993, Reist et al. 1998).

The genus *Stenodus* contains only one species, *S. leucichthys* (Guldenstadt 1772), the inconnu. Inconnu differ from the ciscoes and whitefishes (lake and broad) by having large mouths with many small teeth on the jaws, vomer, and palatine (Scott and Crossman 1973). Two subspecies of inconnu have been described, however, recent taxonomic evidence has brought question to the generic status of this group (Bernatchez et al. 1991, Smith and Todd 1992, Hamada et al. 1997, Hamada et al. 1998, Reist et al. 1998). The evidence suggests that inconnu are closely related to the *Coregonus* group

and should likely be placed within this genus. Bernatchez et al. (1991) found that the inconnu were more closely grouped with the North American cisco group while the remaining studies found they were more closely related to the Eurasian group or that they fell between the two cisco groups (Smith and Todd 1992, Hamada et al. 1997, Hamada et al. 1998, Reist et al. 1998).

Members of the genus *Coregonus* are characterized by having a double nostril flap, no basiobranchial plate, and young lacking parr marks. Whitefish usually differ from cisco by having relatively few and short gillrakers, and small, subterminal mouths (Scott and Crossman 1973). The subgenera *Coregonus* (for the whitefishes) and *Leucichthys* (for the ciscoes) were used by Nelson (1994); however, he did note that these groups were probably not monophyletic. Within the ciscoes there is phylogenetic evidence suggesting the existence of two distinct clades questioning the validity of the *Leucichthys* subgenus (Reist et al. 1998). One clade included all the species endemic to North America as well as the Arctic cisco, *C. autumnalis* Pallas 1776, and the Bering cisco, *C. laurettae* Bean 1882. The second clade contains all of the Eurasian forms as well as the least cisco, *C. sardinella* Valenciennes 1848 (Smith and Todd 1992, Reist et al. 1998).

Ciscoes

The Great Lakes region of North America represents the extreme of cisco radiation (Todd and Smith 1992). A total of eight cisco species are currently recognized from the Great Lakes region including deep and shallow water species; however, some of these have recently been considered extinct. One group included four deepwater species endemic to

the Laurentian Great Lakes including Lake Nipigon: deepwater cisco (*C. johannae* (Wagner 1910)), shortnose cisco (*C. reighardi* (Koelz 1924)), bloaters (*C. hoyi* (Gill 1872)), and kiyi (*C. kiyi* (Koelz 1924)) (Scott and Crossman 1973, Todd and Smith 1992). Shortjaw ciscoes and blackfin ciscoes (*C. nigripinnis* (Gill 1872)) were also abundant in the deep waters of the Great Lakes (Scott and Crossman 1973). The six species mentioned above were collectively referred to as “chubs” and supported a large commercial fishery until the 1950’s when stocks crashed. *Coregonus hoyi* is now the only “chub” species believed to be abundant in the Great Lakes, however, it has been extirpated from Lake Ontario. *Coregonus johannae* and *C. reighardi* are believed to be extinct while *C. kiyi* has been extirpated from lakes Ontario, Huron, and Michigan but remains abundant in Lake Superior. *Coregonus nigripinnis* has been extirpated from lakes Huron and Michigan but remains abundant in Lake Nipigon. *Coregonus zenithicus* is considered to be extirpated from all the Great Lakes with the exception of Lake Ontario where it was never originally reported, Lake Superior where it is rare, possibly Lake Huron, and Lake Nipigon where it remains abundant (Todd and Smith 1992). Todd et al. (1981) suggested *C. alpenae* to be synonymous with *C. zenithicus* based on findings that the major difference between the two species was simply the larger size of *C. alpenae*, beyond this the two were morphologically similar. Submergence of the formal name, *C. alpenae*, as synonymous with *C. zenithicus* is now generally accepted.

Coregonus artedi Le Sueur 1818 (common name cisco) is also part of the cisco “complex” found in the Great Lakes; however, it was not part of the deepwater “chub” fishery (McPhail and Lindsey 1970, Scott and Crossman 1973). Some authors have

previously identified this species as *C. artedii*; however, the current list of common and scientific names of fishes uses *C. artedi* (Nelson et al. 2004). Other names for this species include lake herring (Great Lakes region) and tullibee (Prairie region); however, cisco is currently the only common name recognized by Nelson et al. (2004). Lake herring are now considered rare in Lake Huron, threatened in lakes Ontario, Erie, and Michigan, and abundant in lakes Superior and Nipigon (Todd and Smith 1992). Lake herring are the most widespread cisco species in North America extending northwest to Great Bear Lake (Scott and Crossman 1973).

Prior to human perturbation, the Laurentian Great Lakes ciscoes displayed the greatest amount of cisco diversity in the world (Koelz 1929). These forms likely represented an adaptive radiation to the diverse ecosystems present in the large lakes, which developed in post-glacial times (Todd and Smith 1992). Todd and Smith (1980) considered *C. zenithicus* to be the easiest cisco to identify in Lake Superior. The taxonomic history of the Coregoninae includes many changes due to the difficulties associated with identification and classification. Table 1.1 provides some of the key characters and the geographic distributions of the North American cisco species as well as some of the taxonomic changes that have occurred within the group.

Table 1.1. Taxonomic summary of North American ciscoes, compiled from Koelz (1929), Hubbs and Lagler (1964), McPhail and Lindsey (1970), Clarke (1973), Scott and Crossman (1973), Todd and Smith (1992), Steinhilber (2000).

Species (<i>Coregonus</i>)	Total gillraker count	Lateral line scales	Body profile	Upper jaw position	Arctic	Inland Canada	Great Lakes Region
<i>C. alpenae</i> ^a	33-46	68-96	elliptical	protruding			X
<i>C. artedi</i> ^b	38-64	63-94	elliptical	equal		X	X
<i>C. autumnalis</i>	41-48	82-110	elliptical	equal	X		
<i>C. hoyi</i>	37-50	63-84	elliptical	protruding			X
<i>C. johannae</i> ^c	25-36	67-95	ovate	equal			X
<i>C. kiyi</i>	34-47	71-91	ovate	protruding			X
<i>C. laurettae</i>	33-41	76-95	elliptical	equal	X		
<i>C. nigripinnis</i> ^d	41-54	66-91	ovate	equal		?	X
<i>C. nipigon</i> ^e	54-66	68-82	elliptical	equal			X
<i>C. reighardi</i>	30-43	64-96	elliptical	included			X
<i>C. sardinella</i> ^f	42-53	78-98	elliptical	equal	X	?	X
<i>C. zenithicus</i> ^g	32-46	66-90	elliptical	included		X	X

^a *C. alpenae* was considered synonymous with *C. zenithicus* by Todd *et al.* (1981) and Todd and Smith (1984).

^b *C. artedi* includes approximately 15 synonymous "species" (see Clarke (1973) and Steinhilber (2000)).

^c *C. johannae* is currently considered extinct (Todd and Smith 1992).

^d *C. nigripinnis* is considered extinct in the Great Lakes except for Lake Nipigon, inland populations are considered to be synonymous with *C. artedi* (Clarke 1973, Todd and Smith 1992).

^e *C. nipigon* was considered synonymous with *C. artedi* by Scott and Crossman (1973), but recent work indicates *C. nipigon* may be a valid distinct species (Etnier and Skelton 2003).

^f Specimens from Great Slave Lake, NT, were tentatively identified as *C. sardinella* by the author and N. Mandrak (DFO, Burlington, ON). Steinhilber (2000) also reported *C. sardinella*-like specimens from the Athabasca region of Alberta.

^g *C. nigripinnis cyanopterus* and *C. reighardi dymondi* are considered synonymous with *C. zenithicus* (Todd and Smith 1980).

Validity and Identification of *C. zenithicus*

Is *C. zenithicus* a distinct and identifiable taxon?

Table 1.2 and Figure 1.1 provide some of the characters that have traditionally been used for distinguishing between *C. zenithicus* and *C. artedi*; however, overlap of values is common, especially when comparing forms from different water bodies. *Coregonus zenithicus* are elliptical in shape like most other ciscoes and are laterally compressed with large, smooth, silvery scales. They are generally light in dorsal colouration ranging from tan to light brown and white ventrally. The lower jaw is usually even with or shorter than the upper jaw and the premaxillaries usually make a distinct angle from the horizontal axis of the head (Scott and Crossman 1973, Clarke 1973, Todd and Smith 1980, Steinhilber et al. 2002). Individually these characters are not absolutely diagnostic for identification of *C. zenithicus* but in combination they usually are.

Table 1.2. Key characteristics of *Coregonus artedi* and *C. zenithicus*.

Character	<i>C. zenithicus</i>	<i>C. artedi</i>
Gillraker count ¹	32-46, usually 43 or less	38-64, usually 43 or more
Upper jaw length ^{1,2,3}	middle of eye, 2.1-2.8 in head length	anterior half of eye, 2.5-4 in head length
Head length ^{1,2}	22.8-27% of total length 3.8-4 in standard length	20-26.4% of total length 4.3-5.3 in standard length
Angle of premaxilla ³	55-75 degrees from horizontal axis of head	45-60 degrees from horizontal axis of head
Snout length ³	3.1-4 in head, long	3.3-4.5 in head, moderate
Eye diameter ¹	19.7-25.6% of head length	21-26% of head length
Depth of head ^{1,2}	4-4.75 in head length	3-5 in head length
Dorsal colouration ⁴	tan to greenish	greenish to black
Lateral compression ⁴	greater than most ciscoes	average
Lower jaw position ⁴	included in upper or slightly protruding	often projects beyond upper or equal

¹ Scott and Crossman 1973

² Jordan and Evermann 1909

³ Koelz 1929

⁴ Todd 2003

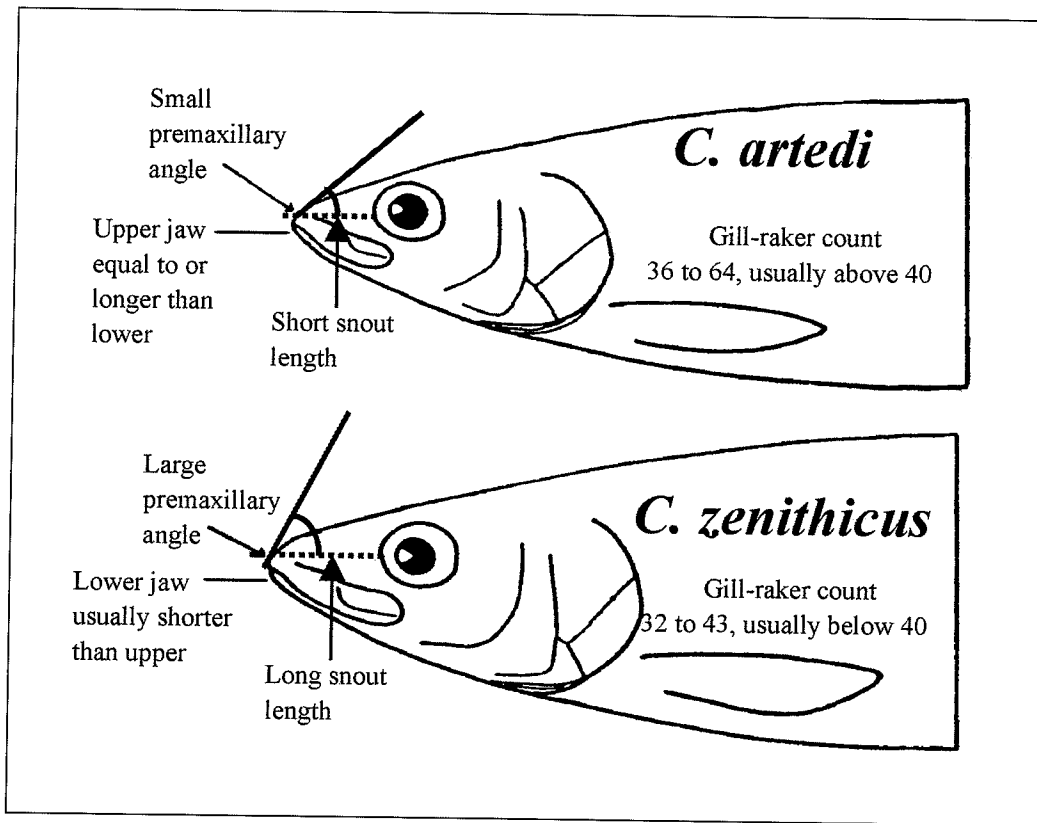


Figure 1.1. Key characters often used to distinguish between *Coregonus zenithicus* and *C. artedi*.

Is *Coregonus zenithicus* a valid species?

Coregonus zenithicus is a member of the subfamily Coregoninae, one of the most widely distributed and taxonomically perplexing of all Canadian freshwater fish. The validity of *C. zenithicus* is widely accepted by researchers, especially within the Great Lakes Region. For lakes beyond this region the existence is accepted, however, some questions still remain about their distribution and genetic relatedness to the Great Lakes populations. Outside the Laurentian Great Lakes, *C. zenithicus* have been reported in approximately 20 lakes extending northwest to Great Slave Lake (Figure 1.2, Table 1.3); however, information pertaining to their abundance, biology, and status is limited (Clarke 1973, Scott and Crossman 1973, Todd 2003). Formerly abundant in most of the Great Lakes, shortjaw ciscoes are now considered to be extinct in all except Lake Superior (where they are threatened) and Lake Nipigon. Recent evidence suggests that they may still be present in Lake Huron (N. Mandrak, Dept. Fish. Oceans Canada, Burlington, ON pers. comm.). Outside of the Great Lakes *C. zenithicus* have received little attention with the exception of a few studies (Dymond 1943, Keleher 1950, Paterson 1969, Clarke 1973, Steinhilber 2000, Steinhilber et al. 2002).

The identification of *C. zenithicus* is often uncertain due to the amount of phenotypic plasticity they display over their geographic range and their morphological similarity to sympatric *C. artedi* (Koelz 1929, Dymond 1943, Scott and Crossman 1973, Clarke 1973, Todd and Smith 1980, Todd and Steinhilber 2002, Steinhilber et al. 2002). The primary means of *C. zenithicus* identification has been based on gillraker counts; *C. zenithicus*

usually having less than 40 short, widely spaced gillrakers while *C. artedi* commonly have 40 or more closely packed, long gillrakers (Todd and Smith 1980).

There is much debate over whether morphologically distinct forms can be referred to as valid species and whether phenotypic similarity between forms reveals genetic relatedness because environment can influence the phenotypic display without causing genetic change (Bernatchez and Dodson 1990a). Phenotypic plasticity has been well documented within the Coregoninae with transplantation experiments consistently showing that few characters remain uninfluenced by changes in environmental conditions (Svardson 1965, Loch 1974, Lindsey 1981). Under allopatric situations, environmental modifications make most characters unsuitable for analysis; however, any character differences found between sympatric populations may be of use for separating putative taxa because they likely developed under similar environmental conditions (Clarke 1969). The question of whether the forms represent distinct species is difficult to ascertain, however, the persistence of some of these forms suggests that some mechanism must be at work maintaining the integrity of the forms.

Gillraker number has been the most important character for coregonine identification with stocks, subspecies, species, and even genera established based on this single character. No other character has been found which consistently separates the Coregoninae as well as gillraker number does. Gillraker number has been used as the primary means of delimiting putative *C. zenithicus* in Manitoba in keys and morphological analyses (Dymond and Pritchard 1930, Dymond 1943, Hinks 1957,

Keleher 1950, Clarke 1969, Clarke 1973). Recent evidence has shown that gillraker number can vary in coregonines in response to environmental influences. Temperature changes have been shown to affect gillraker number during early stages of development in coregonines (Todd 1998). Gillraker number has also been found to vary in response to the presence or absence of other species through adaptive radiation or character displacement, filling the available niches in the system (Kliewer 1970, Lindsey 1981, Todd et al. 1981). However, transplantation studies where eggs or fry of known Coregonine species were reared under different environmental conditions than their parents found gillraker number to be relatively stable (Svardson 1965, Loch 1974, Todd 1998). These studies found that gillraker number becomes fixed at some point in development and environmental conditions no longer have an influence, suggesting that the character has a strong genetic basis. These findings support the taxonomic usefulness of gillraker number for Coregonine identification, however, it would be beneficial to examine if other characters support the arrangement suggested by gillraker number.

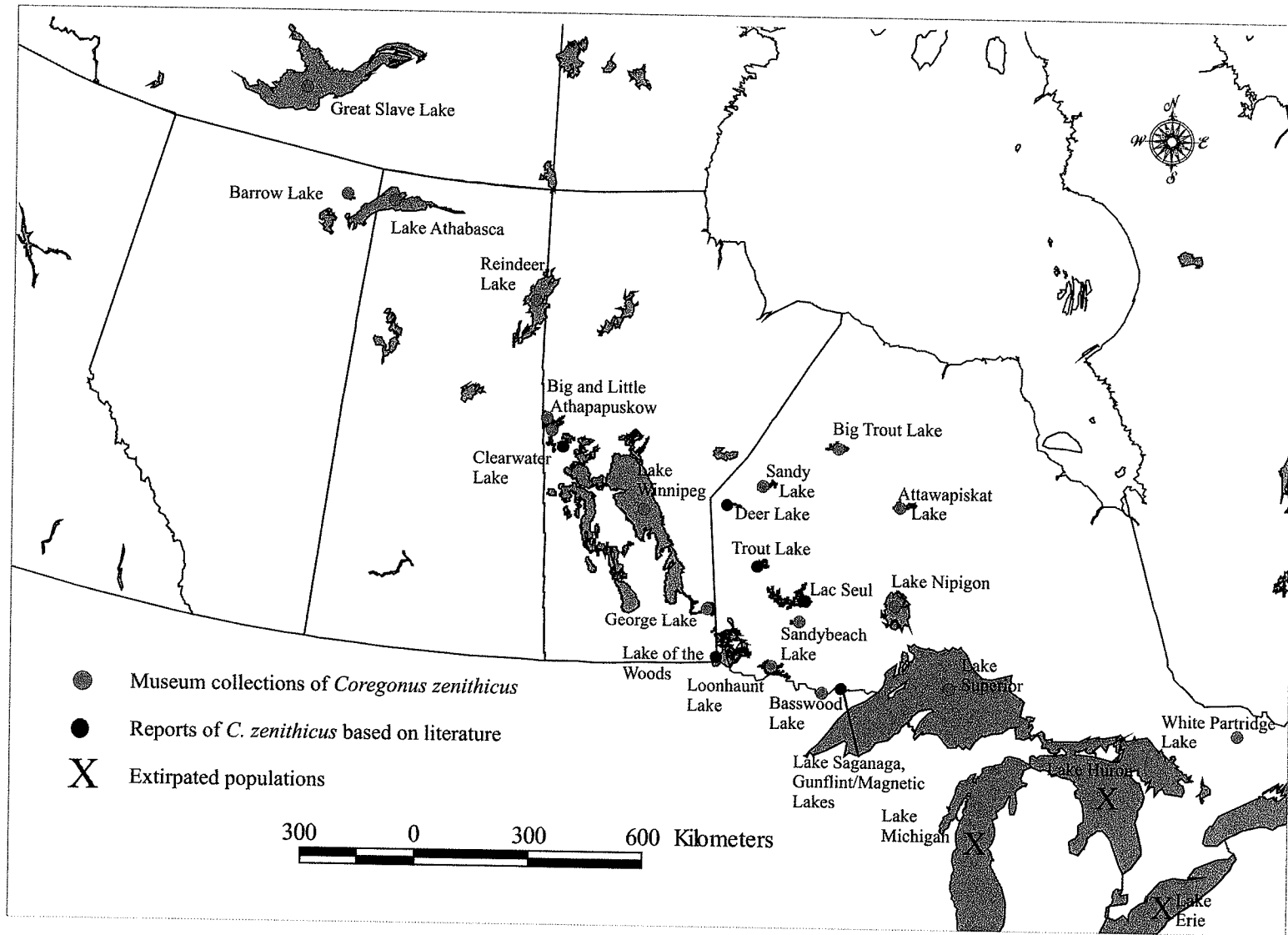


Figure 1.2. Current distribution of putative *Coregonus zenithicus* in Canada.

