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

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

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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*.

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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).

<u>Ciscoes</u>

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

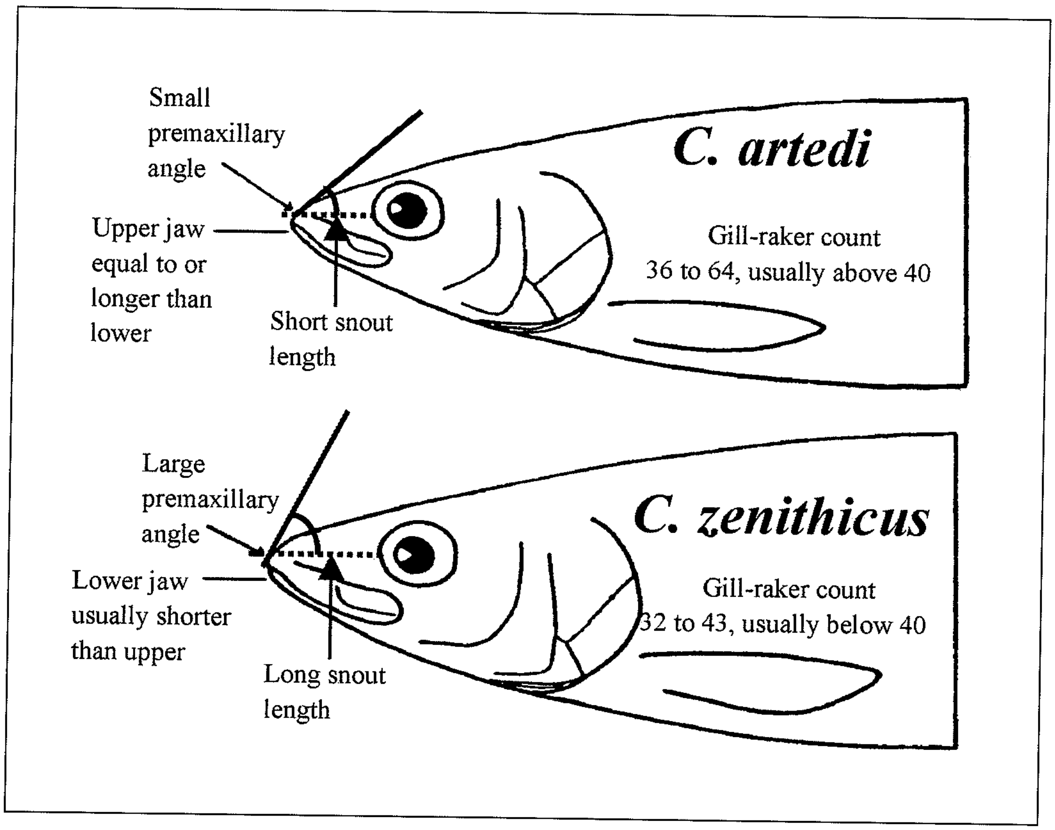


Figure 1.1. Key characters often used to distinguish between *Coregonus zenithicus* and *C. artedi*.

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.

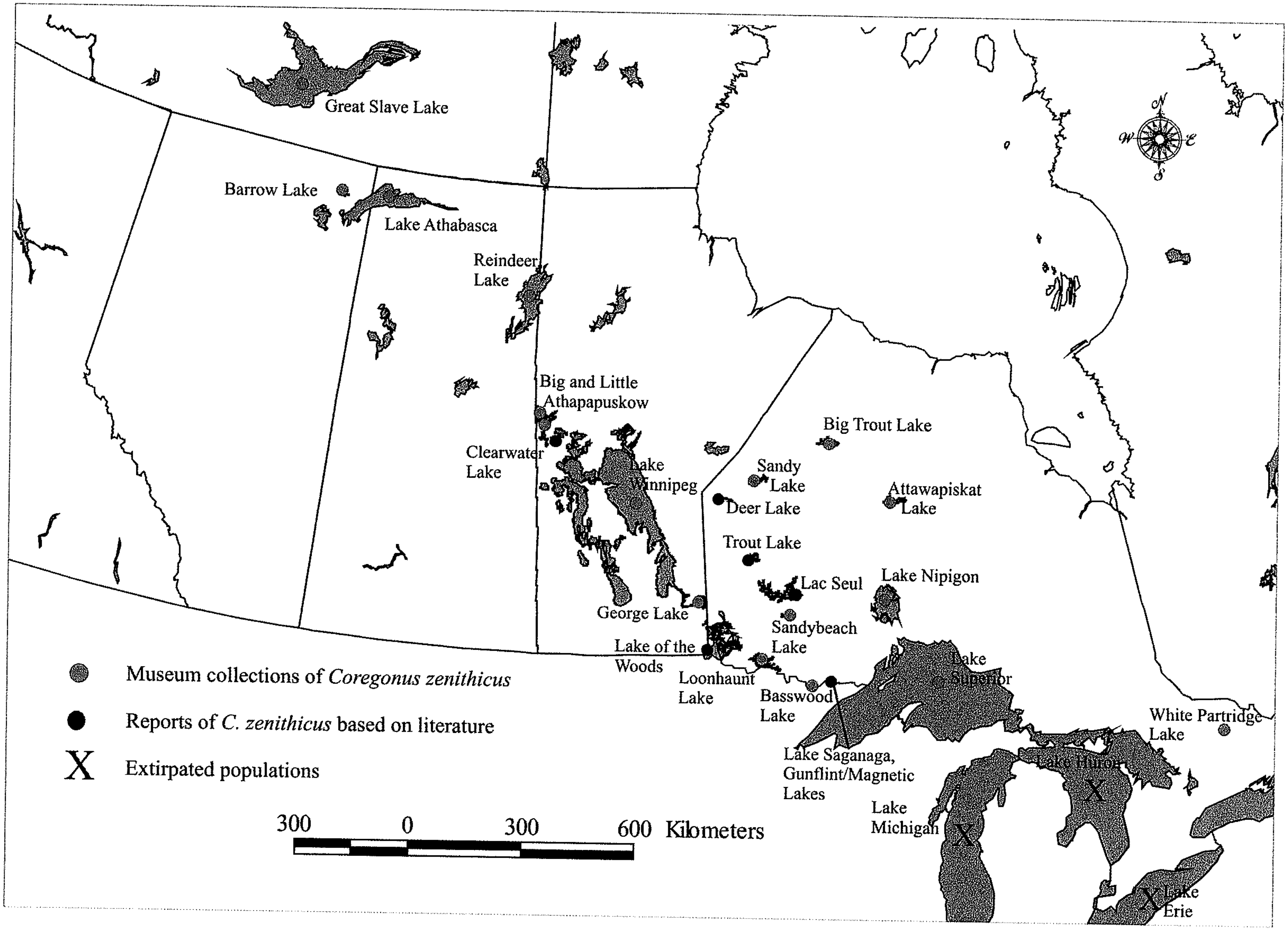


Figure 1.2. Current distribution of putative *Coregonus zenithicus* in Canada.