Table 1.3. Reported occurrences of *Coregonus zenithicus* in North America

Location	Province	Latitude and Longitude	Reference	Location of specimens
Great Slave Lake	NT	61° 37' N 114° 00' W	Harper and Nichols (1919) as <i>L. macrognathus</i> , Dymond (1943), Rawson (1947) as <i>C. zenithicus</i> , Clarke (1973) as <i>C. artedii</i>	ROM ^a
Barrow Lake	AB	59° 15' N 111° 14' W	Paterson (1969)	PMA ^b , UAMZ ^c , ROM
Lake Athabasca	AB	59° 15' N 110° 30' W	Dymond and Pritchard (1930)	
Lake Athabasca	SK	59° 20' N 109° 00' W	Dymond and Pritchard (1930)	ROM
Reindeer Lake	SK	57° 14' N 102° 16' W	Bajkov (1930), Dymond (1943)	ROM
Big Athapapuskow L.	MB	54° 37' N 101° 39' W	Clarke (1969) as <i>C. reighardi</i> ; Clarke (1973) as <i>C. prognathus</i>	ROM
Little Athapapuskow L.	MB	54° 37' N 101° 39' W	Clarke (1969) as <i>C. reighardi</i> ; Clarke (1973) as <i>C. prognathus</i>	ROM
Clearwater Lake	MB	54° 05' N 101° 00' W	Clarke (1973) as <i>C. prognathus</i>	
Lake Winnipegosis	MB	52° 29' N 99° 59' W	Bajkov (1930)	
Lake Winnipeg	MB	52° 08' N 97° 16' W	Bajkov (1930), Bajkov (1932)	ROM
George Lake	MB	50° 15' N 95° 30' W	Gibson and Johnson (1969) as <i>C. hoyi</i> , Clarke (1973) as <i>C. prognathus</i>	UMMZ ^d
Lake of the Woods	ON	49° 16' N 94° 40' W	Hinks (1957)	
Big Trout Lake	ON	53° 45' N 90° 00' W	Ryder et al. (1964)	ROM
Trout Lake	ON	51° 13' N 93° 19' W	Clarke (1973)	ROM
Sandy Lake	ON	53° 02' N 93° 00' W	ROM as <i>C. hoyi</i> , Clarke (1973) as <i>C. prognathus</i>	ROM
Lac Seul	ON	50° 20' N 92° 16' W	Dymond and Pritchard (1930), Clarke (1973) changed to <i>C. prognathus</i>	
Sandybeach Lake	ON	49° 48' N 92° 22' W	Wain (1993)	
Loonhaunt Lake	ON	49° 01' N 93° 30' W	ROM and Murray and Reist (2003)	ROM
Basswood Lake	ON	48° 05' N 91° 35' W	ROM, analyzed by Steinhilber (2000)	ROM

Table 1.2. Cont.

Lake Attawapiskat	ON	52° 18' N 87° 54' W	Ryder et al. (1964)	ROM
Lake Saganga	ON	48° 13' N 90° 55' W	Etnier and Skelton (2003)	ROM, UMMZ
Gunflint and Magnetic Lakes	ON	48° 06' N 90° 41' W	Etnier and Skelton (2003)	ROM, UMMZ
White Partridge Lake	ON	45° 50' N 78° 06' W	ROM and Nick Mandrak (Dept. Fish. Oceans Canada, Burlington ON, pers. comm.	ROM
Lake Nipigon	ON	49° 50' N 88° 30' W	Koelz (1929)	ROM
Lake Superior	ON	48° 00' N 87° 00' W	Jordan and Evermann (1909) type species	ROM, UMMZ
Lake Michigan	ON	44° 35' N 86° 50' W	Koelz (1929)	ROM
Lake Huron	ON	44° 50' N 82° 25' W	Koelz (1929)	ROM
Lake Erie	ON	42° 00' N 81° 20' W	Koelz (1929)	ROM

-
- ^a Royal Ontario Museum
^b Provincial Museum of Alberta
^c University of Alberta Museum of Zoology
^d University of Michigan Museum of Zoology

Do different forms of *C. zenithicus* exist throughout its range?

Coregonus zenithicus populations have been shown to exhibit morphological variability across their range (Clarke 1973, Todd and Steinhilber 2002). Population subdivisions were reported for *C. zenithicus* in Lake Superior and recent studies have suggested the presence of two *C. zenithicus*-forms throughout North America (Todd 2003). The two forms consist of a large-lake form found in the Great Lakes region and Great Slave Lake characterized as larger ciscoes with more and longer gillrakers and a small-lake form found within inland lakes such as George Lake (MB), Lake Athapapuskow (MB), Barrow Lake (AB) and others listed in Table 1.4, characterized by being smaller in size and having shorter, more widely spaced gillrakers (Todd and Steinhilber 2002, Steinhilber et al. 2002, Todd 2003). Recent genetic work has suggested that this morphological variability may not be entirely due to environmental influences on phenotypically plastic characters. Instead, the evidence suggests that individuals identified as *C. zenithicus* in the Great Lakes and Lake Nipigon may be genetically distinct from those populations identified as *C. zenithicus* in inland lakes (Turgeon et al. 1999, Turgeon and Bernatchez 2003, T. Todd, unpublished data). Each location of *C. zenithicus* included in the study (Lake Superior, WS; Lake Nipigon, ON; White Partridge Lake, ON; George Lake, MB; Barrow Lake, AB) was found to be genetically distinct from one another. *Coregonus zenithicus* populations were also found to be more similar to sympatric species than to other *C. zenithicus* populations in the study (Turgeon and Bernatchez 2003). Such information suggests that some populations of *C. zenithicus* are not as closely related as once thought, leading to speculation that the species may be polyphyletic. However, the use of microsatellites for comparing populations from different locations may not be

effective due to the difficulty in establishing homology of the microsatellite alleles (J. Reist, Dept. Fish. Oceans Canada, Winnipeg, MB, pers. comm.). Also, the rapid mutation displayed in microsatellites has the potential to result in allopatric populations (of the same implied species) sharing fewer similarities than co-existing sympatric populations (of different implied species) because of the amount of gene flow that may occur between the latter (O'Connell and Wright 1997). Thus, definitive taxonomic identification based upon microsatellite DNA results is not possible at this time.

Species Descriptions

Coregonus zenithicus

The original shortjaw cisco description was made by Jordan and Evermann in 1909 from a type specimen collected in the deep waters off Isle Royale, Lake Superior, September 1908. The specimen had a total gillraker count of 42 (17 upper and 25 lower gillrakers), however, when examined by Koelz in 1929 he found it to have a total of 45 gillrakers. The gillrakers were noted to be very slender in shape with the longest being divisible 6 times into the head length; the eyes were small and the maxillary long. The mouth was larger than the other cisco species within the lake with the lower jaw usually included in the upper jaw and the snout pointed. The lateral line scale count for the type specimen was 72. The species was reported to live in much deeper water than *C. artedi* in Lake Superior. In 1911, Jordan and Evermann examined additional specimens believed to *Leucichthys zenithicus*. The lower jaws were found to be equal to or longer than the upper jaws and the gillrakers ranged in total count from 37 to 44 while the lateral line scale counts ranged from 76 to 87.

In 1919, Harper and Nichols described three new species *L. entomophagus*, *L. athabascae*, and *L. macrognathus*. All three species were later synonymized with *L. zenithicus* by Dymond (1943) and then with *C. artedii* (Clarke 1973) as described below. *L. entomophagus* was collected from Tazin River, NT, southeast of Great Slave Lake. The type specimen had a gillraker count of 33 and the gillrakers were noted to be relatively long. The specimen had 65 lateral line scales and a small mouth with a maxillary reaching the front of its eye. The profile of its head was low and nearly straight and the lower jaw was included in the upper. *Leucichthys athabascae* was collected from Lake Athabasca and had a total gillraker count of 35 [the gill arch had been cut short so the number is likely lower than it should be (Steinhilber 2000)]. The lateral line scale count was about 66, the head narrow and pointed with a straight, low profile. The mouth was large with a projecting lower jaw and the maxillary extended to below the pupil. The lower jaw had a vertical protuberance at the tip and there was a slight notch in the tip of the upper jaw. The final specimen, *L. macrognathus*, was collected from Great Slave Lake. This specimen had 41 gillrakers and about 68 lateral line scales. The head was narrow and pointed with a low, straight profile. The maxillary reached to the front of the pupil and the lower jaw distinctly projected beyond the upper jaw. The tip of the lower jaw had a vertical protuberance and the upper jaw had a slight notch at the tip.

In 1929, Koelz undertook an extensive survey of the cisco forms present in the Great Lakes. Koelz (1929) described *L. zenithicus* specimens from each lake except Lake Ontario. Also described in this report were *L. reighardi dymondi* (new subspecies), and

L. nigripinnis cyanopterus (Jordan and Evermann 1909) [i.e., the submergence of their species as a formal subspecies of blackfin cisco]. Gillraker number ranged from 31 to 48 and lateral line scale counts ranged from 66 to 96 for *L. zenithicus* specimens for all the Great Lakes. The fish were described as having elongate, sub-terete bodies of moderate size with short maxillae, usually included with the lower jaw (i.e., mandibles as originally used). The snouts were relatively long and the eyes were moderate in size but variable. The average maxillary length was long, usually extending past the anterior margin of the pupil. The premaxillaries were nearly vertical ranging from 55 to 75° from the horizontal axis of the head and the head shape was described as long and shallow. Koelz (1929) described *L. reighardi dymondi* from lakes Superior and Nipigon as on average having longer snouts, heads, and maxillaries than typical *L. reighardi* from lakes Michigan and Ontario. *Leucichthys nigripinnis cyanopterus* were collected from Lake Superior; they had fewer gill-rakers, longer heads, and longer snouts than typical *L. nigripinnis*. All forms were found at moderate depths of 54 to 76 meters, rarely no more than a few miles from shoals that drop abruptly to 144 meters or greater. Koelz (1929) distinguished *L. zenithicus* from *L. artedii* by the former having fewer gillrakers on the first branchial arch, and longer snouts, maxillaries, heads, and paired fins.

In 1930, Dymond and Pritchard identified specimens collected from Lake Athabasca, Alberta as *L. zenithicus*. The specimens had fewer than 43 gillrakers, usually 38 to 40, very large eyes, long maxillaries, and lateral line scale counts from 58 to 69. Of the four species identified from western Canada (*L. nigripinnis*, *L. nipigon*, *L. tullibee* [all later synonymized to *L. artedii* by Clarke 1973], and *L. zenithicus*), *L. zenithicus* was found to

be the smallest on average, with the longest maxillary, narrowest interorbital width, and shortest dorsal fin base.

In 1932, Bajkov reported on a collection of ciscoes he identified as *L. zenithicus* from Lake Winnipeg. The specimens were identified based on gillraker counts ranging from 33 to 42 (seldom 44), large eyes, light dorsal colouration in living specimens, pale paired fins, elliptical bodies, and bottom feeding nature.

In 1943, Dymond re-examined the *L. zenithicus* issue in western Canada by describing them as ciscoes with gillraker counts of 33 to 40, low lateral line scale counts of 64 to 76, and long maxillaries. The body depth and fin length was found to be variable. Dymond (1943) synonymized the three species previously described by Harper and Nichols (1919) (i.e., *L. entomophagus*, *L. athabascae*, and *L. macrognathus*) with *L. zenithicus* on the basis of a combination of characters including gillraker number, maxillary length, and number of lateral line scales.

Hinks (1957) discussed tullibee variation within Manitoba and stated that six cisco species were recognized at that time although commercial fisherman only recognized two, a light-backed and a black-backed form. Gillraker counts were the primary means of identifying the different species along with a few morphological differences such as head length, lower jaw size, and overall body size. Hinks pointed out that the average commercial fisherman placed little importance on counting gillrakers, which likely explained their recognition of only two cisco types. Hinks identified *L. zenithicus* as one

of the larger Manitoba tullibee species having fewer than 43 gillrakers. *L. hoyi* was also described by Hinks as having fewer than 43 gillrakers, however, they were smaller and had a thinner mandible with a hook at the end. Clarke (1973) determined that *L. hoyi* was not present in Manitoba and that previous reports represented populations of *C. zenithicus* or *C. artedii*.

Throughout the late 1940's and early 1950's Keleher described several cisco species from Lake Winnipeg including *L. zenithicus* (Keleher 1950, Keleher 1952, Keleher 1954). In 1947 he described *L. zenithicus* as a light-backed or silver-backed form of cisco with a very silvery appearance and around 20 to 30 centimeters in length. Keleher separated the cisco into groups based on gillraker counts and found that 97% of group 1 (having gillraker counts of 34 to 42) were less than 27.5 cm. Keleher identified four species of cisco (*L. nigripinnis*, *L. nipigon*, *L. tullibee*, and *L. zenithicus*) present in Lake Winnipeg based on Dymond's key (1943).

In 1964, Hubbs and Lagler described *C. zenithicus* in their key of fishes from the Great Lakes. Shortjaw ciscoes were described as having equal upper and lower jaws and occurring at depths of 20 to 180 meters, usually around 64 meters. The gillraker counts ranged from 34 to 43 and they were considered one of the larger cisco species present in the Great Lakes.

In 1969, Paterson identified cisco specimens from Barrow Lake, Alberta as *C. zenithicus*. The identification was based on gillraker counts of 37 to 41, lateral line scales of 69 to

77, head length 4 - 4.5 in fork length, and maxillaries 2 - 2.8 in head length. The predorsal and snout lengths were also found to be significantly longer than sympatric *C. artedii*.

In 1973, Scott and Crossman described *C. zenithicus* over the entire geographic range. This description included gillraker counts of 32 to 46, elongate but not deep heads, moderate-sized eyes (20-25% of head length), snouts usually longer than eyes, relatively long maxillaries that extend to the middle of the eye or beyond. The lower jaw usually protrudes or is included in the upper, and lateral line scale counts range from 58 to 90. Most of the descriptions were based on specimens from Lake Superior, Lake Nipigon, Lake Winnipeg, and Lake Athabasca and focused on the work of Dymond (1929), Koelz (1929), Dymond and Pritchard (1930), and Keleher (1952). The grouping of descriptions from a wide geographic range for a species of uncertain identification has likely added to the taxonomic confusion for *C. zenithicus* due to the potential inclusion of non-*C. zenithicus* forms.

In 1973, Clarke did an extensive study of the cisco variation in western Canada. Clarke suggested using *C. prognathus* instead of *C. zenithicus* based on specimens identified by Smith (1894) with low gillraker counts from the Great Lakes, which he felt had priority over *C. zenithicus* (Jordan and Evermann 1909). Todd (1981) examined the existing specimens of *C. prognathus* and determined that they represented most of the species previously described from the Great Lakes. The combined poor condition of the specimens and the unclear identity of the holotype led him to suggest *C. prognathus* be

considered a *nomen dubium* (Todd 1981). Clarke found *C. zenithicus* to always have fewer gillrakers wherever they co-occurred or, in specific locations only, longer upper jaws, and longer snouts than sympatric *C. artedii*. Clarke found 50% of *C. zenithicus* had 35 or fewer gillrakers while 77% of *C. artedii* had 44 or more across all populations. He also noted that, in comparison to *C. artedii*, the majority of *C. zenithicus* populations had longer heads, shorter gillrakers, larger premaxillary angles from the horizontal head axis (i.e., a greater sloped lateral profile of the tip of the snout), and lower jaws included in the upper jaws.

Todd and Smith (1980) considered cisco subspecies from Lake Superior (*C. nigripinnis cyanopterus* and *C. reighardi dymondi*) to be synonymous with *C. zenithicus*. They found that when 29 morphometric and meristic characters were analyzed using principal components, the only difference between the co-occurring populations was based on size and no other factor. They concluded that these taxa represented large-bodied populations of *C. zenithicus* (Todd and Smith 1980). *Coregonus reighardi dymondi* from Lake Nipigon were also synonymized with *C. zenithicus* (Todd and Smith 1980). In 1981, Todd et al. also synonymized *C. alpenae* from the Great Lakes with *C. zenithicus* based on similar findings that previous distinctions between the two species were based primarily on overall size and not morphometric or meristic differences.

Steinhilber (2000) found that *C. zenithicus* specimens from Barrow Lake, Alberta had shorter gillrakers, smaller eyes, and longer upper jaws than all other Alberta cisco populations in his study. They also possessed longer snouts and a longer adipose fin

origin to caudal fin origin than most populations. Steinhilber also closely examined the three specimens originally described as three new species by Harper and Nichols (1919), synonymized by Dymond as *C. zenithicus*, and later considered to likely represent *C. artedi* (Clarke 1973, McPhail and Lindsey 1970, Scott and Crossman 1973). Although Steinhilber (2000) found their gillraker counts to fall in the range of *C. zenithicus* and *C. artedi*, the poor condition of some specimens especially the gill arch suggested that the counts might be slightly higher than previously reported. An analysis of several truss measurements, gillraker counts, and gillraker length could not give conclusive evidence for taxonomic identification as some characters resembled *C. zenithicus* while others more closely resembled *C. artedi*. The precise taxonomic identity of these specimens is likely unattainable given their condition and new specimens should be collected from the original locations to re-examine the issue. The standard length of the Barrow Lake *C. zenithicus* specimens examined by Steinhilber was similar to that of other *C. zenithicus* populations at around 200 to 250 mm, the upper jaw length and head depth were also similar. The dorsal fin base length was found to be higher in the Barrow Lake specimens while the gillraker length was found to be lower.

Coregonus artedi

The original description of *Coregonus artedi* was made by Le Sueur in 1818. The type locality was Lake Erie, and at Lewiston, upper Canada. They were described as having sub-fusiform bodies that were slightly elevated at the back, relatively small and narrow heads, pointed and short snouts, wide maxillaries, and very small conical teeth at the edge of the jaws in small individuals but not visible in larger specimens. The lateral line was

straight and near the middle of the body. The average length was 25 to 30 cm, with 12 dorsal rays, 16 pectoral rays, 12 pelvic rays, and 13 anal rays.

In 1836, Richardson described three new species, *Salmo (Coregonus) tullibee*, *S. (C.) lucidus*, and *S. (C.) harengus*, all of which are now considered synonymous with *C. artedi*. They were described as highly compressed with rounded bellies, large eyes, more than their own diameter from the snout. They had small mouths with lower jaws slightly protruding beyond the upper jaw, the lower jaw had a knobbed tip that fit into a depression between the premaxillaries. A small plate of minute teeth was noted on the center of their tongues. No gillraker counts were made but the longest gillraker was found to usually be about 1.2 cm in length. The *S. lucidus* specimen was collected from Great Bear Lake and was described as having a larger mouth than any other Coregoninae. The *S. harengus* specimen was collected from Lake Huron and was noted to be similar to *S. lucidus* but with smaller scales and a slightly larger head. Richardson felt the *S. tullibee* specimen had a less pointed snout and less rounded scales than Le Sueur's (1818) *C. artedi*.

Evermann and Smith (1896) described *Argyrosomus artedi* and *A. osmeriformis* (Smith 1894). The gillraker counts for these species were 43 to 58, the structure of the gillrakers was described as long and slender, usually 1-1.5 in eye length. The bodies were slender, and mouths large with lower jaws projecting beyond the upper or equal. The maxillaries usually extended to the front of the pupil. The lateral line scale counts ranged from 62 to 87 (usually 74 to 83). The *A. osmeriformis* specimens were collected from Seneca and

Skaneateles lakes in New York State. These specimens usually had large heads, large eyes, and premaxillaries not at an angle to the dorsal margin of the head. Evermann and Smith (1896) also examined *A. lucidus* and *A. tullibee*, describing the former as having a small head, almost vertically truncate snout, lower jaw included in upper, and a maxillary extending to the just beyond the front of the pupil. The latter was described as also having a small head, a projecting lower jaw, and maxillaries extending to the anterior edge of the pupil.

In 1911, Jordan and Evermann further expanded the number of cisco species recognized and further described previously identified species. All of the following are now considered to be synonymous with *C. artedi*. Newly described species at that time included *Leucichthys ontariensis*, *L. manitoulinus*, and *L. supernas*. Previously identified species included *L. artedi*, *L. harengus*, *L. osmeriformis*, *L. sisco* (Jordan 1875), *L. lucidus*, *L. eriensis* (Jordan and Evermann 1909), *L. nigripinnis* (Gill 1872), and *L. tullibee*. The diversity of the above was based mainly on their geography, size and robustness of body, adipose fin size, and colouration. The gillraker counts ranged from 37 to 55 and the lateral line scales ranged from 67 to 87. *L. artedi* had oblique premaxillaries and maxillaries extending to or slightly beyond the front margin of the pupil. *Leucichthys harengus* were characterized by having lower jaws projecting beyond their upper jaws, maxillaries that did not quite extend to the front of the pupil, and short dorsal fin bases, usually shorter than their eye. The *L. ontariensis* specimens were collected from Lake Ontario and Cayuga Lake. These specimens were described as having a mandible slightly projecting beyond the upper jaw and maxillaries extending to

below the anterior edge of the pupil. The *L. lucidus* specimens were collected from Great Bear Lake and were described as having short heads, small eyes, mandibles included in the upper jaw, maxillaries extending to midway between the front and the middle of the pupil, and vertically truncate snouts. The *L. eriensis* specimens were collected from Lake Erie and they were described as having blunt snouts, mandibles included in the upper jaw, and maxillaries extending to the front of their pupils. The *L. manitoulinus* specimens were collected from the north channel of Lake Huron and were described as having lower jaws not included in the upper jaw and maxillaries extending to the anterior one-third of the eye. The *L. supernas* specimens were collected from Lake Superior and were described by Jordan and Evermann as being very similar to *L. artedi* and *L. harengus* but with shorter maxillaries and deeper bodies. *L. nigripinnis* was described as large in size with black on all fins. The *L. tullibee* specimens were collected in Lake Winnipeg and Lake Superior and were described as having very deep bodies, lower jaws included in the upper jaw, maxillaries not extending to the anterior edge of the pupil, and premaxillaries projecting forward. The large number of species described here displays the considerable amount of morphological variation present in ciscoes and helps explain why so much confusion existed about where species boundaries should be drawn.

In 1929, Koelz took a closer look at the cisco variation within the Great Lakes and considered many previously described species as synonymous with *L. artedi* and where suitable he suggested subspecies designations. Koelz described *L. artedi* as having 41 to 66 gillrakers, 64 to 89 lateral line scales, short maxillaries averaging between 2.5 to 3.3 in head length, short snouts around 3.3 to 4.5 in head length, premaxillaries usually at an

angle of 45-60° from the horizontal axis of the head, and heads broadly triangular in side view. Three subspecies were recognized including *L. artedi artedi* (widespread), *L. a. albus* (lakes Erie, Superior, and Ontario), and *L. a. manitoulinus* (north channel of Lake Huron). The subspecies were found to differ in body depth, eye size, head length, gillraker number, and lateral line scales.

In 1930, Dymond and Pritchard re-described several previously identified coregonine species including *L. tullibee*, *L. nigripinnis*, and *L. nipigon*. The gillraker counts ranged from 41 to 62. *Leucichthys tullibee* was considered to have a shorter head, smaller eyes, shorter snout, and shorter maxillary than the other species. Dymond and Pritchard (1930) believed that the western Canadian *L. tullibee* were distinct from *L. artedi* from the Great Lakes, the former being larger, deeper bodied, and faster growing.

In 1931, Koelz expanded his coregonine work beyond the Great Lakes and identified 14 different subspecies of *L. artedi*. The basis of these subspecific identifications was small regional morphological differences that were not enough to warrant the level of species. The subspecific name, common name, and locations where the specimens were found are listed in Table 1.3. The subspecific level of identification in coregonines has been widely abandoned by most authors due to the overlap in characters used to identify them and because many of the characters are environmentally influenced (Hubbs and Lagler 1964).

In 1932, Bajkov examined *L. artedi* and *L. tullibee* specimens from Lake Winnipeg and considered *L. tullibee* to be a subspecies of *L. artedi*. The gillraker range for this group

was 37 to 66. Bajkov found *L. a. tullibee* to vary in body shape from slim and elongate to deep bodied with no distinct difference from typical *L. artedi* of the Great Lakes. He also found that *L. nipigon* specimens had more gillrakers, larger maxillaries and snouts, and smaller eyes than *L. artedi*. *L. nigripinnis* was also found to have a larger head on average than *L. artedi*.

In 1943, Dymond examined several cisco species including *L. artedi*, *L. lucidus*, *L. tullibee*, and *L. nigripinnis*. The gillraker count for *L. artedi* was 40 to 52 and the premaxillaries were described as being nearly vertical. Dymond synonymized *L. lucidus* with *L. artedi*. Although he re-examined *L. tullibee*, Dymond was unable to determine if it was closer to *L. nigripinnis* or *L. artedi*.

In 1964, Hubbs and Lagler recognized 22 subspecies within *C. artedi* (Table 1.4). In general they described *C. artedi* as having 43 to 52 gillrakers, which are usually long, equal jaws, and medium length fins. The majority of these subspecies were originally identified by Koelz (1931). It is important to note that many of these subspecies have been abandoned by most authors due to the taxonomic confusion they create and that many of the key characters overlap and have been found to be subject to environmental effects.

In 1969, Paterson compared two sympatric forms of cisco from Barrow Lake and determined that *C. artedii* in that lake had 42 or more gillrakers and 64 to 74 lateral line

scales. He also observed that the *C. artedii* forms had longer predorsal lengths and longer snout lengths compared to sympatric *C. zenithicus*.

In 1970, McPhail and Lindsey dealt with the *C. artedii* problem by referring to them as the *C. artedii* complex. In their view, this complex consisted of ciscoes with 41-51 gillrakers and lateral line scales counts of 67-89. The bodies were usually elongate and somewhat compressed, the head moderately long, about one-quarter of the standard length. The upper jaw extended to around the middle of the pupil, the snout length was approximately equal to the eye diameter, the premaxillaries were in line with the forehead, and the tip of the lower jaw projected beyond the upper jaw.

Clarke (1973) included *C. nigripinnis*, *C. nipigon*, and *C. hoyi* in his "high group" of ciscoes from central Canada. He considered *C. prognathus* (= *zenithicus*) and *C. artedii* to be the only two cisco species present beyond the Great Lakes in central Canada. With the exception of George Lake and Sandy Lake where *C. hoyi* was considered to be *C. zenithicus*, all other species identified from central Canada were synonymized with *C. artedii*. This *C. artedii* group was described as having long gillrakers with mean numbers ranging from 39.3 to 62.9, short heads, and short upper jaws.

In 1973, Scott and Crossman described *C. artedii* as having gillraker counts of 36 to 64, the lateral line scale counts ranged from 63 to 94, and their head lengths were about 20-24% of their total length. The eyes were considered moderate in size at around 21-26% in head length; the snouts were usually longer than the eyes. The lower jaw usually

projected beyond the upper and the maxillaries extended to below the anterior half of their eye. *Coregonus nigripinnis* were considered to have similar characteristics but at the upper end of the size range from *C. artedii*.

The current scientific name recognized in the “Common and Scientific Names of Fishes from the United States, Canada, and Mexico” is *C. artedi* (Nelson et al. 2004). The second “*i*” was dropped based on Lesueur’s original 1818 description of this species. Cisco was the only common name recognized in the new edition as the name lake herring was dropped.

Table 1.4. Examples of the prolific identification of *Coregonus artedii* subspecies in the past (from Hubbs and Lagler 1964).

Subspecific name	Common name	Location	Reference
<i>greeleyi</i>	Torch Lake cisco	Typical races from Torch and Elk lakes, Ontario	Koelz
<i>huronicus</i>	Rush Lake cisco	Rush Lake, Michigan	Koelz
<i>annensis</i>	Lake Anne cisco	Lake Anne, Michigan	Koelz
<i>sargenti</i>	Sargent Lake cisco	Sargent and Richie lakes on Isle Royale, Ontario	Koelz
<i>russeli</i>	Pine Lake cisco	Pine Lake, Michigan	Koelz
<i>atikamek</i>	Whitefish Lake cisco	Whitefish Lake, Michigan	Koelz
<i>mackayi</i>	Ontario cisco	Inland lakes in the Great Lakes basin of Ontario	Koelz
<i>clarensis</i>	Clear Lake cisco	Clear Lake and other inland lakes of Wisconsin and Michigan	Koelz
<i>clemensi</i>	Nipigon cisco	Lake Nipigon, Ontario	Koelz
<i>lowei</i>	Hulbert Lake cisco	Hulbert Lake, Michigan	Koelz
<i>microcephalus</i>	Gogebic Lake cisco	Gogebic Lake, Michigan	Koelz
<i>woodi</i>	Twin Lake cisco	North Twin Lake and other lakes in Wisconsin and Minnesota	Koelz
<i>winnipegosis</i>	Lake Winnipegosis cisco	Lakes Winnipegosis and Wabigoon, Manitoba	Koelz
<i>birgei</i>	Green Lake cisco	Green Lake, Wisconsin	Wagner
<i>artedii</i>	Great Lakes cisco	In all the Great Lakes and some inland lakes in the area	LeSueur
<i>osmeriformis</i>	Seneca Lake cisco	Seneca Lake, New York	Smith
<i>bisselli</i>	Rawson Lake cisco	Rawson Lake and other Michigan inland lakes	Bullman
<i>albus</i>	Lake Erie cisco	Type from Lake Erie, also in Lakes Ontario and Superior	LeSueur
<i>arcturus</i>	Lake Superior cisco	Lake Superior	Jordan and Evermann
<i>sisco</i>	Tippecanoe Lake cisco	Tippecanoe Lake and inland lakes of Michigan and Indiana	Jordan and Evermann
<i>manitoulinus</i>	North Channel Tullibee	North Channel of Georgian Bay	Jordan and Evermann

Coregonus nigripinnis

C. nigripinnis (blackfin cisco) were originally identified by Gill (*in* Hoy 1872) from specimens collected from Lake Michigan (Scott and Crossman 1973). Koelz (1929) reported that the type specimen was no longer extant; however, upon examination of variability in this group he considered that four subspecies should be recognized: *C. nigripinnis nigripinnis* (Gill 1872), found in Lake Michigan and Lake Huron; *C. nigripinnis regalis* (Koelz 1929), in Lake Nipigon; *C. nigripinnis cyanopterus* (Jordan and Evermann 1911), in Lake Superior; and *C. nigripinnis prognathus* (Smith 1895), in Lake Ontario. With the exception of Lake Nipigon, all Great Lakes populations of *C. nigripinnis* are now considered extinct (Scott and Crossman 1973). Dymond (1943) made the first report of *C. nigripinnis* outside of the Great Lakes from several lakes in Ontario, Manitoba, Saskatchewan, and Alberta. The identification was based primarily on the presence of darkly pigmented fins; however, coregonines caught in inland lakes have been noted to have darker fin colouration than the same species in the Great Lakes (Scott and Crossman 1973).

The presence of *C. nigripinnis* in Lake Nipigon and its previous existence in the Great Lakes seems to be widely accepted (T. Todd, U. S. Geological Service, Ann Arbor, Michigan, pers. comm. 2002). However, the existence of inland populations remains in question, due to the difficulty in discerning them from *C. artedi* and the lack of detailed taxonomic studies. The gillraker counts for *C. nigripinnis* and *C. artedi* overlap considerably throughout their respective ranges. Scott and Crossman (1973) felt that the inland populations identified as *C. nigripinnis* should more appropriately be considered

members of the more widespread and morphologically variable *C. artedi* and this grouping has been accepted by many (Clarke 1973, Todd and Steinhilber 2002, Turgeon and Bernatchez 2003, Stewart and Watkinson 2004).

Radiation and Evolution in North America of *Coregonus zenithicus*

There are two main hypotheses regarding the origin and evolutionary history of *C. zenithicus* in North America. One hypothesis is that *C. zenithicus*, along with *C. artedi*, represented the two original, colonizing lineages radiating out from the Mississippian refugium to northwestern Canada following the Pleistocene glaciation, i.e., Two-Species Model based on allopatric origin for local diversity. Another hypothesis that has garnered recent genetic support is that *C. artedi* and possibly *C. zenithicus* radiated into the Great Lakes region following glaciation; however, only *C. artedi* radiated out from the Great Lakes into western Canada where adaptive divergence and parallel speciation led to the formation of different morphotypes recognized by many authors as distinct species-level taxa, i.e., One-Species Model based on sympatric origin for local diversity (McPhail and Lindsey 1970, Smith and Todd 1984, Douglas et al. 1999, Turgeon and Bernatchez 2003, Todd and Steinhilber 2002, Steinhilber et al. 2002). Similar modes of divergence have been proposed to explain the origins of sympatric forms in other North American freshwater fishes (Lindsey et al. 1970, Foote et al. 1992, Bernatchez and Dodson 1991, Bodaly et al. 1992, Taylor and Bentzen 1993, Wilson and Hebert 1998).

Pleistocene glaciation events undoubtedly played a major role in the current distribution and diversification seen in salmonids including North American cisco species (Behnke

1972). The late Wisconsinan glaciation was the most extensive of these events and was probably the most disruptive to fish populations. Conditions created by the glacial advances and retreats would have provided numerous cold-water habitats with conditions suitable for ciscoes through the formation of ice dams and the drainage or flooding of ice-margin lakes (Dyke and Prest 1987, Pielou 1991, Wilson and Hebert 1998). Extensive water connections provided links from the Mississippi headwaters region as far north as the lower Mackenzie River (McPhail and Lindsey 1970, Teller 1987, Rempel and Smith 1998; Figure 1.3). The Great Lakes region experienced a series of advances and withdrawals of the Laurentide ice sheet from its maximum extent approximately 18 000 years ago to 8 000 years ago when the region became ice-free (McPhail and Lindsey 1970). Of particular importance to Manitoba cisco distribution was glacial Lake Agassiz, which was intermittently connected to proglacial lakes in the Great Lakes region between 12 800 and 9 000 years ago (Lindsey and McPhail 1986, Dyke and Prest 1987, Smith and Fisher 1993, Rempel and Smith 1998, Leverington and Teller 2003). Lake Agassiz had two major expansion periods, the first was from 13 900 to 12 600 years ago and the second was from 11 000 to 9 900 years ago (Lowell and Teller 1994). The maximum extent of the lake occurred approximately 9 900 years ago when the surface area reached 350 000 km² (Teller 1987). The total area covered by the lake over its 5 000 year history was 1.5 million km², which included all of the lakes in this study at different times (Teller 1987; Figure 1.4).

The widespread distribution of *C. zenithicus* in North America has led some researchers to speculate that they were one of the original colonizers along with *C. artedi* following

glaciation (Clarke 1973, Bailey and Smith 1981, Smith and Todd 1984, Todd and Smith 1992). Under this allopatric, two-species model of evolution, the sympatric pairs represent evolutionarily distinct lineages that have come into secondary contact. Therefore, genetic evidence should demonstrate that each phenotype shares more genetic similarities with phenotypically similar allopatric populations than with their sympatric phenotypically divergent pair (Chouinard et al. 1996, Douglas et al. 1999). This model has been supported for salmoniform fishes (Bernatchez 1997), including coregonines (Bernatchez and Dodson 1990b, Bernatchez et al. 1996). Under this hypothesis, *C. zenithicus* and *C. artedi* survived Pleistocene glaciation within the Mississippian refugium and then a stock of each species radiated into inland Canada (Bailey and Smith 1981). Bailey and Smith (1981) felt that *C. zenithicus* and *C. artedi* likely diverged some time during the 70 000 years of the Wisconsinan glaciation, however, they did not rule out the possibility of a post-glacial origin of *C. zenithicus*.

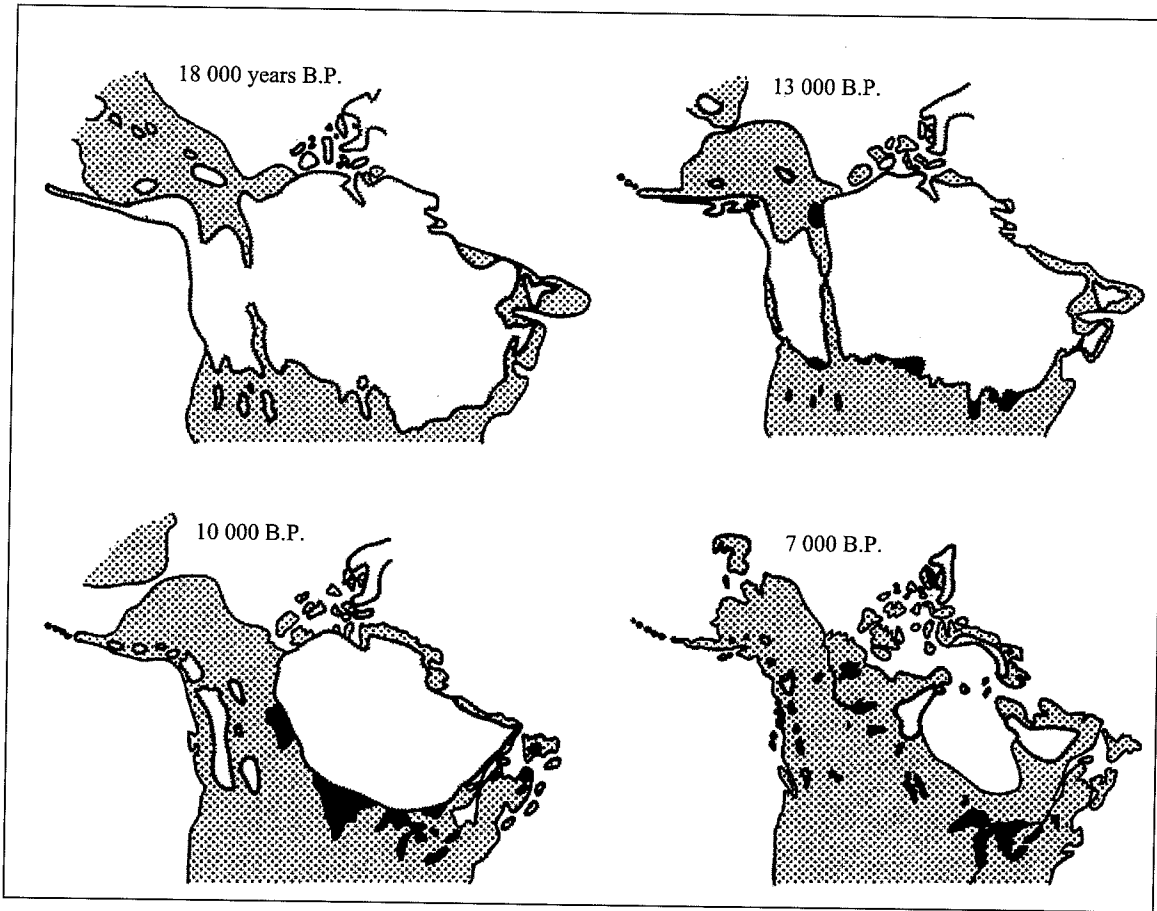


Figure 1.3. Recession of the North American glacial ice sheets from the most recent maximum 18 000 years B.P. to 7 000 years B.P. White areas represent glaciers; shaded areas represent land surfaces; black areas represent water bodies (after Pielou 1991).