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 *L.macrognathus*, Dymond (1943), Rawson (1947) as *C. zenithicus*, Clarke (1973) as *C. artedii*	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 *C. reighardi;* Clarke (1973) as *C. prognathus*	ROM
Little Athapapuskow L.	MB	54° 37' N 101° 39' W	Clarke (1969) as *C. reighardi;* Clarke (1973) as *C. prognathus*	ROM
Clearwater Lake	MB	54° 05' N 101° 00' W	Clarke (1973) as *C. prognathus*	
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 *C. hoyi,* Clarke (1973) as *C. prognathus*	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 *C. hoyi*, Clarke (1973) as *C. prognathus*	ROM
Lac Seul	ON	50° 20' N 92° 16' W	Dymond and Pritchard (1930), Clarke (1973) changed to *C. prognathus*	
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

<u>Do different forms of *C. zenithicus* exist throughout its range?</u>

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. artedi* 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 Smith1980). *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 artedi* subspecies in the past (from Hubbs and Lagler 1964).

Subspecific name	Common name	Location	Reference
greeleyi	Torch Lake cisco	Typical races from Torch and Elk lakes, Ontario	Koelz
huronicus	Rush Lake cisco	Rush Lake, Michigan	Koelz
annensis	Lake Anne cisco	Lake Anne, Michigan	Koelz
sargenti	Sargent Lake cisco	Sargent and Richie lakes on Isle Royale, Ontario	Koelz
russeli	Pine Lake cisco	Pine Lake, Michigan	Koelz
atikamek	Whitefish Lake cisco	Whitefish Lake, Michigan	Koelz
mackayi	Ontario cisco	Inland lakes in the Great Lakes basin of Ontario	Koelz
clarensis	Clear Lake cisco	Clear Lake and other inland lakes of Wisconsin and Michigan	Koelz
clemensi	Nipigon cisco	Lake Nipigon, Ontario	Koelz
lowei	Hulbert Lake cisco	Hultbert Lake, Michigan	Koelz
microcephalus	Gogebic Lake cisco	Gogebic Lake, Michigan	Koelz
woodi	Twin Lake cisco	North Twin Lake and other lakes in Wisconsin and Minnesota	Koelz
winnipegosis	Lake Winnipegosis cisco	Lakes Winnipegosis and Wabigoon, Manitoba	Koelz
birgei	Green Lake cisco	Green Lake, Wisconsin	Wagner
artedii	Great Lakes cisco	In all the Great Lakes and some inland lakes in the area	LeSueur
osmeriformis	Seneca Lake cisco	Seneca Lake, New York	Smith
bisselli	Rawson Lake cisco	Rawson Lake and other Michigan inland lakes	Bullman
albus	Lake Erie cisco	Type from Lake Erie, also in Lakes Ontario and Superior	LeSueur
arcturus	Lake Superior cisco	Lake Superior	Jordan and Evermann
sisco	Tippecanoe Lake cisco	Tippecanoe Lake and inland lakes of Michigan and Indianna	Jordan and Evermann
manitoulinus	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 though 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 withdrawls 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 km^2 (Teller 1987). The total area covered by the lake over its 5 000 year history was 1.5 million km^2, 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*.

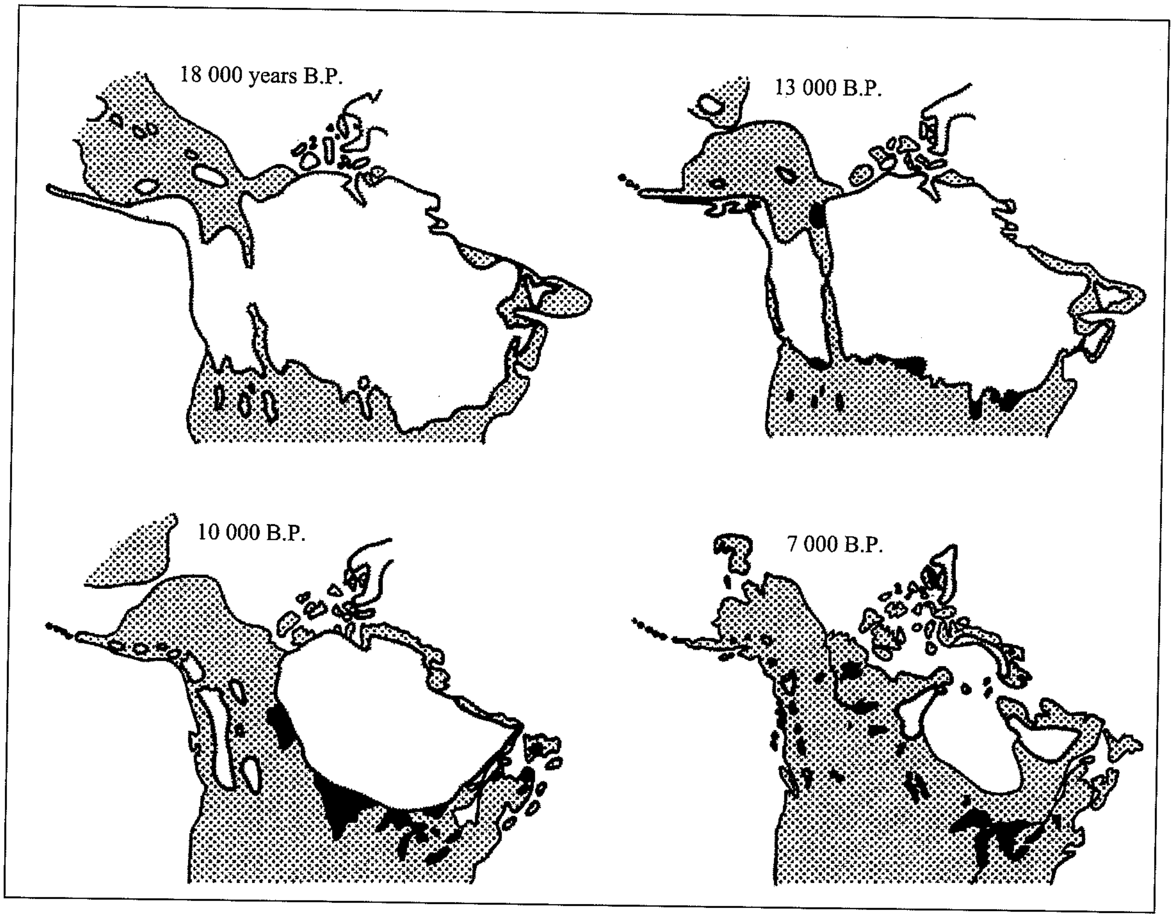


Figure 1.3. Recession of the North American glacial ice sheets from the most recent maximum 18 000 years B.P. to 7 000 years B.P. White areas represent glaciers; shaded areas represent land surfaces; black areas represent water bodies (after Pielou 1991).