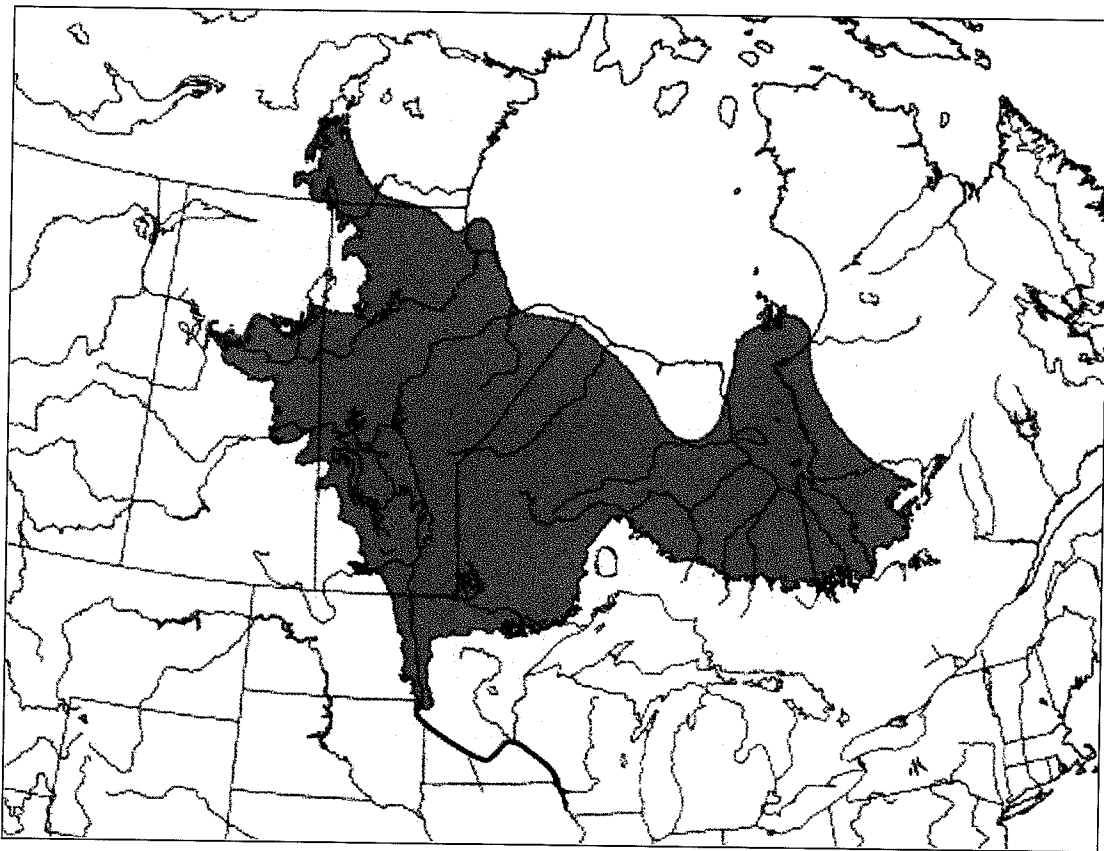


Figure 1.4. Total area covered by glacial Lake Agassiz over its 5 000 year history; approximately 1.5 million km². The size of the lake fluctuated over its lifespan, gradually shifting from south to north following the recession of the Laurentide Ice Sheet (after Leverington and Teller 2003).

An alternate hypothesis regarding the origin of *C. zenithicus* is the one-species model, which considers it to be a polymorphic species beyond the Great Lakes (including Lake Nipigon). In this case, *C. artedi* was the lone inland lake invader and where suitable habitat conditions occurred it diverged into different morphotypes through parallel speciation. Some genetic evidence has been found to support the early divergence between *C. zenithicus* and *C. artedi* discussed above (Turgeon et al. 1999). This evidence was limited to lakes Nipigon and Superior, however; and was not supported by populations from inland lakes (Turgeon and Bernatchez 2003). The hypothesis suggests that morphologically divergent forms within each lake are the result of phenotypic plasticity within a single gene pool (Douglas et al. 1999). If, however, divergence within each lake is significant enough to warrant identification to the level of species then adaptive radiation leading to sympatric speciation has occurred (Schluter 2000). Phenotypic plasticity in the form of recent parallel and local divergence within *C. artedi* has been suggested by some as the most plausible scenario for the significant morphological polymorphisms displayed in North America (Turgeon and Bernatchez 2003).

Species Concepts and Criteria

One, if not the major, goal of systematics is to produce a reference system, where the species taxon is identified as the lowest-level most-inclusive formally named group within the biological hierarchy. To accomplish this, an appropriate criterion for grouping organisms is needed on which some categorical rank and a method of naming the recognized categories can be applied (i.e., species). A species concept provides the

general criteria necessary to determine where species boundaries likely exist for any given case. It is important to have a precisely defined and consistently applied species concept for ecological studies of diversification that provide valuable information about the processes of speciation (Shaw 1998).

The scientific literature has been inundated with species concepts with a particular flourish of concepts and definitions in the last 40 years (Mayr 1963, Dobzhansky 1970, Bush 1975, Wiley 1978, Paterson 1985, Templeton 1989, Cracraft 1989, Nixon and Wheeler 1990, Baum and Shaw 1995, Mallet 1995). In general most of these concepts agree that speciation is a process requiring gene flow to be limited and hybridization to be disadvantageous for diverging populations (Bush 1975). How reproductive barriers are established has often been debated. Some speculate that the barriers are a direct result of selection for reproductively isolating mechanisms between populations while others feel that the barriers are the result of selection for traits that increase reproductive cohesion or niche specialization within populations. The debate over product versus process has been problematic to understanding the mechanisms of divergence and multiplication of species (Templeton 1989).

The Biological Species Concept has been defined in several ways. Mayr (1963) defines it as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. Dobzhansky (1970) defines it as a system of populations, where the gene exchange between them is limited or prevented in nature by a reproductive isolating mechanism or by a combination of such mechanisms.

The Recognition Species Concept, as defined by Paterson (1985), proposes that species are the most inclusive population of individual biparental organisms, which share a common fertilization system. Templeton (1989) defined the Cohesion Species Concept as the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. The Phylogenetic Species Concept defines a species as an irreducible cluster of organisms, diagnosably distinct from other such clusters, within which there is a parental pattern of ancestry and descent (Cracraft 1989). Nixon and Wheeler (1990) defined a species as the smallest aggregation of populations or lineages diagnosable by a unique combination of character states in comparable individuals. The Genealogical Species Concept is defined as exclusive groups of organisms, where an exclusive group is one whose members are all more closely related to each other than to any organism outside the group (Baum and Shaw 1995). The Evolutionary Species Concept as defined by Wiley (1978) states that a species is a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. The Genotypic Species Cluster Definition states that species are distinguishable groups of individuals that have few or no intermediates when in contact. Clusters are recognized by a deficit of intermediates, both at single loci and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters) (Mallet 1995).

One of the oldest species concepts is the Typological concept, which is based on the belief that distinct and constant forms exist for species and any morphological variation

from these forms is due to imperfection (Mayr and Ashlock 1991). Species are identified from one another in this concept through the use of morphological similarities and differences. Modern taxonomists have tried to move away from this type of concept. However, difficulties associated with establishing whether or not reproductive isolation truly exists between populations in nature makes the selection of alternative species concepts relying on this condition uncertain. Thus, in practice taxonomists often use morphological similarities and differences as a basis for taxonomy at the species level despite their theoretical shortcomings (Steinhilber 2000).

Under the Biological Species Concept co-occurring species are separated into reproductive communities by reproductive isolating mechanisms that preserve the genetic makeup of each species by reducing gene flow to a minimum. The mechanisms can be either pre-zygotic (spatial, temporal, or behavioural isolation) or post-zygotic (physical, gamete incompatibility, and hybrid sterility or inviability). Under the biological species concept, isolating mechanisms are believed to evolve following the adaptive divergence of physically separated populations. If gene flow does occur between the sympatric populations, it is believed that hybrid inferiority or sterility act as isolating mechanisms to protect the gene pool of biological species (Mayr and Ashlock 1991).

An approach that minimizes bias by comparing external morphological characters from across the body was used in this study. Multivariate analyses with no *a priori* character weighting towards traits with theoretical or speculated importance for competition have been used as a means to remove this bias (Steinhilber et al. 2002). Identifying species

based on continuous quantitative differences requires a means of delimiting taxa that reduces subjectivity and is not arbitrary (Cracraft 1989). To accomplish this, multivariate methods such as Principal Components Analysis or Discriminant Function Analysis effectively reduce the amount of subjectivity bias. These objective multivariate methods are suitable for situations where no single morphometric or meristic character is available for discriminating phenotypically plastic taxa (Todd et al. 1981, Reist et al. 1992).

Principal Components Analysis has been found to separate closely related cisco species into distinct, non-overlapping clusters on component projections (Todd et al. 1981).

Membership of individuals to a potential species can be hypothesized using one or a few characters such as gillrakers, which show some delimiting properties; however, these hypotheses should be tested by comparing them to the results of analyses using a combination of additional useful characters.

Study Objectives and Approach

North American ciscoes represent one of the most decimated groups of freshwater fishes in the northern hemisphere. The center of the diversity of this group is the Laurentian Great Lakes; however, this is the region where the greatest impacts and permanent loss of diversity have occurred. North American ciscoes account for 7 % of the fish species listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), either as extinct, threatened, or of special concern (Todd 2003). *Coregonus zenithicus* is one of the cisco species listed by COSEWIC as threatened and this status is based primarily on their situation in the Great Lakes and the lack of knowledge available on them beyond this region (Todd 2003). Outside of the Great Lakes region the status of *C.*

zenithicus is met with uncertainty due to the issues surrounding the taxonomic validity of the local forms. In Manitoba, it is considered to be a species of special concern due to its limited distribution and taxonomic uncertainty (Stewart and Watkinson 2004). If the inland form of *C. zenithicus* appears to be more consistent with *C. artedi* than the Great Lakes form of *C. zenithicus* then the status issue should be restricted to the Great Lakes region. If, however, the inland and Great Lakes *C. zenithicus* forms appear to be equivalent then the status issue extends beyond the Great Lakes and the populations outside of the Great Lakes represent surviving stocks of a declining species (Stewart and Watkinson 2004).

The objectives of this study were to examine a combination of morphometric and meristic characters in ciscoes from four lakes with prior evidence of multiple cisco forms being present to determine: 1) if multiple forms are indeed present in each lake, 2) if so then how similar are particular forms across all lakes, 3) what is the most likely taxonomic identity of the forms.

The approach used in this study was to collect cisco specimens from each lake and examine them initially using key taxonomic characters. Gillraker counts and structure have historically been the primary characters used for cisco identification and these characters were examined in this study for potential cisco forms. Other key characters including body shape, dorsal colouration, and mouth position and morphology were then examined to determine whether they were in agreement with the forms suggested by gillraker count and structure. A combination of morphometric and meristic characters

were then analyzed multivariately by Principal Component Analysis for potential grouping structure in phenetic space. Finally, the groups identified in the above steps were tested by Analysis of Variance and Discriminant Analysis. The focus here is on the products of evolution in the form of taxonomic diversity in ciscoes and whether the diversity is at the species level or not. The basic operational assumption was that different character suites within a lake separate the sympatric forms. Agreement between character suites among lakes suggests taxonomic affinity of the allopatric members. Key character values such as gillraker count for the forms were then compared to the character values for *C. zenithicus* and *C. artedi* from other locations and from the literature for potential identification of the forms.

2. MATERIALS AND METHODS

Study Sites

Lake Athapapuskow

Lake Athapapuskow is located in northern Manitoba near the town of Flin Flon at approximately 54° 35'N, 101° 35'W. The lake consists of three basins, a small north basin, a larger middle basin commonly referred to as Little Athapapuskow, and the south basin, which is the largest and appropriately referred to as Big Athapapuskow (Figure 2.1). The three basins have a combined surface area of 270.3 km². Big and Little Athapapuskow are connected by Mink Narrows, a 32 m wide, 90 m long, and 4 m deep channel. Drainage is from north to south with the majority of inflowing water coming from Pineroot, Mistik, and Schist creeks. Outflow water leaves Lake Athapapuskow through the Goose River (Day 1983). Some physical characteristics of Lake Athapapuskow are listed in Appendix 1-1.

The lake lies in the transition area between Precambrian and Ordovician rock. The south shores of Big Athapapuskow are Ordovician with dolomitic limestone. The other lake basins are mostly Precambrian consisting of granites and other varieties of igneous rock (Day 1983). The bottom of the lake is mainly mud and the shorelines are mostly rocky with a few sandy beaches. Depth contours for Lake Athapapuskow are fairly irregular with many shallow rocky reefs and small islands throughout. The eastern sides of Little and Big Athapapuskow are more shallow and rocky than those on the western side, especially around the eastern arm of Big Athapapuskow (Figure 2.1).

Thermal stratification usually begins in June with the thermoclines becoming established by early July in all basins. Maximum thermocline depth was found to occur around late August for all basins and was deepest in Big Athapapuskow. The highest oxygen levels were found within Big Athapapuskow for all strata where they were always saturated or supersaturated (Day 1983).

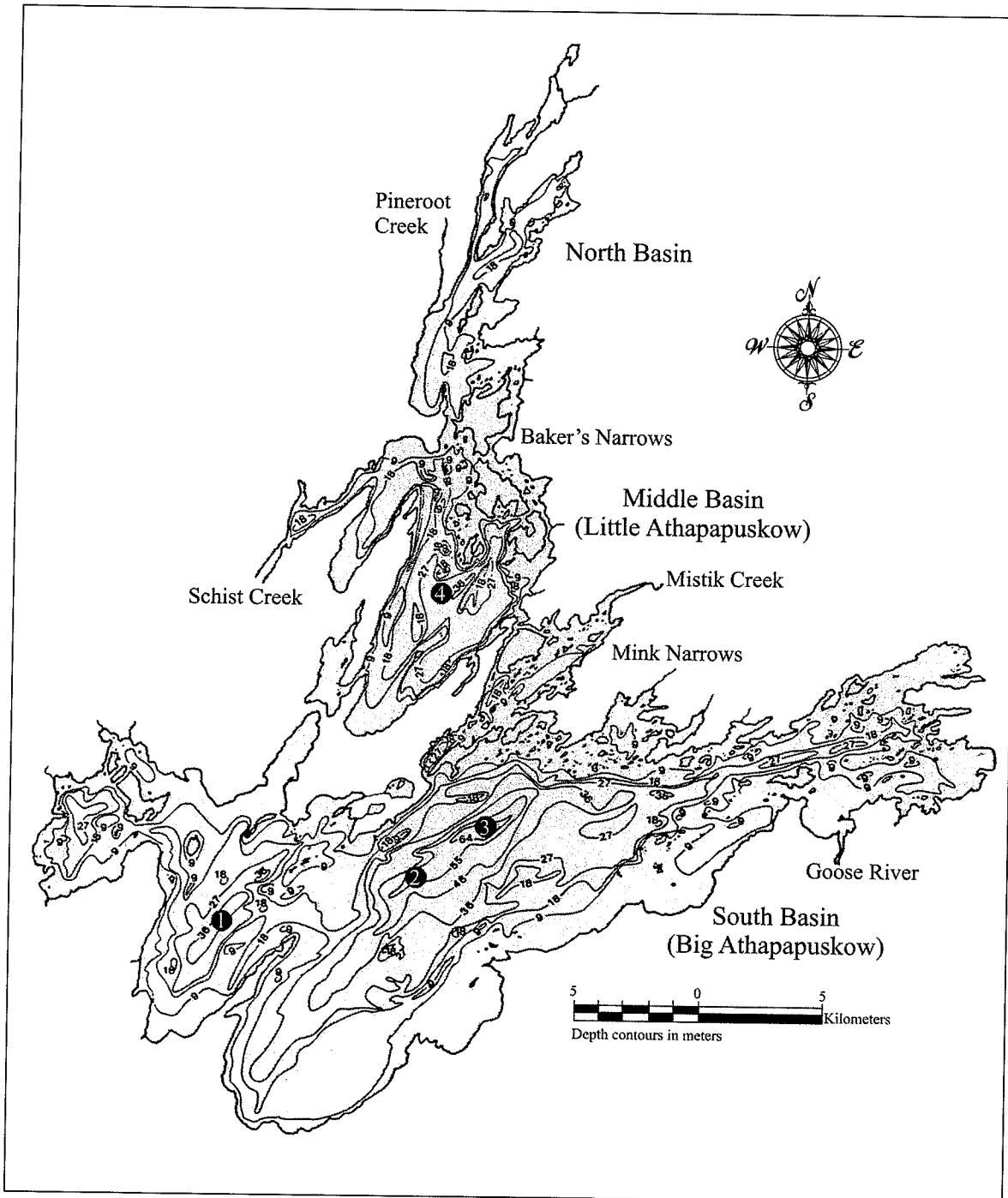


Figure 2.1. Lake Athapapuskow map (Adapted from Day 1983). Numbered dots indicate set number and set information is presented in Appendix 1-1.

Reindeer Lake

Reindeer Lake is in northern Manitoba and Saskatchewan with approximately 84% of the lake located on the Saskatchewan side of the border (Dean 1975, Figure 2.2). The longitudinal boundaries of the lake are $101^{\circ} 30'$ and $103^{\circ} 15'$ W and the latitudinal boundaries are $56^{\circ} 15'$ and $58^{\circ} 10'$ N. It is the tenth largest freshwater lake in North America with a surface area of around $5\,300\text{ km}^2$. The length of the lake is approximately 225 km and the mean width is 23.5 km. The lake has many small islands (approximately 5 500) creating over 9 000 km of heavily indented shoreline. The mean depth of the lake is approximately 18 m with a maximum depth of 215 m occurring in Deep Bay of the south basin resulting from a meteorite impact. The total volume of water in the lake is approximately $95 \times 10^9\text{ m}^3$. The drainage area of the lake is extensive at approximately 65 km^2 . The main rivers include the Reindeer River, which drains the lake at Southend (Figure 2.2) flowing into the Churchill River system, and Cochrane River, which flows from Wollaston Lake entering Reindeer Lake at Brochet. A number of small streams enter the lake including Sawbill, Paskwachi, and Wapus rivers on the eastern side and Swan and Wathaman rivers on the western side (Figure 2.2). Some physical characteristics of Reindeer Lake are provided in Appendix 1-2.