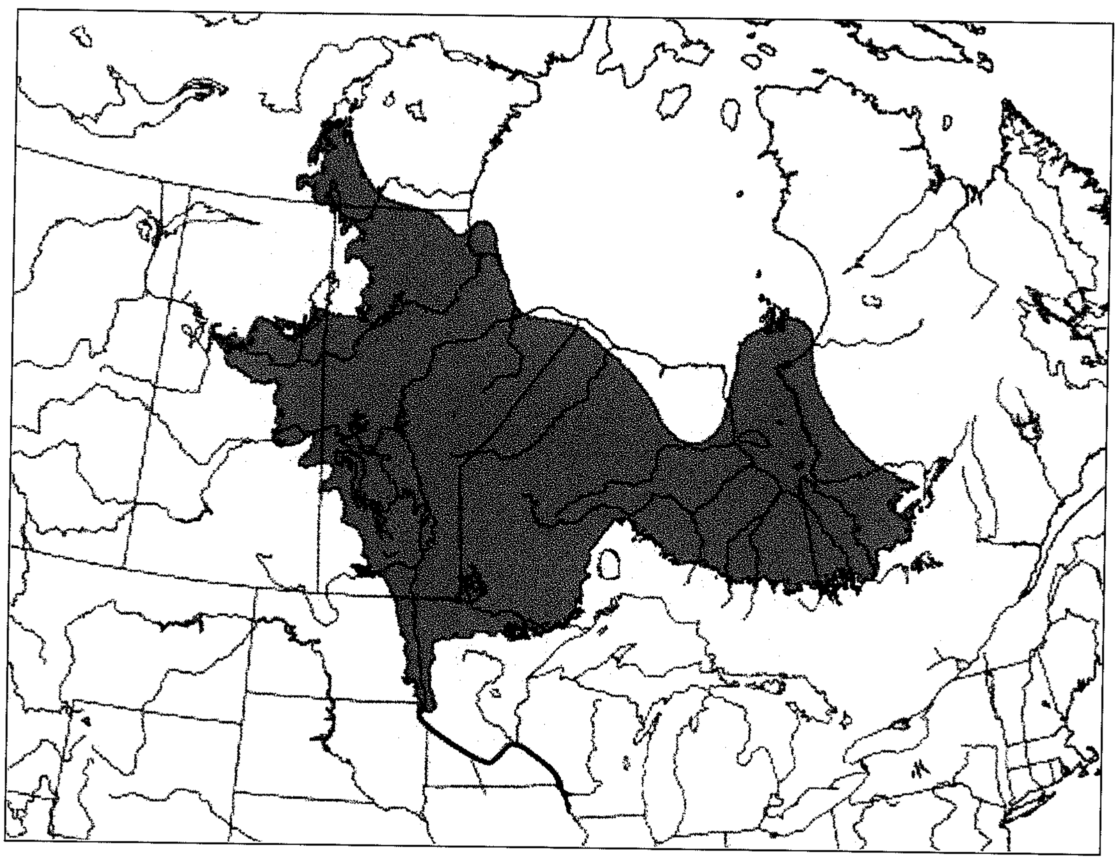


Figure 1.4. Total area covered by glacial Lake Agassiz over its 5 000 year history; approximately 1.5 million km^2. The size of the lake fluctuated over its lifespan, gradually shifting from south to north following the recession of the Laurentide Ice Sheet (after Leverington and Teller 2003).

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 km^2. 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).

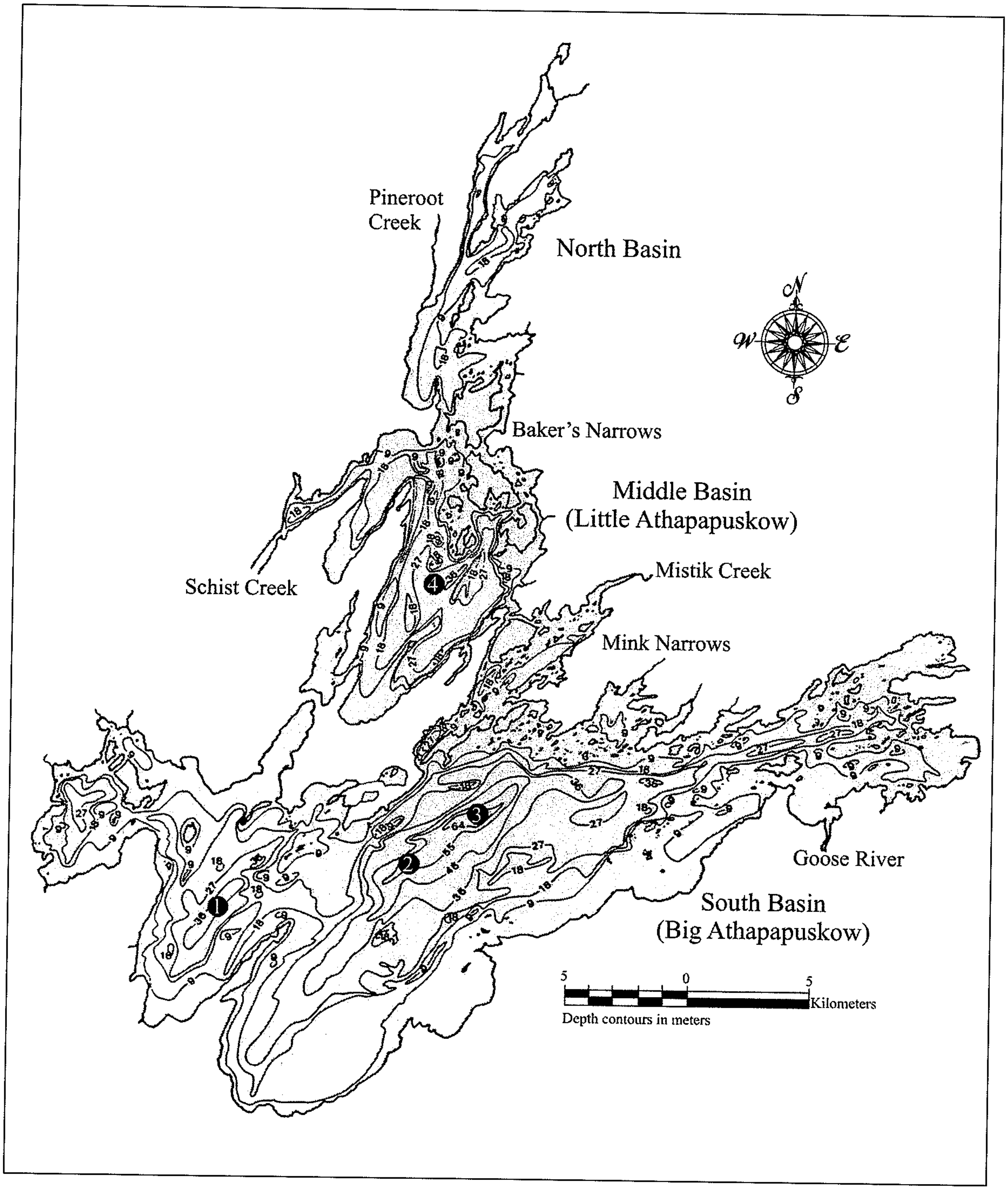


Figure 2.1. Lake Athapapuskow map (Adapted from Day 1983). Numbered dots indicate set number and set information is presented in Appendix 1-1.

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° 30' and 103° 15' W and the latitudinal boundaries are 56° 15' and 58° 10' N. It is the tenth largest freshwater lake in North America with a surface area of around 5 300 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 x 10^9 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).

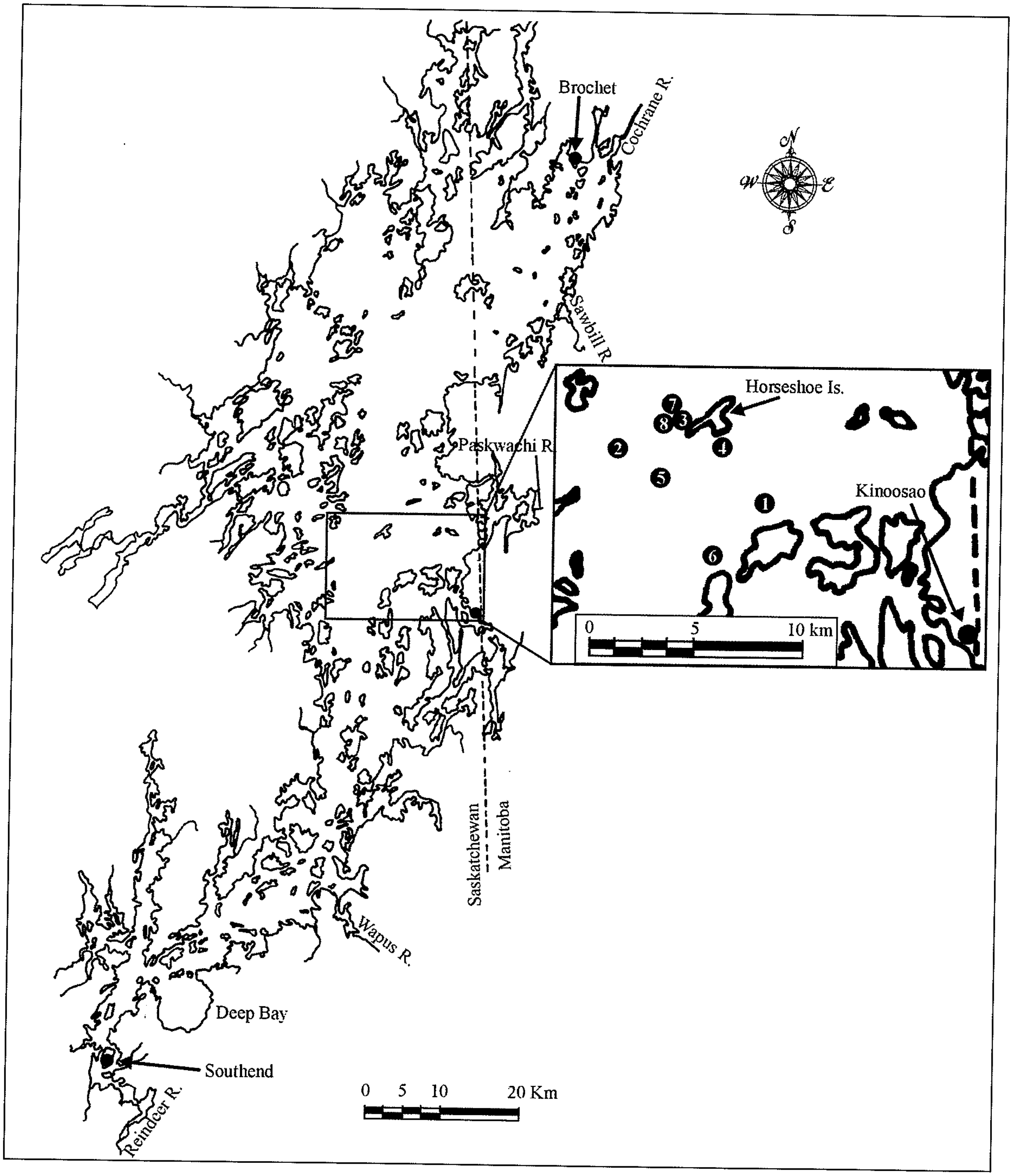


Figure 2.2. Map of Reindeer Lake (after Dean 1975). Enlarged region shows the focus of sampling effort with sets indicated by numbered dots. Note: set information is presented in Appendix 1-2.

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 x 10^7 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).