Precambrian crystalline rocks such as granite and quartz diorite make up the bedrock of Reindeer Lake. The surface deposits in the area are primarily glacial drift of till and granitic boulders (Schlick 1971). Depth contours for Reindeer Lake are fairly irregular with many shallow rocky reefs and bays, small islands, and deep basins throughout.

Thermal stratification usually begins in early July with maximum thermoclines occurring in August in most regions of the lake. Maximum thermocline depth was found to be around 20 to 30 meters for most regions of the lake. Oxygen was found to be abundant at all depths during the summer within Reindeer Lake (Dean 1975).

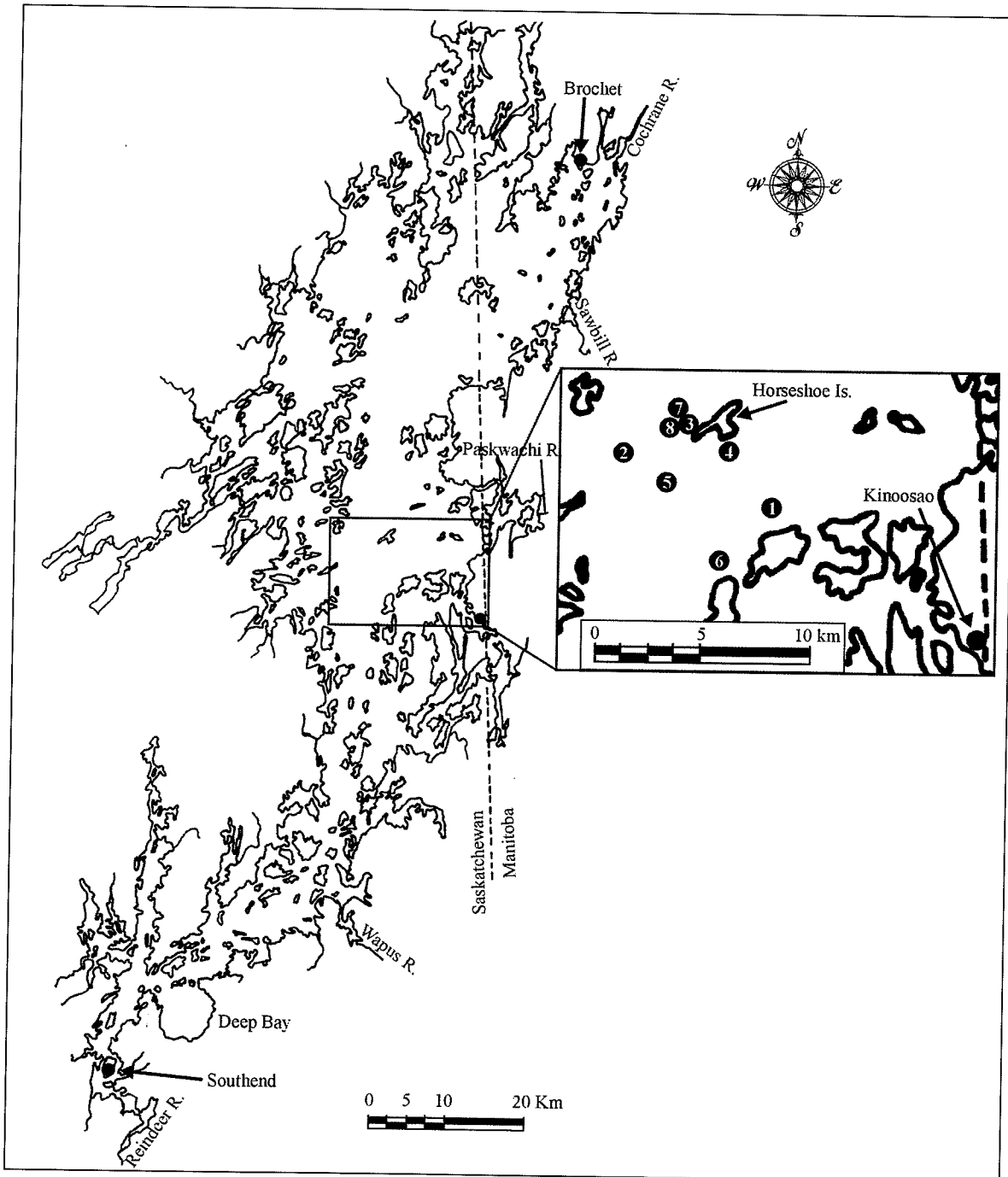


Figure 2.2. Map of Reindeer Lake (after Dean 1975). Enlarged region shows the focus of sampling effort with sets indicated by numbered dots. Note: set information is presented in Appendix 1-2.

George Lake

George Lake is located in southeastern Manitoba within the Whiteshell Provincial Park at approximately 50° 15' latitude and 95° 30' longitude (Figure 2.3). The nearest town is Point Du Bois, which is accessible by road; however, you have to cross the Winnipeg River and then portage approximately 2.5 km either by foot or with the aid of the local outfitters to get to the lake. The lake is approximately 12.2 km in length and has a mean width of 1.75 km (Gibson and Johnson 1969). The lake consists of three basins, the deepest and largest basin is at the north end of the lake while the mid and south basins are much smaller and shallower. The morphometry of each is presented in Appendix 3. The lake has a few small islands and the shoreline length for the entire lake including islands is approximately 48 km (islands alone have shoreline length of 32 km). The mean depth of the lake is approximately 12 m with a maximum depth of 45 m. The total volume of water in the lake is approximately $26.6 \times 10^7 \text{ m}^3$. The drainage area of the lake is relatively small, with a few lakes draining into it including Forbes Lake, North Sailing Lake, and Horseshoe Lake. A number of small streams enter the lake including Forbes and McMurray creeks on the east, Williams Creek on the west, and Beck's Creek at the southeast corner. The outlet of George Lake is Tie Creek found at the southwest corner of the lake (Figure 2.3) (Gibson and Johnson 1969). The physical characteristics of George Lake are shown in Appendix 1-3.

George Lake lies in the Precambrian Shield. The surface terrain consists of igneous and metamorphic rock outcrops and is relatively hilly (Gibson and Johnson 1969). The altitude is approximately 290 m and mixed woods are the predominant vegetation (mostly

spruce and aspen) (Gibson and Johnson 1969). Depth contours for George Lake are fairly regular with the most variation occurring in the north basin where shallow bays, islands, and the deepest region of the lake occur (Figure 2.3, Gibson and Johnson 1969).

Thermal stratification was found in all three basins of the lake (measurements taken in July) (Gibson and Johnson 1969). Thermocline depth was found to be around 6 to 12 m for the north basin, 7.5 to 13 m for the mid basin, and 8.5 to 10.5 for the south basin. Oxygen was found to be abundant at all depths during the summer within George Lake (Gibson and Johnson 1969).

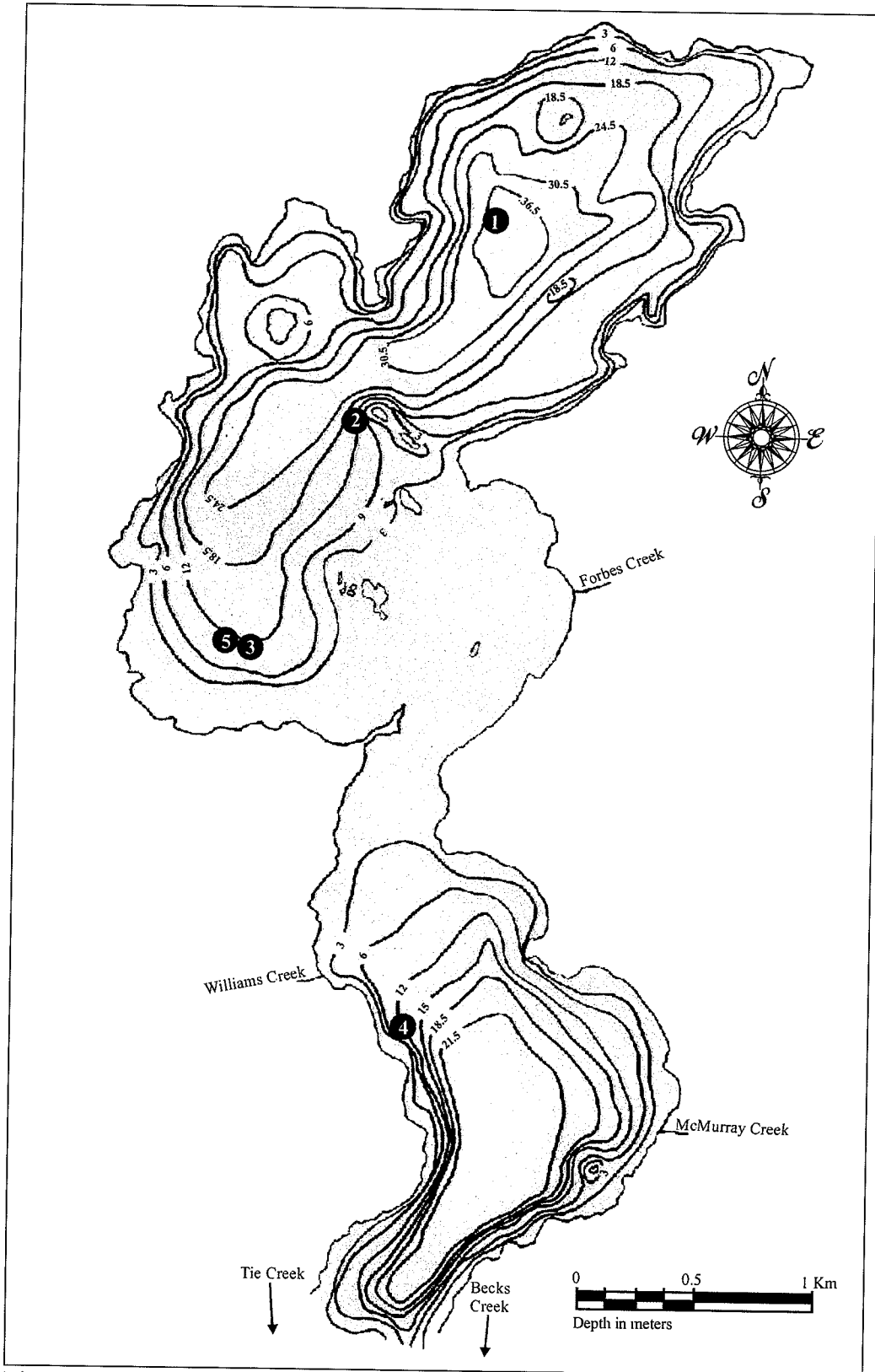


Figure 2.3. Bathymetric map of George Lake (adapted from Gibson and Johnson 1969). Note: collection sites are indicated and set information is presented in Appendix 1-3.

Clearwater Lake

Clearwater Lake is located in northern Manitoba near The Pas approximately 54° 00'N and 101° 00'W. The lake is relatively square in shape measuring approximately 16 km long and 16 km wide with an area of around 290 km² (Schlick 1978). The lake is readily accessible by road from the south where a provincial park, campground, several lodges, and cabins are present. The western side of the lake slopes gradually to a depth of approximately 12 m where it becomes more irregular. The eastern side of the lake slopes much more rapidly to a depth of 12 m. The deepest regions of the lake are located in the north central area and consist of four distinct areas with depths greater than 30 m (Figure 2.4). The maximum-recorded depth for the lake is 42.5 m. Some physical characteristics for Clearwater Lake are presented in Appendix 1-4. The drainage area of the lake is relatively small with the watershed limited to a few kilometers from the shoreline. A number of small seasonal streams enter the lake on the west side, draining from the end moraine and muskeg to the west (Schlick 1978). The outlet of Clearwater Lake is found at the northeast corner and flows into Cormorant Lake (Figure 2.4). Some islands are found in the northern part of the lake and reefs are numerous throughout the lake but only along the shoreline.

The bedrock surrounding Clearwater Lake was formed in Silurian times with Ordovician bedrock primarily confined to the northeast region of the lake. The surface terrain consists of glacial drift that is predominantly limestone; an end moraine lies to the west, part of which is used by Provincial Highway #10 (Schlick 1978). The vegetation around the lake is primarily Northern Coniferous Forest dominated by black spruce (Gibson and

Johnson 1969). Schlick (1978) found in 1970 that the thermocline occurred successively deeper as summer progressed. In late July, Schlick (1978) found that the thermocline ranged from 9 to 14 m, in early August the range had changed from 18 to 22 m, and late August the thermocline had dropped to between 22 and 25 m.

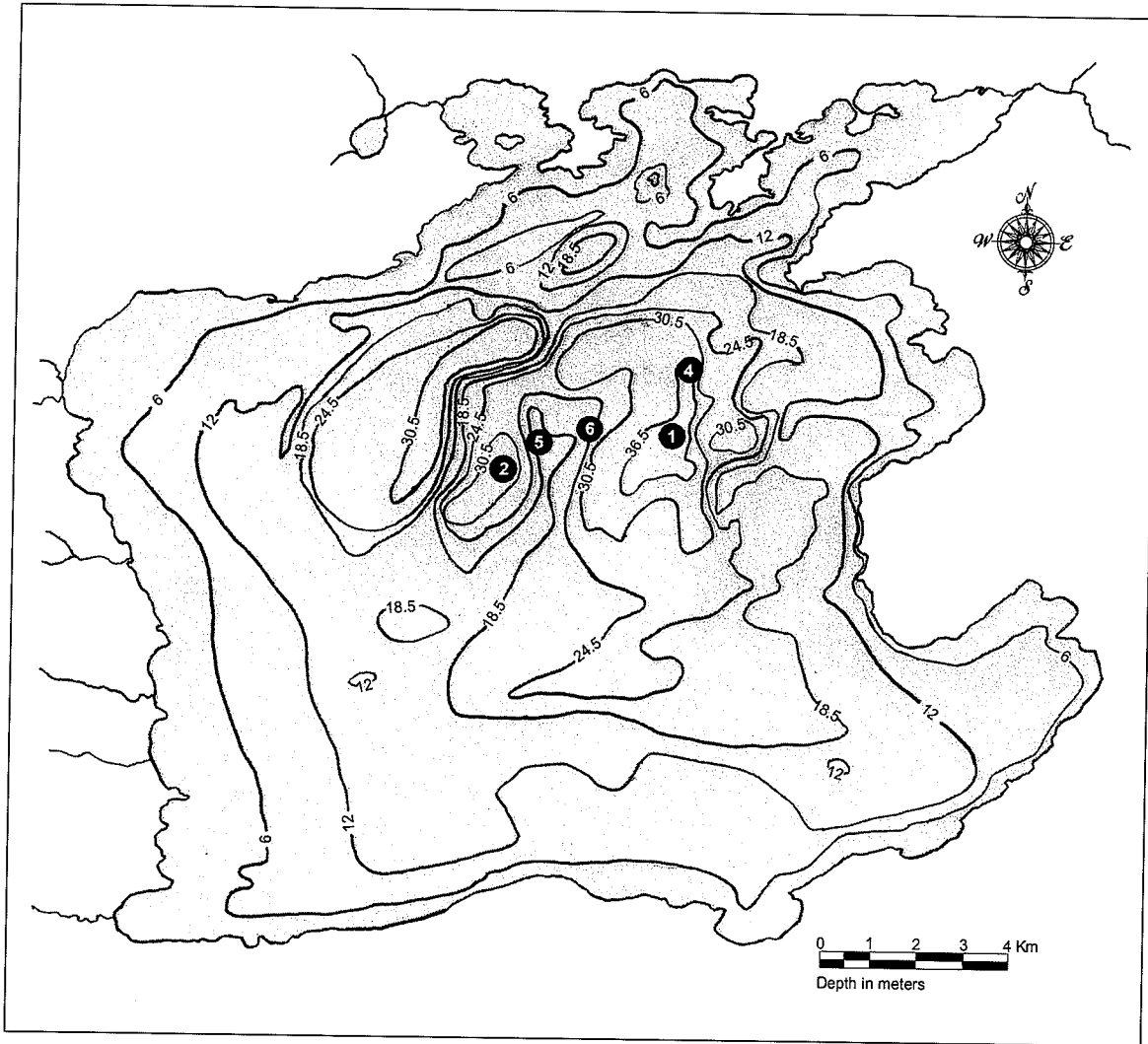


Figure 2.4. Bathymetric map of Clearwater Lake (Adapted from Schlick 1978). Numbered dots indicate set numbers; set information is presented in Appendix 1-4. Note: Sets 1 and 2 were conducted in 2000; sets 3 – 6 were conducted in 2002. Note: sets 1 and 3 were made at the same location.

Specimen Collection

Ciscoes were collected from the four lakes described above based on their having previous accounts of *C. zenithicus* and *C. artedi*. Cisco sampling in all of the lakes was focused towards deeper regions in an effort to catch the deepwater forms of ciscoes in each lake, thus enhancing the probability that the catch would include putative shortjaw cisco. The sites were located using bathymetric maps, a Garmin GPS unit, local knowledge of the area, and a depth finder. All sets were approximately 18 to 24 hours in duration. Location coordinates and other species collected during sampling are presented in Appendices 2-1 to 2-4. Attempts were made to collect a reasonable sample size for each form present in a lake ($n > 50$).

The collection sites for Lake Athapapuskow included three deep areas in Big Athapapuskow and the deepest region in Little Athapapuskow (Figure 2.1). The sets used for all four collection sites consisted of two nets tied together set at the bottom of the lake. The first net was 82.3 m (90 yards) long, 3.66 m (4 yards) deep, and had three mesh sizes (25.4 mm, 38.1 mm, and 44.5 mm stretched measure). The second net was 120 m long, 1.83 m deep, and had six panels with mesh sizes ranging from 10 to 25 mm (stretched measure).

Cisco sampling in Reindeer Lake was focused upon deep regions of the lake within close proximity to the town of Kinoosao. A total of eight sets were made with the majority in close proximity to Horseshoe Island (Figure 2.2). Four of the collection sites consisted of two 60 m nets tied together set at the bottom of the lake. The first net consisted of six

panels with mesh sizes ranging from 10 to 25 mm (stretched measure) and the second net had six mesh panels ranging from 10 to 60 mm. The other four sets consisted of a 120 m long, 1.83 m deep net with panels ranging from 10 to 25 mm (stretched measure) in mesh size.

Ciscoes were collected from George Lake in 2000 and 2001. In 2000 the deeper north basin was sampled while in 2001 the shallower regions of the north and mid basin were sampled in an attempt to collect other cisco forms that may be present. One set was made in 2000 using a 120 m net with mesh sizes ranging from 10 to 25 mm (stretched measure). The sets in 2001 consisted of 60 m nets with mesh sizes ranging from 10 to 60 mm (stretched measure) for some sites and 10 to 25 mm (stretched measure) for other sites (Appendix 2-3).

Cisco sampling in Clearwater Lake focused on the north central location where deep basins are located (Figure 2.4). In October of 2000, two sets were made in this deep region; however, only 24 ciscoes were collected. To increase the sample size four additional sets were made in September, 2002. In 2000 sets consisted of a 120 m net with mesh sizes ranging from 10 to 25 mm (stretched measure) and an 82.3 m net with mesh sizes of 25.4, 38.1, and 44.5 mm. In 2002 sets were made using a 120 m net with mesh sizes from 10 to 25 mm, with the exception of one set which consisted of an additional 60 m net ranging in mesh size from 10 to 25 mm (Appendix 2-4).