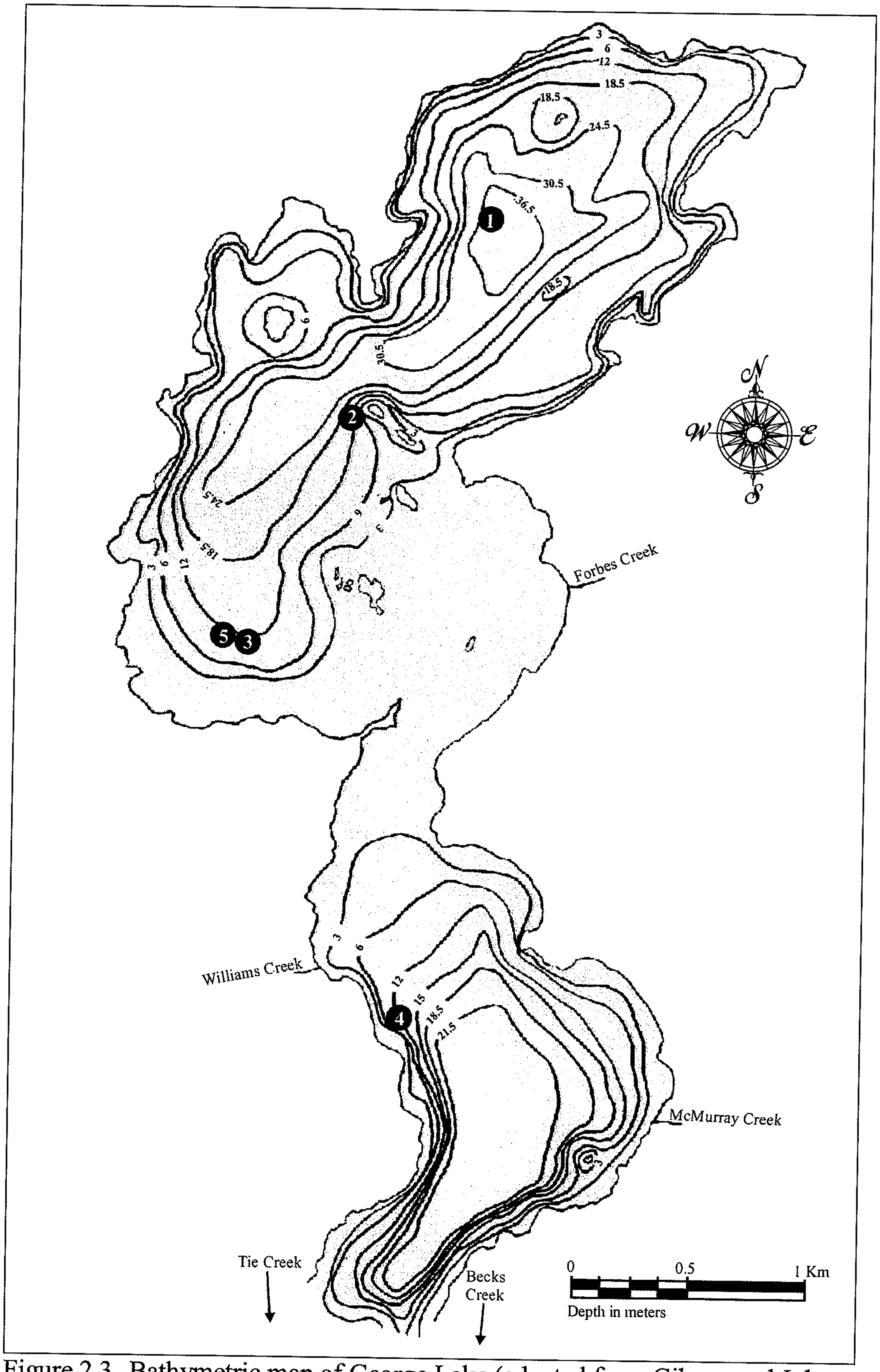


Figure 2.3. Bathymetric map of George Lake (adapted from Gibson and Johnson 1969). Note: collection sites are indicated and set information is presented in Appendix 1-3.

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 km^2 (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.

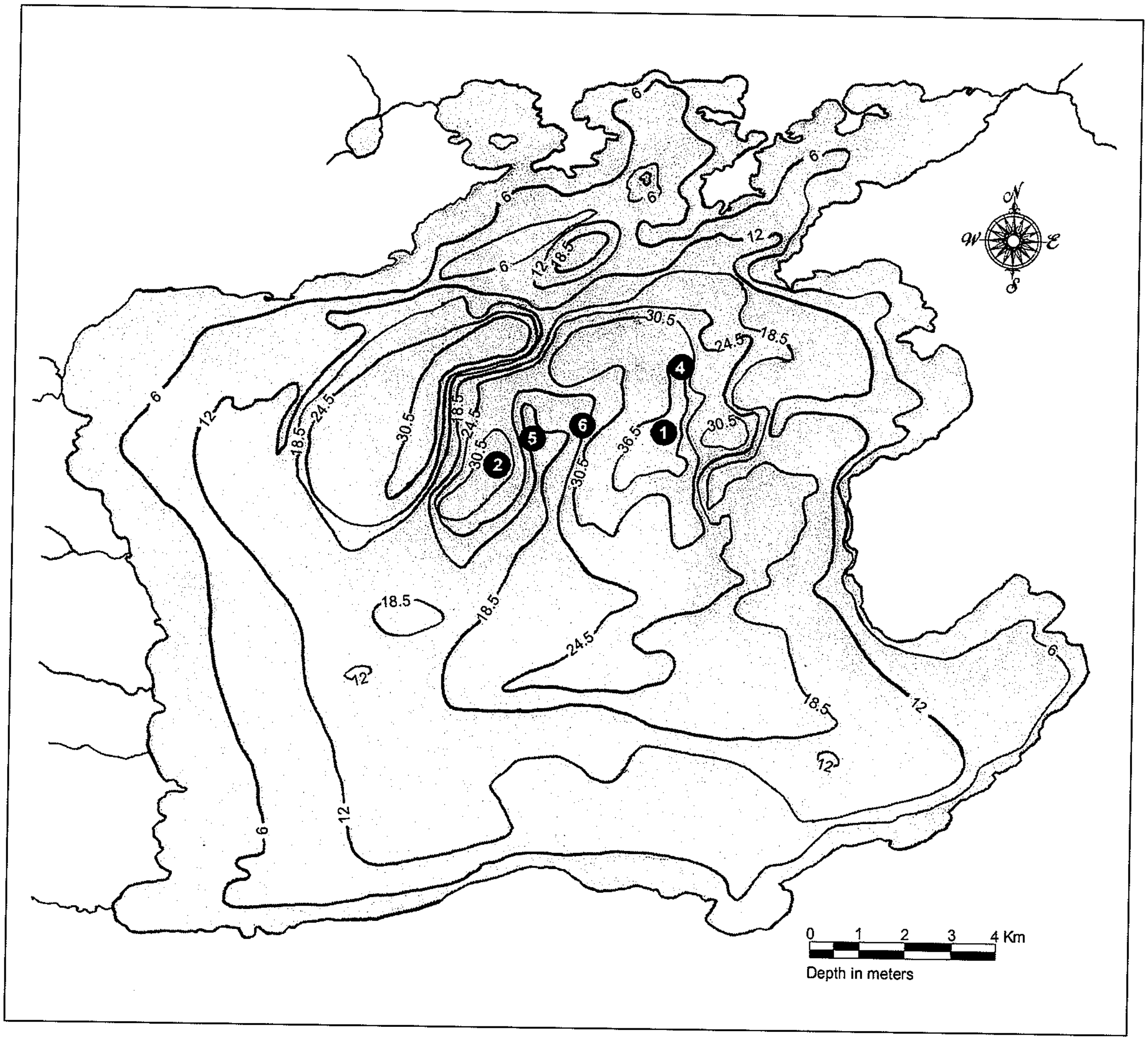


Figure 2.4. Bathymetric map of Clearwater Lake (Adapted from Schlick 1978). Numbered dots indicate set numbers; set information is presented in Appendix 1-4. Note: Sets 1 and 2 were conducted in 2000; sets 3 – 6 were conducted in 2002. Note: sets 1 and 3 were made at the same location.

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 Garvin 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) Preobital 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

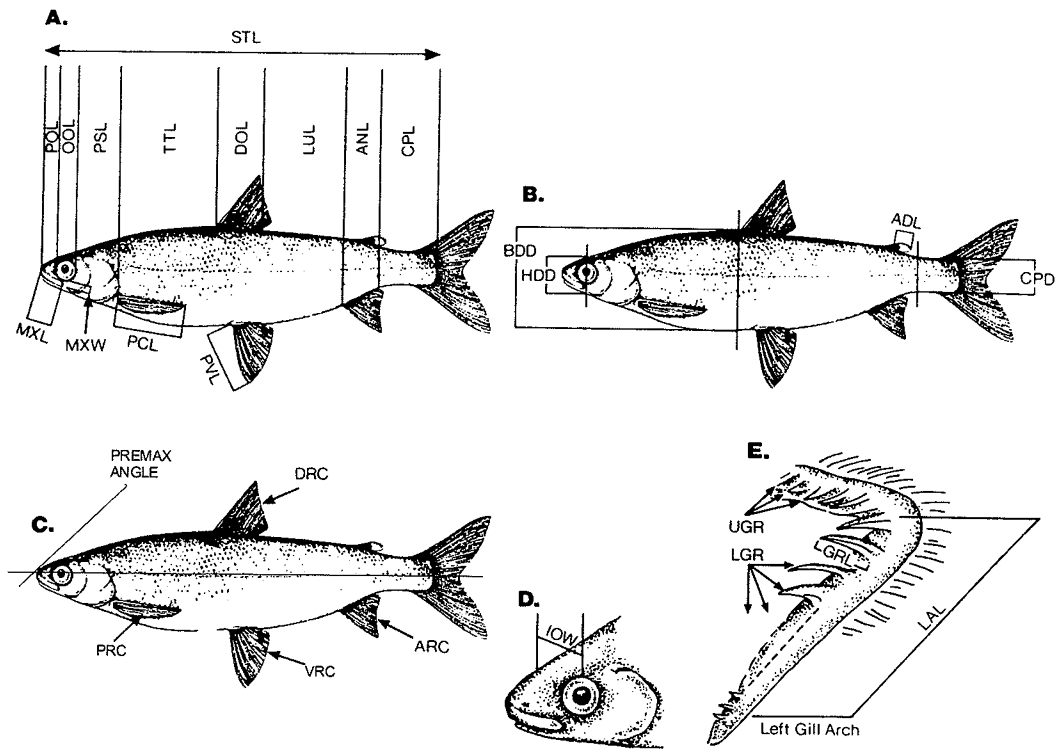
4) Pelvic ray count: all rays in the left pelvic fin counted