Biological, Morphometric and Meristic Characters

Gillraker count and structure was examined initially to search for potential forms within each lake. These characters were selected because the historic importance they have played in the identification of cisco species. Other key characters including body shape, dorsal colouration, and mouth position and morphology were then examined to determine whether they were in agreement with the forms suggested by gillraker count and structure.

Morphometric and meristic characters were measured on all ciscoes in order to examine morphological variation. All morphometric characters were measured on the left side of the body with digital dial calipers and recorded to the nearest 0.1 mm following Vuorinen et al. (1993) except standard length, which was measured using a measuring board (Figure 2.5). Six meristic characters were counted from the left side of the body (Figure 2.5). Another character, premaxillary angle, was measured by determining the angle of the premaxillaries from the horizontal axis of the head following Clarke's (1973) work (Figure 2.5). Other characters were recorded including weight, sex, and maturity.

Measurements

- 1) Standard length: tip of the premaxilla to the caudal flexure
- 2) Preorbital length: tip of the premaxilla to the anterior fleshy margin of the orbit
- 3) Orbital length: distance between anterior and posterior fleshy margins of the orbit
- 4) Post orbital length: posterior fleshy margin of the orbit to posterior bony margin of the operculum

- 5) Trunk length: distance along the horizontal axis of the body between the posterior margin of the operculum and the origin of the dorsal fin
- 6) Dorsal length: origin of the dorsal fin to the posterior edge of the fin behind the final ray
- 7) Lumbar length: distance along the horizontal axis of the body between the end of the dorsal fin and the origin of the anal fin
- 8) Anal length: distance along the horizontal axis of the body between the origin of the anal fin and the posterior edge of the fin
- 9) Caudal peduncle length: distance along the horizontal axis of the body between the posterior of the anal fin and the caudal flexure
- 10) Head depth: vertical distance through the pupil of the eye from the dorsal surface of the cranium to the ventral edge of the gular region
- 11) Body depth: vertical distance from the dorsal origin to the ventral surface of the body
- 12) Caudal peduncle depth: the least vertical depth of the caudal peduncle
- 13) Interorbital width: shortest distance of bone between the upper rims of the orbits
- 14) Maxillary length: anterior point of premaxillae to posterior end of the maxilla
- 15) Maxillary width: greatest width along the maxillary
- 16) Pectoral length: extreme base of outermost ray to farthest tip of fin
- 17) Pelvic length: extreme base of outermost ray to farthest tip of fin
- 18) Adipose length: distance from the point where skin and scales meet at the anterior end of the fin to the free posterior margin of the fin
- 19) Middle gillraker length: length of the gillraker on the ceratobranchial-epibranchial joint on the first arch

20) Lower arch length: length from the start of the lower arch to the base of the middle gillraker

21) Premaxillary angle: angle between the horizontal axis of the head and the premaxillae

Counts

- 1) Dorsal ray count: all rays in the dorsal fin including rudimentary rays
- 2) Anal ray count: all rays in the anal fin including rudimentary rays
- 3) Pectoral ray count: all rays in the left pectoral fin counted
- 4) Pelvic ray count: all rays in the left pelvic fin counted
- 5) Upper gillraker count: number of gillrakers, including all rudiments, on the first, left epibranchial including the raker on the ceratobranchial-epibranchial joint (Bodaly 1979)
- 6) Lower gillraker count: number of gillrakers, including all rudiments, on the first, left ceratobranchial (Bodaly 1979)
- 7) Total gillraker count: sum of upper and lower gillrakers

All fin ray counts were made according to the methods of Hubbs and Lagler (1964).

Rudimentary rays were included for both dorsal and anal counts, branched rays were counted as one and the last two rays were counted as one under the assumption that they share a common base. For the paired fins, all rays were counted including the smallest one at the lower end of the fin base (Hubbs and Lagler 1964).

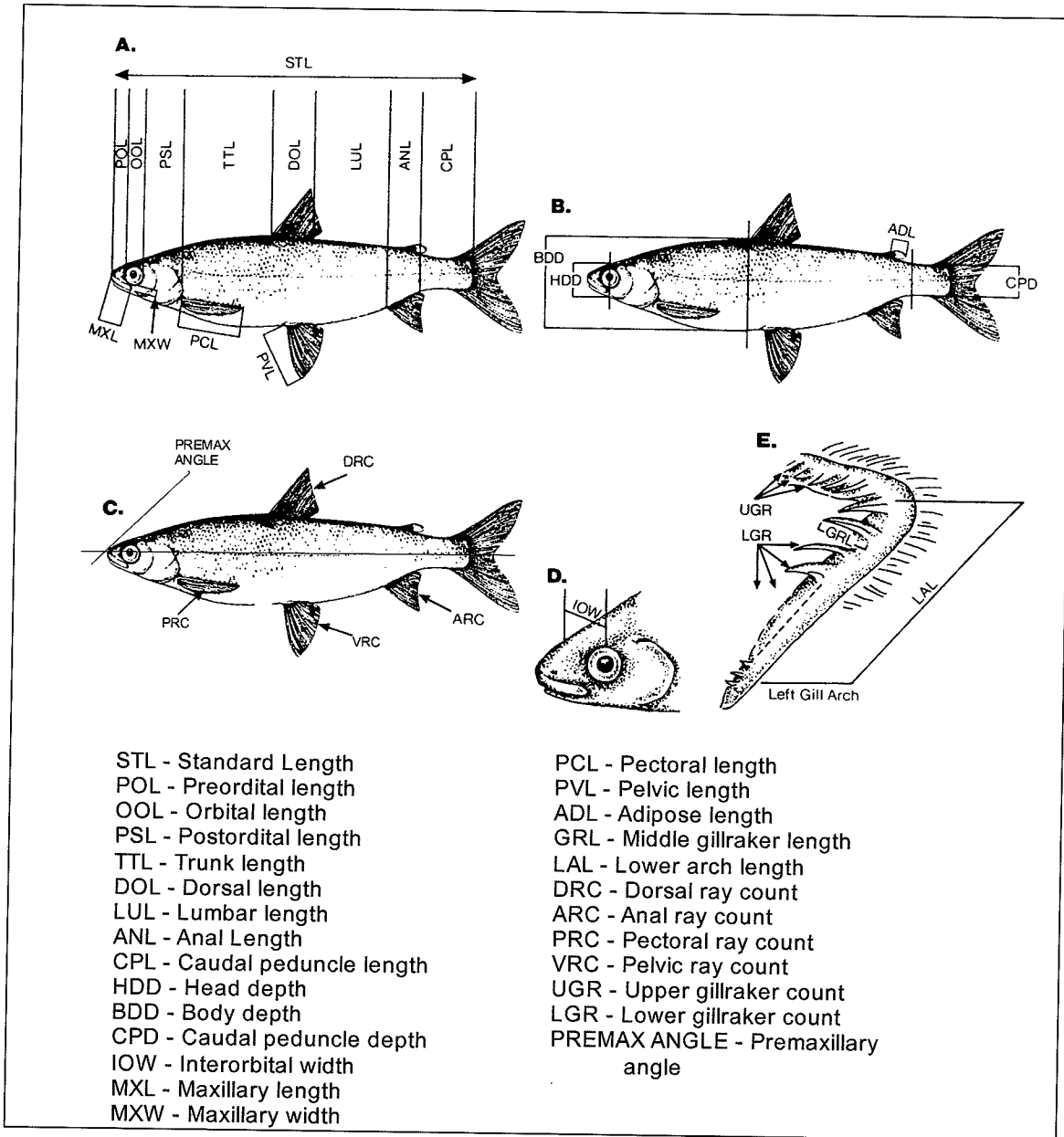


Figure 2.5. Morphometric and meristic measurements used in this study (from Vuorinen et al. 1993).

Aging Structure

Ages were determined by removing and examining otolith structure. Otoliths were removed from the fish during processing and then aged using the break and burn method by Laura Heuring (Stevenson and Camapana 1992). Annuli were counted using magnification. The ages were not validated so they may be subject to some measurement error; however, they were considered accurate enough for determination of relative length-at-age relationships.

Adjustment of Morphometric Data to Account for the Effects of Body Size

When analyzing morphometric data from organisms with indeterminate growth, such as fishes, the effect of size must be accounted for and adjusted in some way to enable direct comparisons of individuals with different body lengths. Ratios have been one of the most commonly used methods for creating size-free shape variants; however, several statistical problems are associated with their use in this way. One major problem has been that ratios have proven ineffective in removing size effects in some studies (Atchley et al. 1976, Albrecht 1978, Dodson 1978). Ratios effectively reduce all individuals to the same size but they are not able to remove the undesired size effects as they keep the size-dependent shape caused by allometric growth. Under isometric growth conditions the use of ratios for removing body size may be effective but for organisms with allometric growth such as fish they are inappropriate (Leonart et al. 2000). Subsequent use of ratio values in data analysis would then have confounding effects on the power of statistical tests, ultimately leading to an increased probability of Type II errors occurring and causing differences between samples to be missed (Atchley 1978, Pimental 1979). In this

study ratios were used in an exploratory sense for preliminary data examination before a more statistically appropriate and effective method of size adjustment was applied to the data.

The most efficient and effective methods of removing the effects of body size incorporate regression techniques to derive shape measures from the relationship between body parts (Reist 1985, Reist 1986). Their use as a technique for accounting for the effects of body size has been supported by Gould (1966), Atchley et al. (1976), Atchley (1978), and Reist (1985). The method incorporated in this study is the common within-group residual method recommended by Reist (1985, 1986). Reist's (1985, 1986) work provides an in-depth evaluation of several size adjustment techniques commonly used by systematists. His findings were that regression residual transformation protocol is superior to most other techniques. A regression line was calculated for each character from an Analysis of Covariance with gillraker form as the fixed factor and standard length as the independent variable. This resulted in a regression slope common to all groups (common-within-groups slope), that was then used as a common standard for comparing the relative body size of all populations combined. The difference between the group mean of the dependent variable for each population (calculated by the ANCOVA) and the grand mean for each dependent variable across all groups was subtracted from the residual values from the common-within-groups regression line. The resulting adjusted residuals were used as the new morphometric variables for all subsequent analyses.

The intra-group frequency distributions of adjusted variables were examined for evidence of non-linearity. Reist (1985), in an empirical test of size removal techniques in *Esox lucius* (northern pike), found that the distribution of 5 of 10 morphometric characters was non-normal following regression residual transformation. However, he cites studies demonstrating that the effects of non-normality are not serious when sample sizes are reasonably large or when descriptive multivariate techniques like principal components analysis are used.

Statistical Analysis

A Principal Component Analysis (PCA) was used at various stages of this study to examine morphometric and meristic differences within and among populations. This multivariate method is used to reduce the complex interactions of many variables into fewer components (Pimental 1976). These components retain the key underlying influences from the original data and allow it to be visualized in a more manageable way. Principal Components Analysis does not require prior knowledge of grouping structure making it a suitable exploratory analysis. Groups that may have been identified prior to the PCA using other methods or characters can then be identified *a posteriorily* for comparison. The procedure is robust and has few assumptions about data distribution and homogeneity of variance among populations (Sneath and Sokal 1973, Pimental 1979).

Discriminant Analysis (DA) was also used at different stages of this study. This statistical method is used to examine the amount of separation between predetermined

groups and to place individuals of uncertain group membership into the most statistically appropriate group. Separation among the groups is maximized relative to the within group variation using a linear combination of objectively weighted characters (Sneath and Sokal 1973, Pimental 1979).

The main goal of this study was to examine ciscoes collected from lakes with previously reported sympatric populations and determine if in fact they are distinct. The null hypothesis for each lake was that the ciscoes examined were part of a single population and the analyses were used to support or refute this hypothesis. Because PCA requires no *a priori* grouping structure it was a more appropriate choice for preliminary data exploration in this study. Discriminant Analysis assumes homogeneity of variance (Pimental 1979) and results from the Levene's tests found that several characters failed to meet this assumption. Despite failing to meet this assumption, DA was still used in this study to test the results of the PCA groupings with the knowledge that the significance of the results may be reduced. All statistical analyses were performed using the Statistical Package for the Social Sciences for Windows (SPSS 2001).

3. RESULTS - COMPARISON OF LAKE ATHAPAPUSKOW CISCOES

General Biology

A total of 192 ciscoes were collected from Lake Athapapuskow that were in suitable condition for analysis. The collection information for each set is summarized in Appendix 2-1. The descriptive statistics for all ciscoes collected from Big Athapapuskow and Little Athapapuskow are presented in Appendix 3-1. The size range for the 181 individuals analyzed from Big Athapapuskow was 77 to 191 mm in standard length with a mean of 117 mm and 6 to 114 g in weight with a mean of 27 g. The 11 ciscoes collected from Little Athapapuskow ranged in size from 122 to 181 mm in standard length with a mean of 152 mm and 27 to 93 g in weight with a mean of 55 g (Appendix 3-1). The frequency distribution for standard length suggests that two modes are present in the data, one around 95 mm and one around 150 mm (Appendix 3-2). When standard length and weight are plotted together along with the location of capture, no difference other than size was apparent (Appendix 3-3). The age distribution for all ciscoes collected from Lake Athapapuskow is heavily skewed towards individuals between one and three years of age (Appendix 3-4). The sex ratio was examined by looking at the distribution of total gillraker counts versus standard length for all individuals identified by sex (Figure 3.1). Two main groups were suggested, one with high gillraker counts and shorter standard lengths and the other with low gillraker counts and greater standard lengths. The high gillraker group consisted of mostly males while the low gillraker group was mostly females, however, both sexes were present in each group ruling out sex as a basis for gillraker number. When sexual maturity was plotted on the graph of total

gillraker counts versus standard length most of the males were mature, including the majority of males with high gillraker counts and standard lengths less than 100 mm (Appendix 3-5). The females were found to be mostly mature; however, several were immature or resting females.

A preliminary examination of the general biology of all ciscoes collected from Lake Athapapuskow suggested the presence of at least two sympatric forms. The size difference between the two forms is most likely due to variation in ages as the majority of the high gillraker forms were found to be age classes one or two. Sexual dimorphism was ruled out as a factor because there were some large males with low gillraker counts as well as smaller females with high gillraker counts (Figure 3.1). The two high gillraker ciscoes collected from set one appear to be outliers in Figure 3.1, these individuals either represent older members of the high gillraker form or members of a third cisco form within the lake.

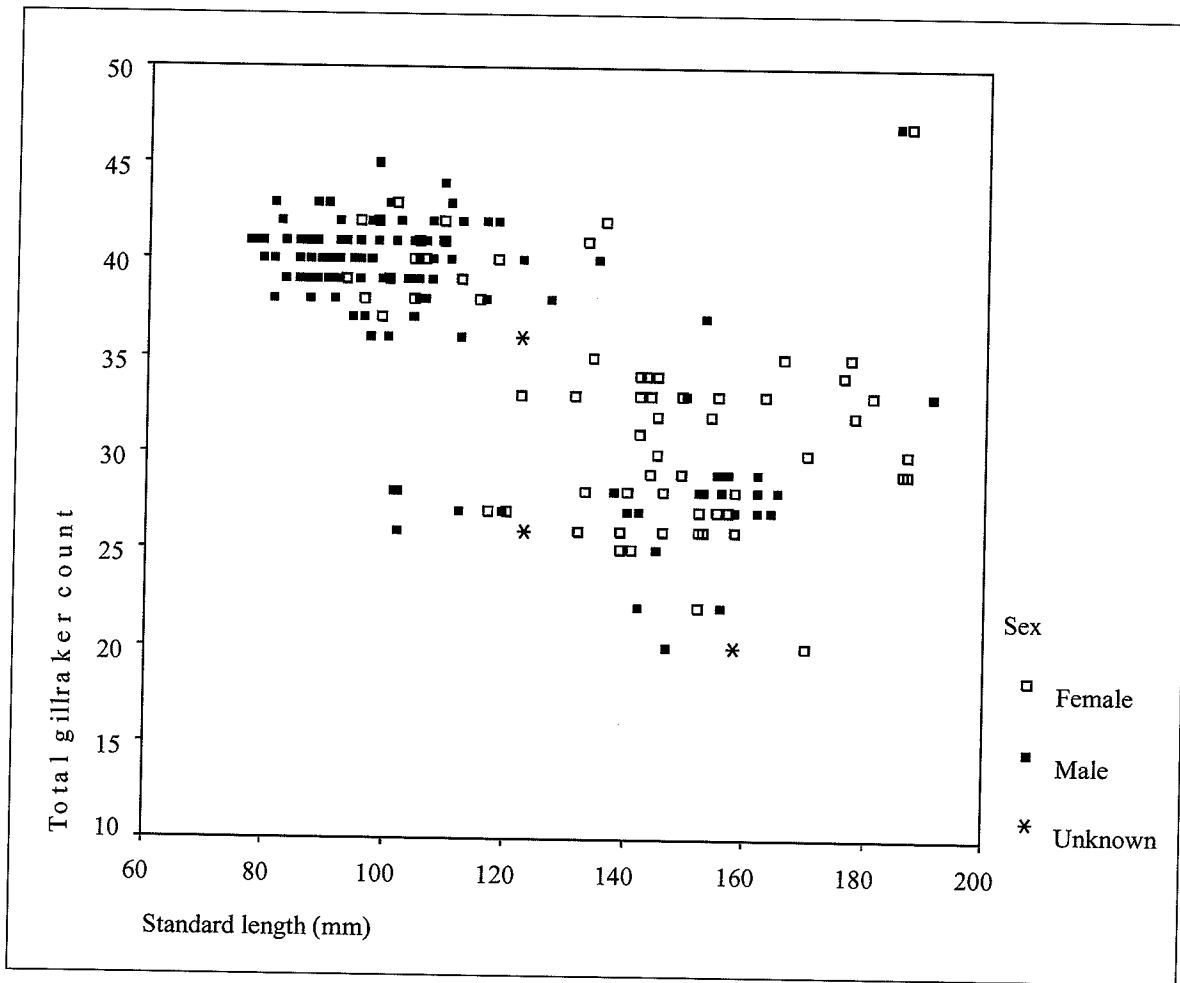


Figure 3.1. Relationship between total gillraker count and standard length for Lake Athapuskow ciscoes with individuals identified by sex.

Discrimination of Cisco Forms

Individuals from Lake Athapapuskow were tentatively placed into high or low gillraker forms initially on the basis of gillraker number and to a lesser extent standard length (figures 3.2 and 3.3). A separation was apparent around the 35 to 36 gillraker range (Figure 3.3). Individuals with a total gillraker count of 35 or less were considered members of the low gillraker form and those with 36 or greater were placed in the high gillraker form. The separation provided by this variable was used as the logical choice for defining the forms. Other characters were found to distinguish the forms in the field along with gillraker counts including dorsal colouration (darker for the high gillraker group), jaw position (usually superior in the high gillraker form and inferior to terminal in the low gillraker form), and gillraker arrangement (tightly packed and long gillrakers in the high form and widely spaced short gillrakers in the low form (Figure 3.3). The low gillraker form from Big Athapapuskow (n=60) had a mean gillraker count of 27.9 (20-35) and a mean standard length of 150.8 mm (112-191). The high gillraker form from Big Athapapuskow (n=121) had a mean gillraker count of 40.1 (36-47) and a mean standard length of 100.5 (77-187). One form was considered present in Little Athapapuskow based on the distribution of individuals produced by plotting standard length against gillraker count (Figure 3.2). The single form from Little Athapapuskow (n=11) had a mean gillraker count of 33.7 (32-37) and a mean standard length of 152 mm (122-181). The specimens from Little Athapapuskow were grouped with the low form from Big Athapapuskow because all but one individual had gillraker counts of 35 or less. The one individual from Little Athapapuskow with a gillraker count of 37 was considered to be a member of the low gillraker form based on it having short, widely spaced gillrakers, light

dorsal colouration, and an inferior jaw position. The combined low gillraker form had a mean gillraker count of 28.8 (20-37) and a mean standard length of 151 mm (112-191). The gillraker structure of the two different forms is shown in Figure 3.4 and the external appearance of the two forms is shown in Figure 3.5.