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).



STL - Standard Length
POL - Preordital length
OOL - Orbital length
PSL - Postordital length
TTL - Trunk length
DOL - Dorsal length
LUL - Lumbar length
ANL - Anal Length
CPL - Caudal peduncle length
HDD - Head depth
BDD - Body depth
CPD - Caudal peduncle depth
IOW - Interorbital width
MXL - Maxillary length
MXW - Maxillary width

PCL - Pectoral length
PVL - Pelvic length
ADL - Adipose length
GRL - Middle gillraker length
LAL - Lower arch length
DRC - Dorsal ray count
ARC - Anal ray count
PRC - Pectoral ray count
VRC - Pelvic ray count
UGR - Upper gillraker count
LGR - Lower gillraker count
PREMAX ANGLE - Premaxillary angle

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 (Lleonart 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.

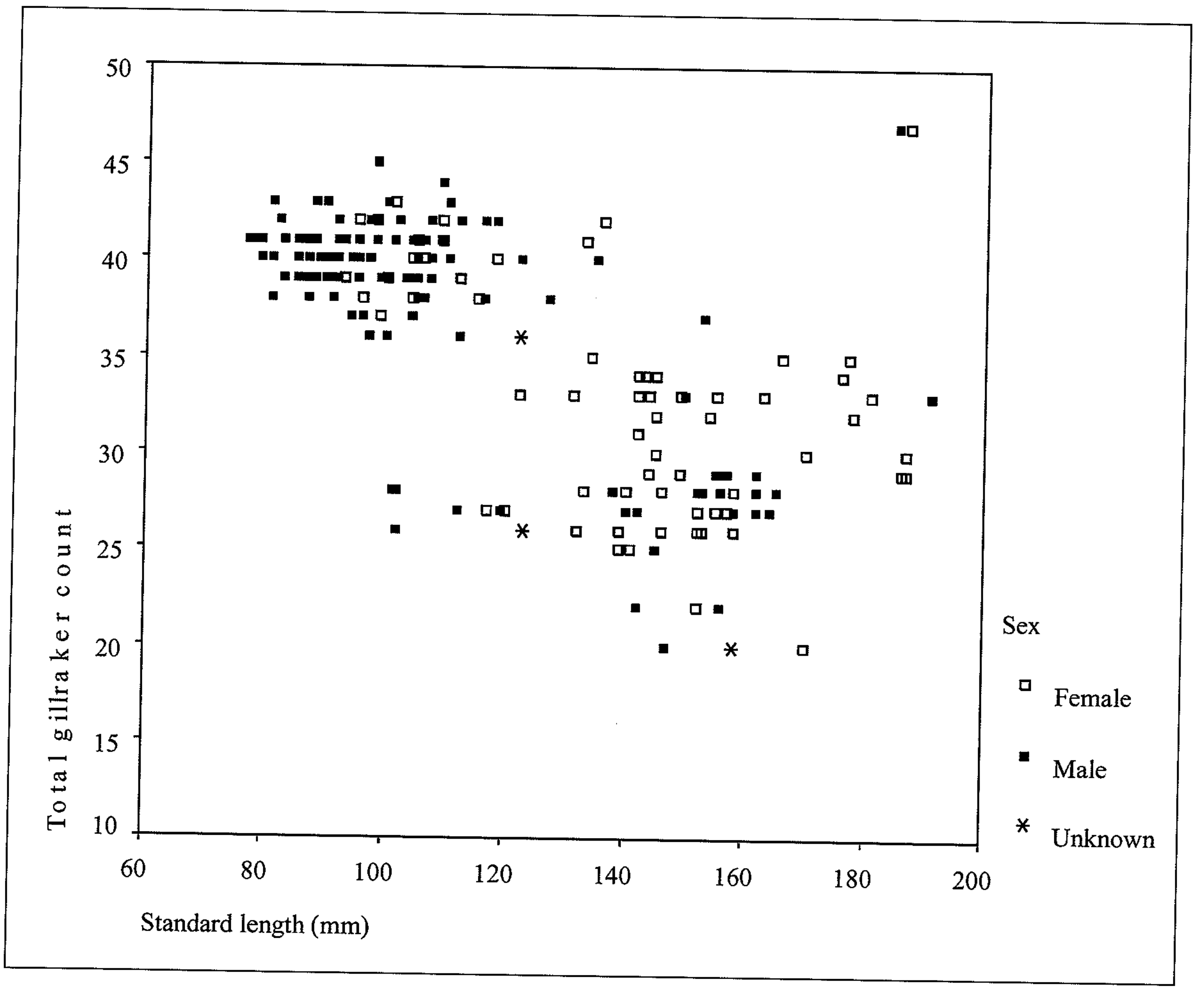


Figure 3.1. Relationship between total gillraker count and standard length for Lake Athapapuskow ciscoes with individuals identified by sex.

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.