The majority of the low forms were collected from the deepest regions of Big and Little Athapapuskow (Figure 3.6). In Big Athapapuskow set three was the deepest at 65 m and this set consisted almost entirely of individuals with 35 or less gillrakers. Only one set was made in Little Athapapuskow at a depth of 38 m and only one individual had greater than 35 gillrakers. The majority of individuals with gillrakers counts over 35 were collected from set 2 at a depth of 47.5 m. The descriptive statistics of the two forms from Lake Athapapuskow (Big and Little Athapapuskow combined) for all morphometric and meristic characters are listed in Table 3.1. The size-at-age for each form was plotted and the results are shown in Appendix 3-6. It is difficult to compare the two forms by this character due to the lack of older individuals from the high gillraker form.

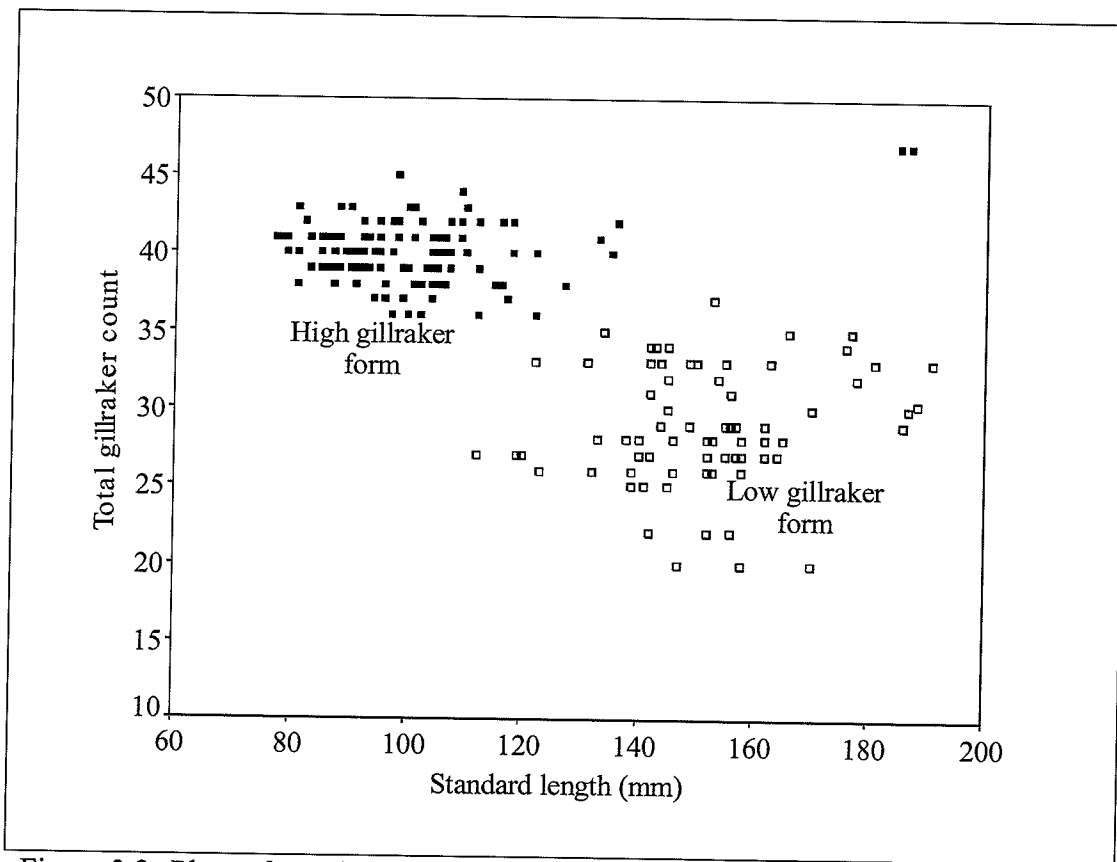


Figure 3.2. Plots of standard length versus gillraker number for all Lake Athapapuskow ciscoes showing forms suggested by gillraker counts.

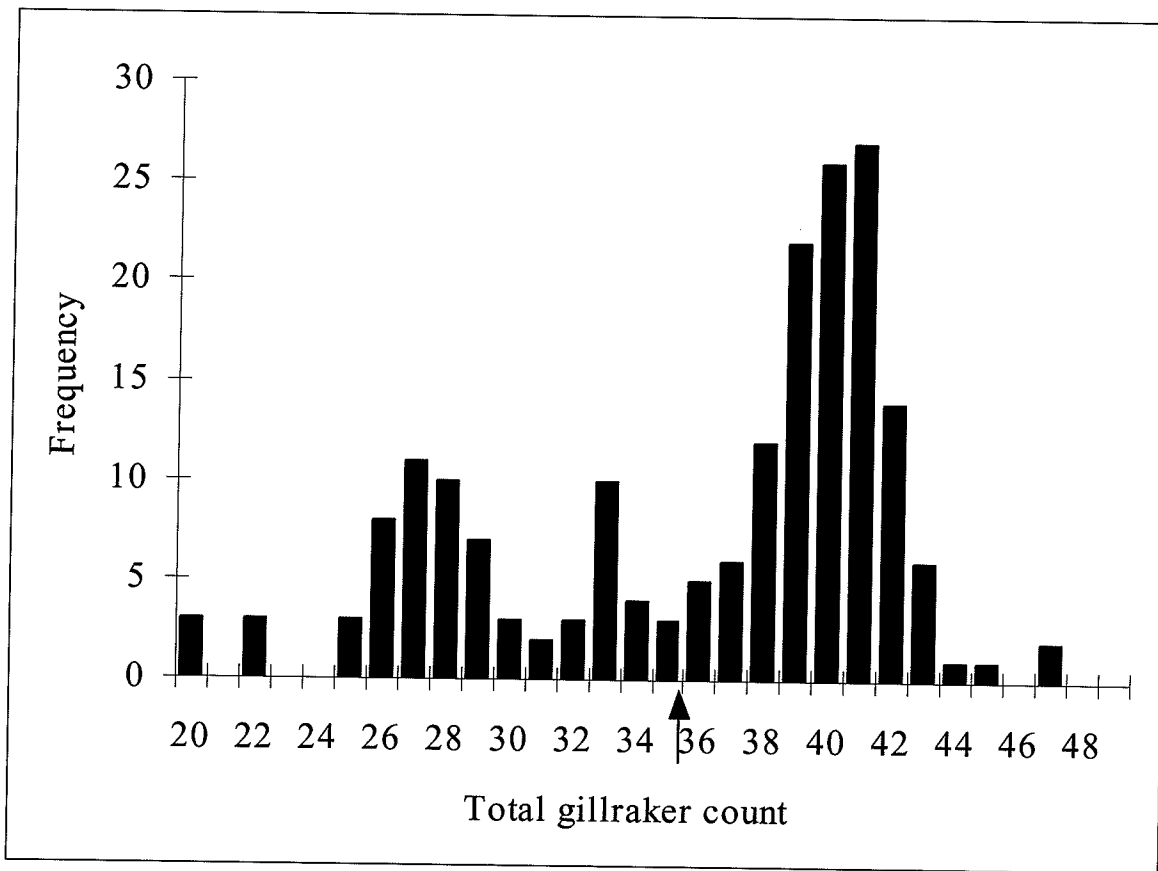


Figure 3.3. Frequency distribution of total gillraker counts for all ciscoes from Lake Athapapuskow. All individuals with counts 35 or less were placed in the low group and 36 or more were placed in the high group with the exception of one individual from Little Athapapuskow with 37 gillrakers which was placed in the low group. The arrow indicates the point of separation between groups.

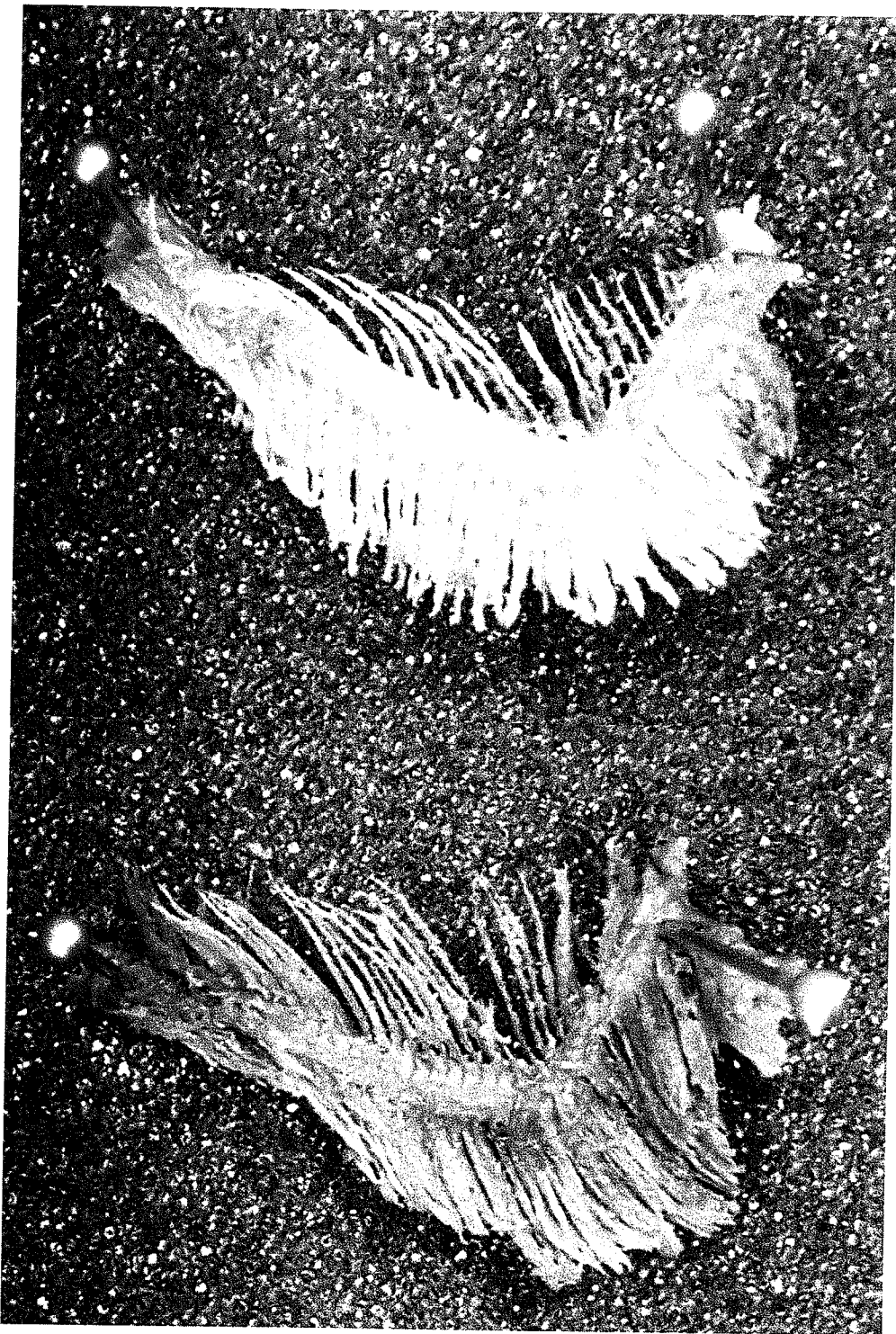


Figure 3.4. Gill arches removed from Lake Athapapuskow ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes and lower panel of high-gillrakered ciscoes from Lake Athapapuskow.

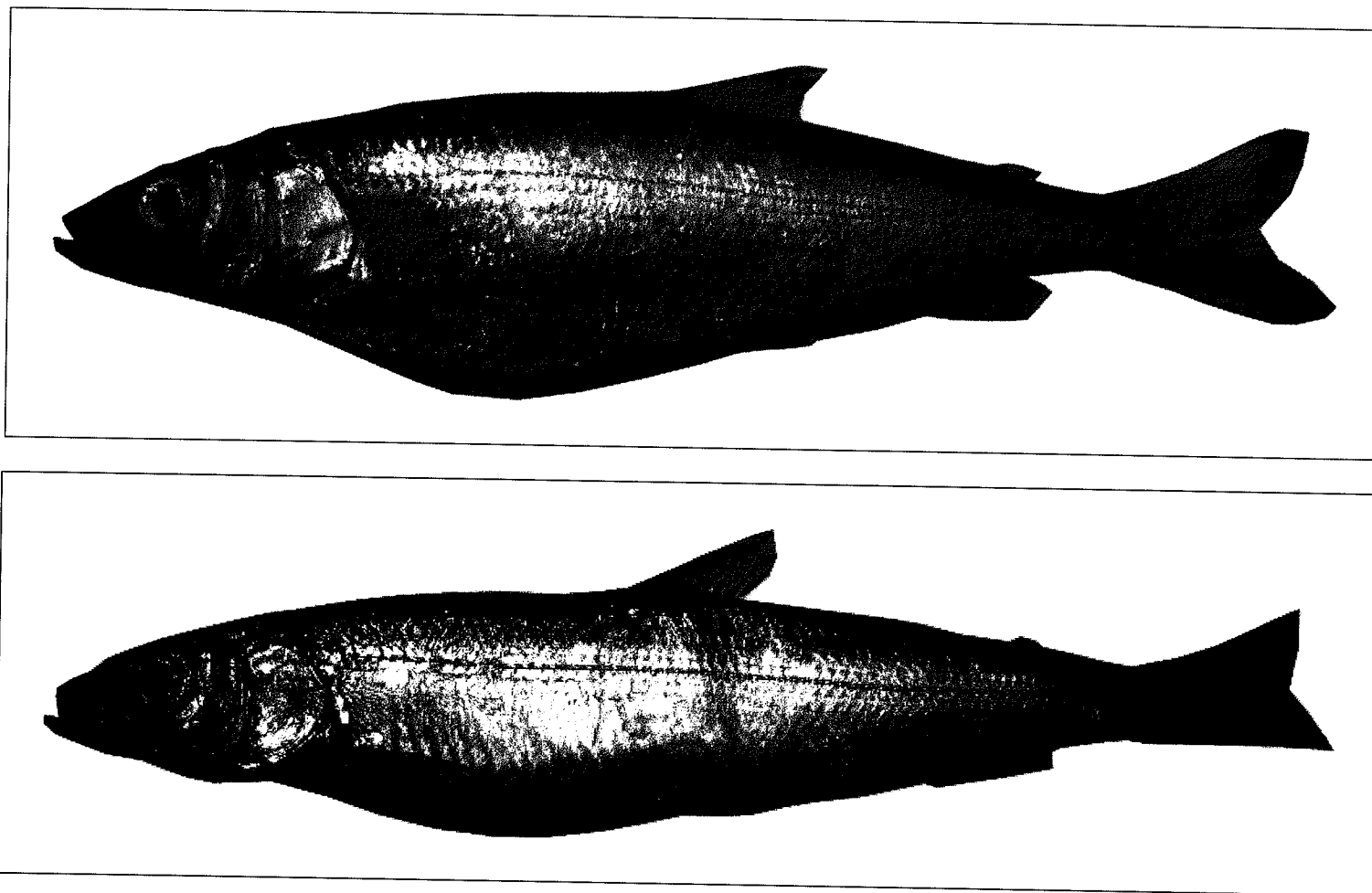


Figure 3.5. General appearance of Lake Athapapuskow ciscoes. The fish in upper panel had a standard length of 187 mm and 30 gillrakers and is representative of the low form. The fish in lower panel had a standard length of 99 mm and 39 gillrakers and is representative of the high form. Note: previously frozen specimens.

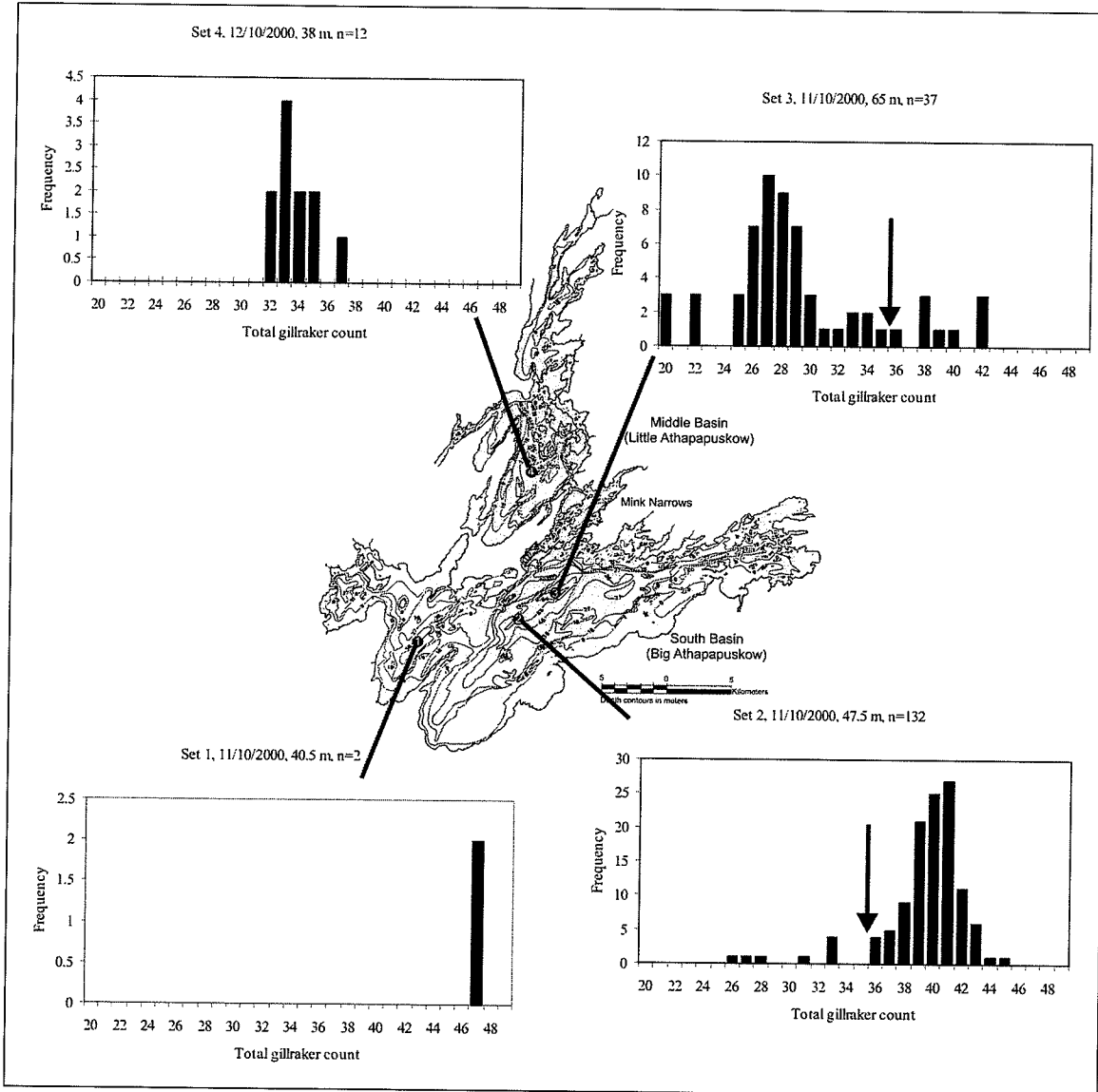


Figure 3.6. Total gillraker count distributions for all Lake Athapuskow collection sites. Arrows indicate separation between groups for sets 2 and 3 based on key characters. Each panel indicates set number, date, depth, and number of fish captured (see also Appendix 2-2).

Table 3.1. Descriptive statistics for the low and high gillraker forms collected from Lake Athapapuskow. All variables are represented by raw, untransformed values.

	Low gillraker form			High gillraker form		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Total gillraker count	20	37	28.8	36	47	40.1
Upper gillraker count	8	13	10.2	9	16	13.3
Lower gillraker count	10	25	18.6	22	32	26.8
Premaxillary angle	35	65	48.4	25	55	42.4
Dorsal ray count	8	12	10.9	9	12	10.6
Anal ray count	10	14	12.2	10	14	12.4
Pectoral ray count	14	18	16.4	11	18	16.3
Pelvic ray count	10	13	11.1	10	13	11.4
Age	3	17	10.0	1	15	1.9
Weight	21	114	53.6	6	98	14.6
Standard length	112.0	191.0	151.0	77.0	187.0	100.5
Fork length	131.0	216.0	168.9	85.0	216.0	112.6
Gillraker length	3.1	7.0	4.9	2.7	8.5	4.4
Lower arch length	11.6	27.9	16.8	7.0	23.5	9.8
Preorbital length	6.7	15.2	10.1	3.9	13.0	6.2
Orbital length	7.7	12.5	9.8	4.9	12.2	6.4
Post orbital length	13.6	25.1	18.6	8.3	24.3	11.6
Trunk length	25.6	52.6	38.2	15.5	47.2	24.1
Dorsal length	11.1	22.0	16.1	7.4	24.3	11.4
Lumbar length	17.7	31.9	25.3	8.4	36.0	15.4
Anal length	11.1	18.7	14.3	6.5	23.5	9.9
Caudal peduncle length	11.9	22.6	17.0	7.2	22.4	11.3
Head depth	11.9	24.8	17.7	8.8	22.7	11.6
Body depth	24.3	51.5	36.2	13.1	43.1	19.9
Caudal peduncle depth	8.8	13.3	10.7	5.2	14.2	6.9
Interorbital width	5.0	11.3	7.9	3.6	13.0	5.5
Maxillary length	9.5	19.3	13.2	6.6	16.4	8.2
Maxillary width	2.4	6.6	4.0	1.7	5.6	2.9
Pectoral length	17.9	31.3	24.3	11.3	28.7	15.6
Pelvic length	18.4	32.3	24.8	11.1	28.8	15.9
Adipose length	5.5	13.3	9.4	3.5	11.9	5.6

Morphological Confirmation of Differences

A series of PCAs were performed to examine if the forms identified from Lake Athapapuskow were confirmed by multivariate analysis. Initially only individuals from Big Athapapuskow were compared and the analysis included using only meristic characters including gillraker counts (appendices 3-7 and 3-8). The two extracted components explained nearly 60% of the total variation with upper and lower gillraker counts accounting for most of the variation positively and premaxillary angle negatively on component one (31.6%)(Appendix 3-8). Component two (27.1%) was influenced most by dorsal, pectoral, and anal ray counts. The next PCA consisted of 19 morphometric characters adjusted by ratios (appendices 3-9 and 3-10). The first two components suggested some separation between the Big Athapapuskow forms (Appendix 3-9). Postorbital length, lower arch length, and maxillary length accounted for most of the variation on component one (19%) (Appendix 3-10). Gillraker length and dorsal length were positively correlated with the second component and lumbar length and body depth were negatively correlated (14.4%).

The results of the PCA using a combination of meristic characters (including gillraker counts) and morphometric characters adjusted by ratios (26 characters in total) provided the best separation between the two forms. Together, components one and two provided complete separation between the two forms (Figure 3.7). The variation shown by component one was primarily accounted for by a contrast between upper and lower gillraker count, body depth and lower arch length versus gillraker length (Table 3.2). The character loadings for these components are provided in Table 3.2.

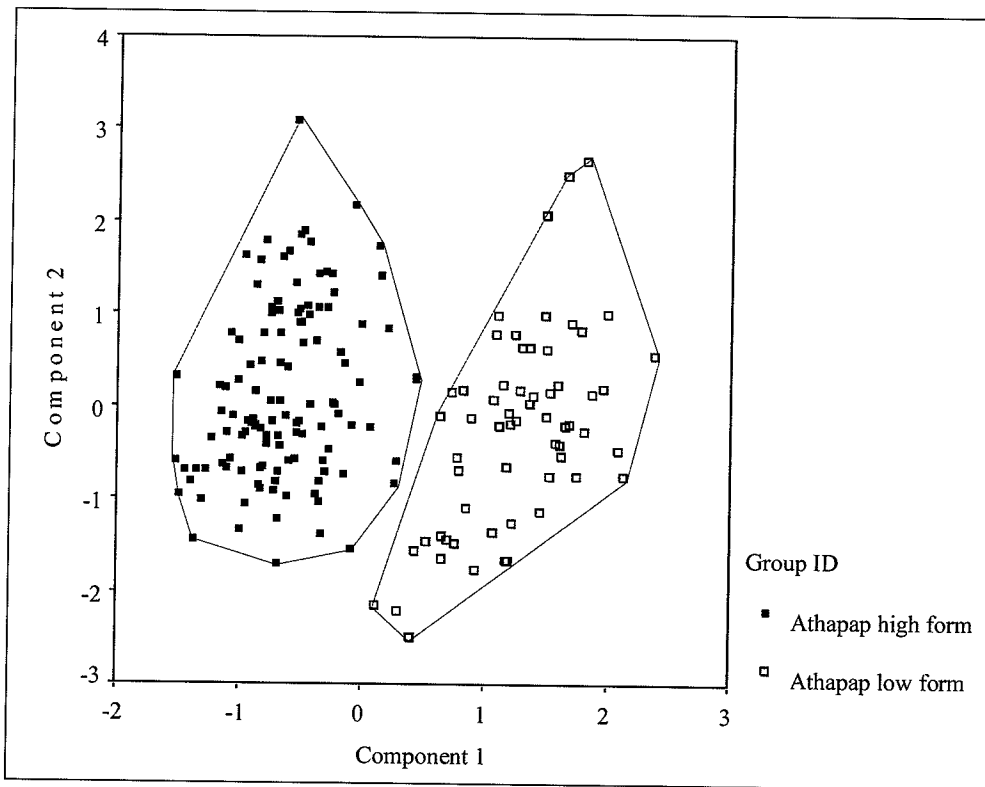


Figure 3.7. PCA plots for ciscoes from Big Athapuskow based upon meristic and morphometric characters adjusted by ratios. Variable loadings are described in the text. Form was assigned *a posteriori* using key character criteria outlined in the text.

Table 3.2. Character loadings and variance explained by PCA on Big Athapapuskow ciscoes using meristic and morphometric characters adjusted by ratios.

	Component	
	1	2
Preorbital length	0.42	0.46
Orbital length	0.14	0.22
Post orbital length	0.52	0.45
Trunk length	0.45	-0.18
Dorsal length	-0.29	0.43
Lumbar length	0.41	-0.52
Anal length	-0.29	0.30
Caudal peduncle length	0.16	0.30
Head depth	0.15	0.55
Body depth	0.77	-0.17
Caudal peduncle depth	0.43	0.46
Interorbital width	-0.04	0.68
Maxillary length	0.44	0.45
Maxillary width	-0.14	0.42
Pectoral length	0.20	0.06
Pelvic length	0.28	0.02
Adipose length	0.40	0.19
Lower arch length	0.60	0.31
Gillraker length	-0.66	0.24
Premaxillary angle	0.47	-0.36
Dorsal ray count	-0.03	-0.42
Anal ray count	-0.28	-0.39
Pectoral ray count	-0.08	-0.33
Pelvic ray count	-0.39	-0.22
Upper gillraker count	-0.83	0.22
Lower gillraker count	-0.78	0.33
Eigenvalues	4.88	3.48
Percent of Variance	18.77	13.40
Cumulative Percent	18.77	32.17

The final PCA for Big Athapapuskow did not include any of the meristic characters. Both upper and lower gillraker values were used to initially identify the forms that were used to calculate the common within-group residual adjusted morphometric characters used in this analysis. The fin ray counts were not found to be of any use in separating the forms and were not included in this analysis. The results of the PCA supported two forms being present; however, there was some overlap between them (Appendix 3-11). Components one and two provided the most separation between forms when plotted and components three and four provided no separation. Component one accounted for 20 % of the variation in the data and maxillary length, postorbital length, lower arch length, preorbital length, and orbital length (eye diameter) accounted for most of this variation (Appendix 3-12). Component two accounted for 13 % of the variance and interorbital width and gillraker length had high positive loadings on this component while pelvic length had a high negative loading (Appendix 3-12).

The above principal components analyses consistently supported two forms being present within Big Athapapuskow based on the specimens analyzed. The differences between the two forms were only supported by the first one or two components in the analyses. Some individuals with gillraker counts just above or below 35 (the point used to define forms) were found to more closely resemble the opposite group in which they were originally placed.

Analysis Including Little Athapapuskow Ciscoes

A PCA was performed including forms from both Big and Little Athapapuskow. This analysis did not include upper and lower gillraker counts but it did include the four remaining meristic characters, premaxillary angle, and the common-within-group residuals for 19 morphometric characters. When scores from components one and two were plotted the individuals from Little Athapapuskow grouped closer to the low gillraker form from Big Athapapuskow (Figure 3.8). The correlating characters between the low form and the Little Athapapuskow individuals for component one (16.2 % of variance) were postorbital length, maxillary length, lower arch length, preorbital length and orbital length. For component two (12.3 % of variance) interorbital width, head depth, and gillraker length were negatively correlated and premaxillary angle, dorsal ray count, pelvic and pectoral length were positively correlated (Table 3.3). Components three and four were did not provide any separation between the high and low forms (not presented).

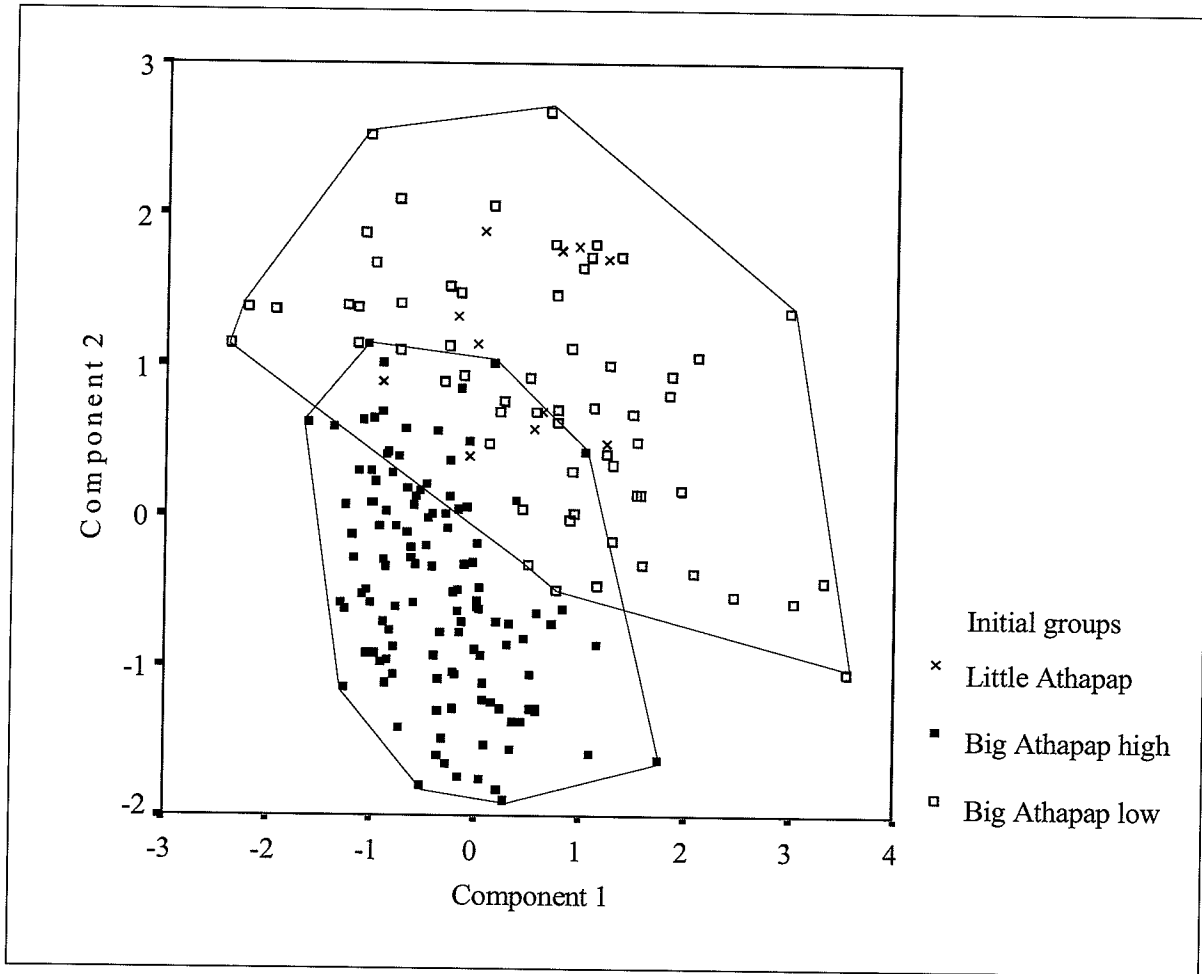


Figure 3.8. Plot of scores from PCA of all ciscoes from Lake Athapuskow using meristic characters (not including gillraker counts) and morphometric characters adjusted by common within-group residuals.

Table 3.3. Character loadings and eigenvalues from PCA of all Lake Athapapuskw ciscoes using meristic and morphometric characters adjusted by common-within-group residuals.

	Component	
	1	2
Premaxillary angle	0.06	0.51
Dorsal ray count	-0.13	0.51
Anal ray count	-0.34	0.28
Pectoral ray count	-0.19	0.31
Pelvic ray count	-0.35	-0.01
Preorbital length	0.66	-0.09
Oribtal length	0.57	0.32
Postorbital length	0.78	-0.05
Trunk length	-0.12	-0.10
Dorsal length	0.21	-0.11
Lumbar length	-0.18	0.38
Anal length	0.19	-0.14
Caudal peduncle length	0.25	-0.17
Head depth	0.47	-0.45
Body depth	0.25	0.39
Caudal peduncle depth	0.56	0.18
Interorbital width	0.17	-0.76
Maxillary length	0.70	0.01
Maxillary width	0.15	-0.42
Pectoral length	0.36	0.53
Pelvic length	0.32	0.57
Adipose length	0.43	0.13
Lower arch length	0.67	-0.05
Gillraker length	-0.14	-0.40
Eigenvalues	3.88	2.95
Percent of variance	16.17	12.28
Cumulative percent	16.17	28.44

Hypothesis Testing of Form Differences

The next step was to examine whether the two forms suggested by gillraker counts, key external characters, and by the PCAs were supported by statistical tests such as ANOVA and DA.

The results of the ANOVA testing mean differences between the two forms for each character and the Levene's test of homogeneity of variance are presented in Table 3.4 for all ciscoes combined (Big and Little Athapapuskow). The analysis included all meristic and morphometric characters with the morphometric values adjusted using common within-group residuals. A total of 18 characters were found to be significantly different between the low and high forms when equality of variances was not assumed and 19 characters when variances were assumed to be equal ($P < 0.05$). The Levene's test of equality of variances revealed that 18 characters failed to have equal variances ($P < 0.05$). Although the assumption of equivalency of variance was violated for many characters, the Anova results still provide strong evidence supporting the presence of multiple groups.

Table 3.4. ANOVA probability values between cisco forms from Lake Athapapuskow and Levene's test for homogeneity of variance. Values in bold indicates significance at $P < 0.05$.

	Levene's test of	Anova test of Equality of Means	
	Equality of Variance	Variance Equal	Variance Not Equal
	Sig.	Sig.	Sig.
Premaxillary angle	0.296	0.000	0.000
Dorsal ray count	0.061	0.021	0.022
Anal ray count	0.031	0.144	0.130
Pectoral ray count	0.356	0.349	0.354
Pelvic ray count	0.044	0.001	0.002
Upper gillraker count	0.317	0.000	0.000
Lower gillraker count	0.012	0.000	0.000
Preorbital length	0.136	0.000	0.000
Orbital length	0.000	0.000	0.000
Post orbital length	0.000	0.000	0.000
Trunk length	0.052	0.958	0.961
Dorsal length	0.004	0.182	0.225
Lumbar length	0.058	0.005	0.007
Anal length	0.000	0.357	0.401
Caudal peduncle length	0.001	0.490	0.527
Head depth	0.000	0.244	0.311
Body depth	0.000	0.000	0.000
Caudal peduncle depth	0.067	0.000	0.000
Interorbital width	0.008	0.000	0.000
Maxillary length	0.000	0.000	0.000
Maxillary width	0.040	0.032	0.045
Pectoral length	0.002	0.000	0.000
Pelvic length	0.000	0.000	0.000
Adipose length	0.000	0.043	0.088
Gillraker length	0.000	0.001	0.005
Lower arch length	0.026	0.000	0.000

Discriminant Analysis was used as a quantitative test of all characters simultaneously to determine if the forms initially identified were supported and to test the placement of the Little Athapapuskow individuals with the low form from Big Athapapuskow. Upper and lower gillrakers were not included in the character suite because they were used to identify the initial forms. Two separate analyses were performed, one with the low form from Big Athapapuskow and the ciscoes from Little Athapapuskow combined into a single low form and another with the Little Athapapuskow cases treated separately. A single function was calculated from the data for the first analysis (Table 3.5). The best discriminating characters for this function were negatively correlated interorbital width and gillraker length, and positively correlated orbital length and caudal peduncle depth. The analysis resulted in 97.4% of the originally grouped cases being classified correctly. Three individuals originally identified as low forms were classified as high forms and two high forms were considered to be low forms based on the discriminant results (Table 3.5). The second analysis treated the ciscoes from Little Athapapuskow separately from the two groups identified from Big Athapapuskow and resulted in two functions that supported the presence of multiple groups ($P < 0.001$, $df = 24$). The best discriminating characters for the first function were the same as the previous analysis (Table 3.5). For the second function the best discriminating characters were adipose length and lower arch length (negatively correlated). When the discriminant scores were plotted, the first function separated the high form from the majority of low gillrakered individuals (including the Little Athapapuskow ciscoes) while function two provided some separation between the Big Athapapuskow low form and the Little Athapapuskow ciscoes (Figure 2.20). The classification results do not completely support the combining