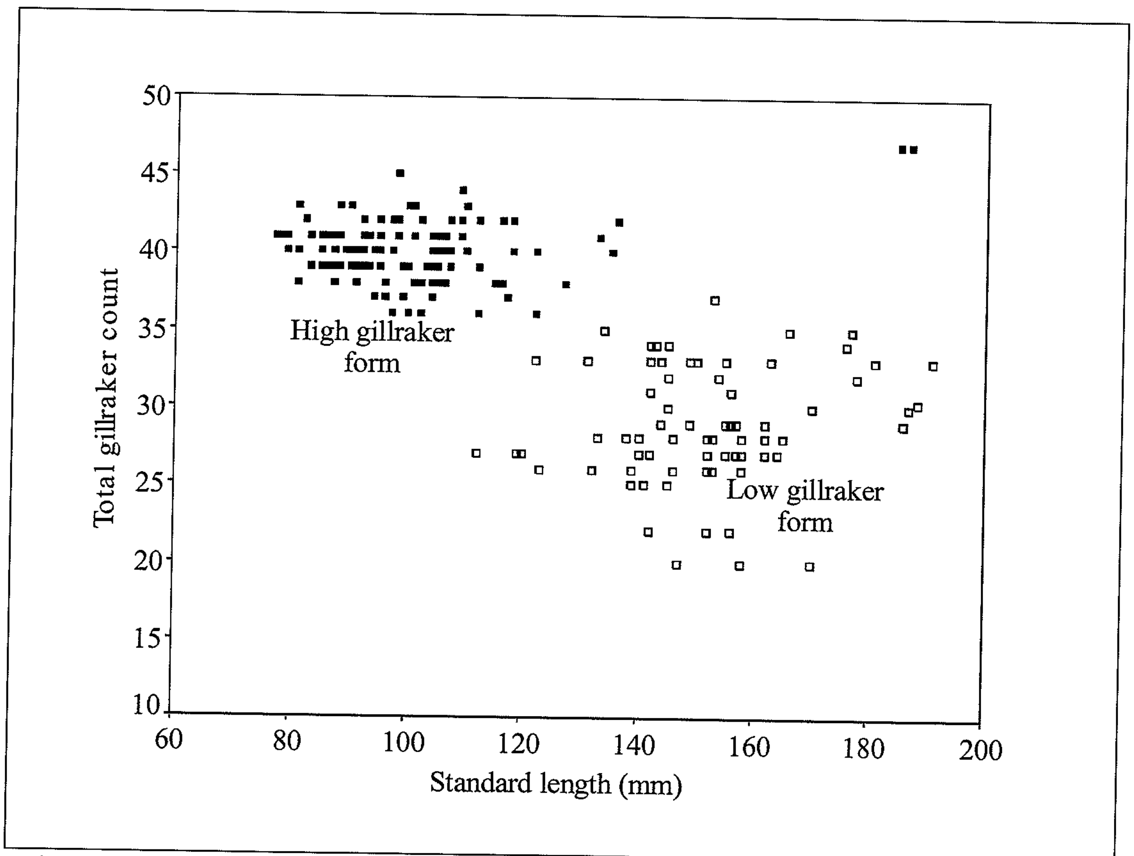


Figure 3.2. Plots of standard length versus gillraker number for all Lake Athapapuskow ciscoes showing forms suggested by gillraker counts.

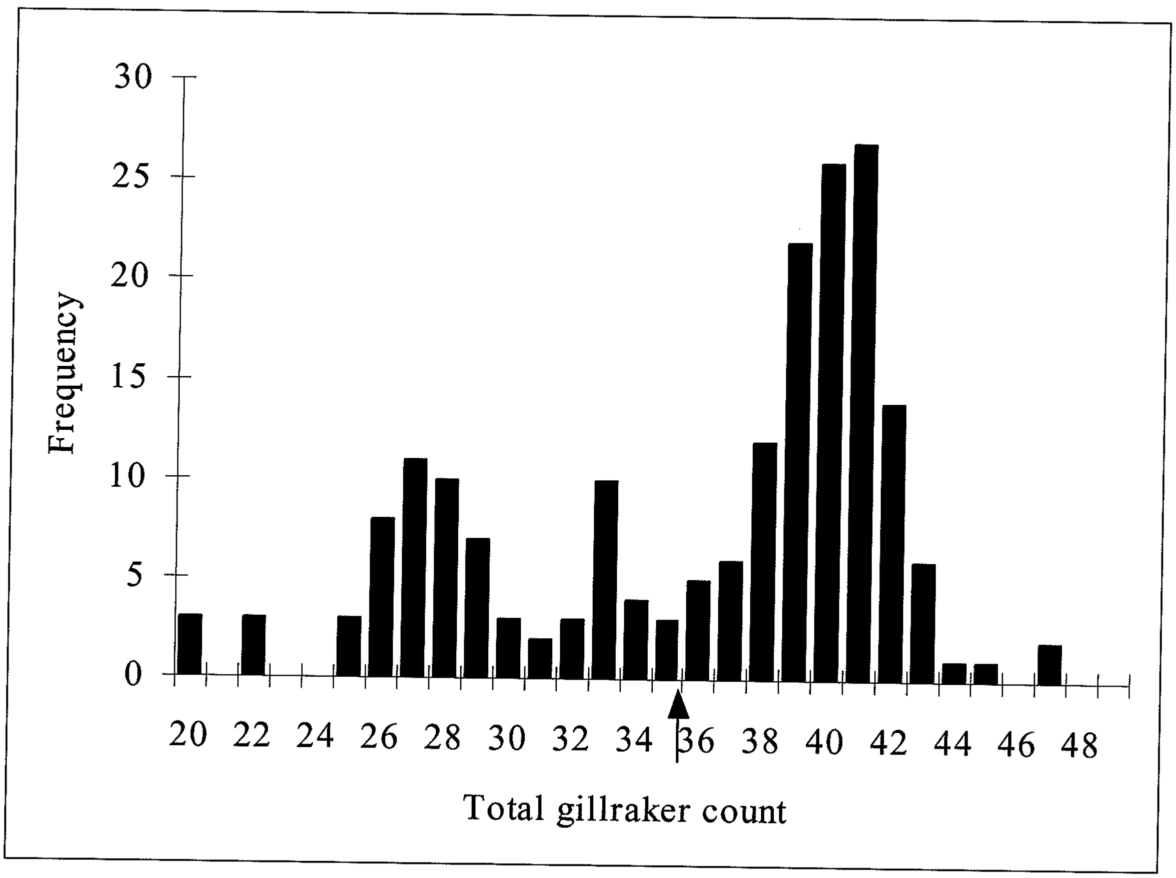


Figure 3.3. Frequency distribution of total gillraker counts for all ciscoes from Lake Athapapuskow. All individuals with counts 35 or less were placed in the low group and 36 or more were placed in the high group with the exception of one individual from Little Athapapuskow with 37 gillrakers which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

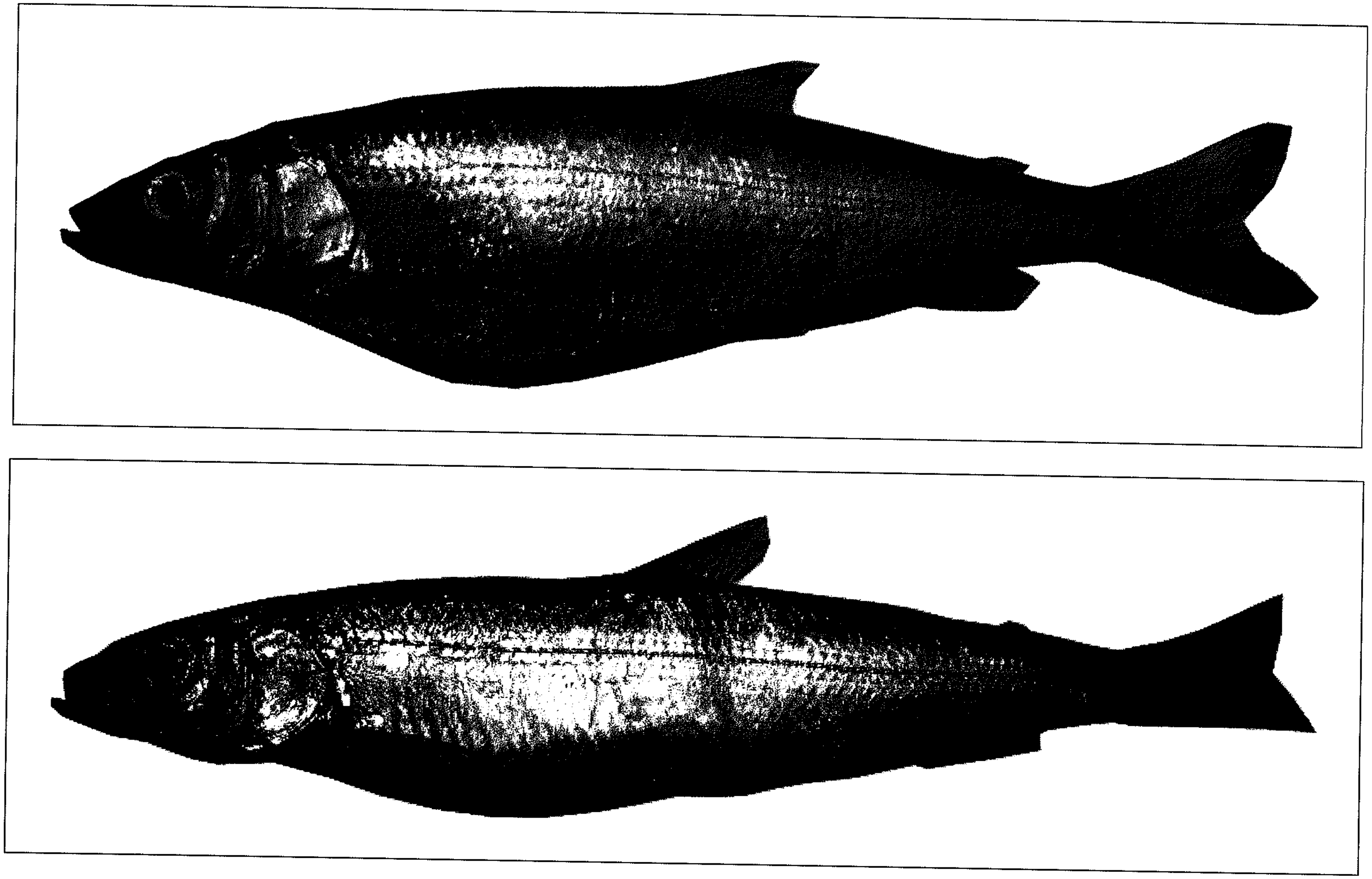


Figure 3.5. General appearance of Lake Athapapuskow ciscoes. The fish in upper panel had a standard length of 187 mm and 30 gillrakers and is representative of the low form. The fish in lower panel had a standard length of 99 mm and 39 gillrakers and is representative of the high form. Note: previously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

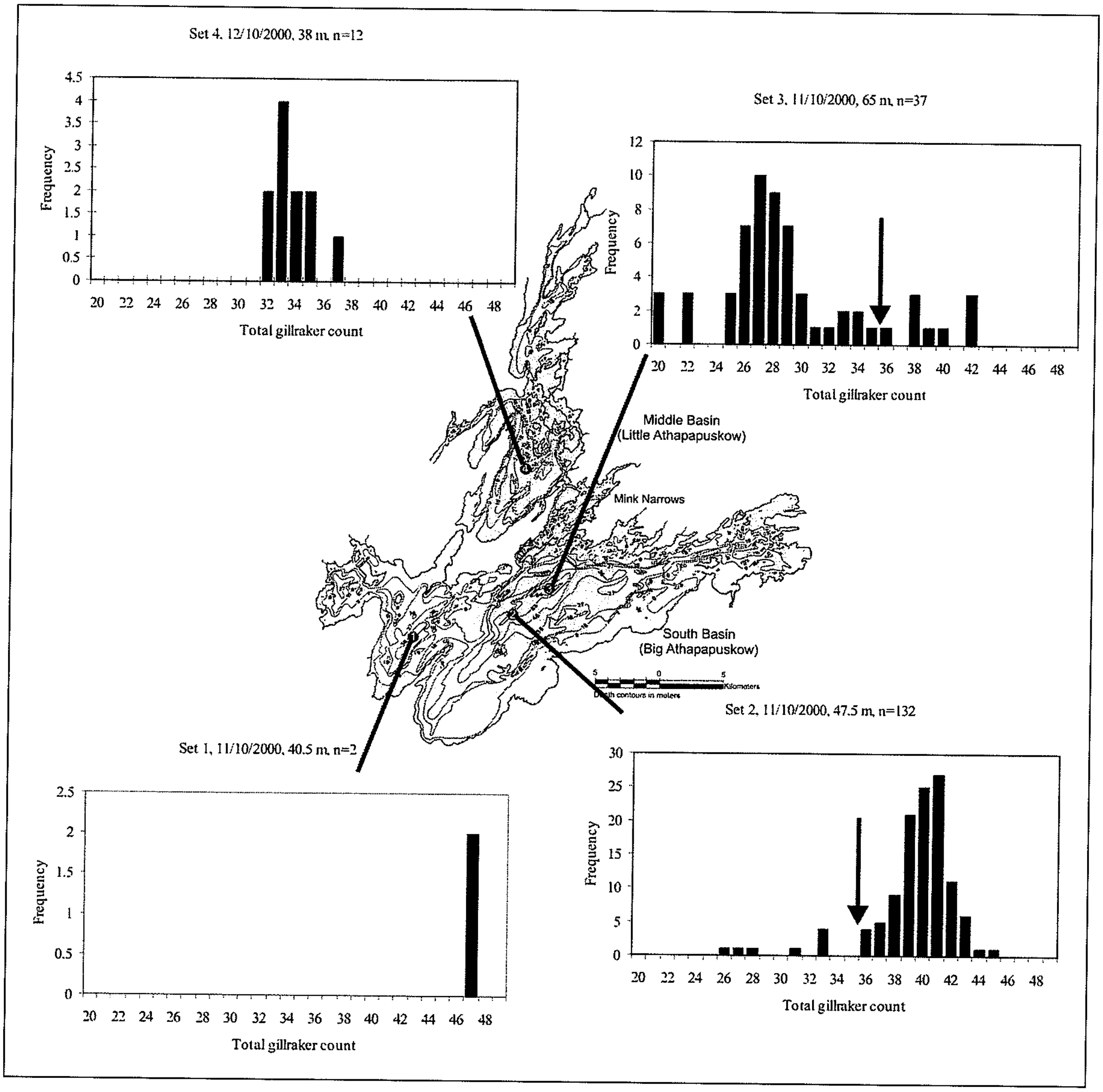


Figure 3.6. Total gillraker count distributions for all Lake Athapapuskow collection sites. Arrows indicate separation between groups for sets 2 and 3 based on key characters. Each panel indicates set number, date, depth, and number of fish captured (see also Appendix 2-2).

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.

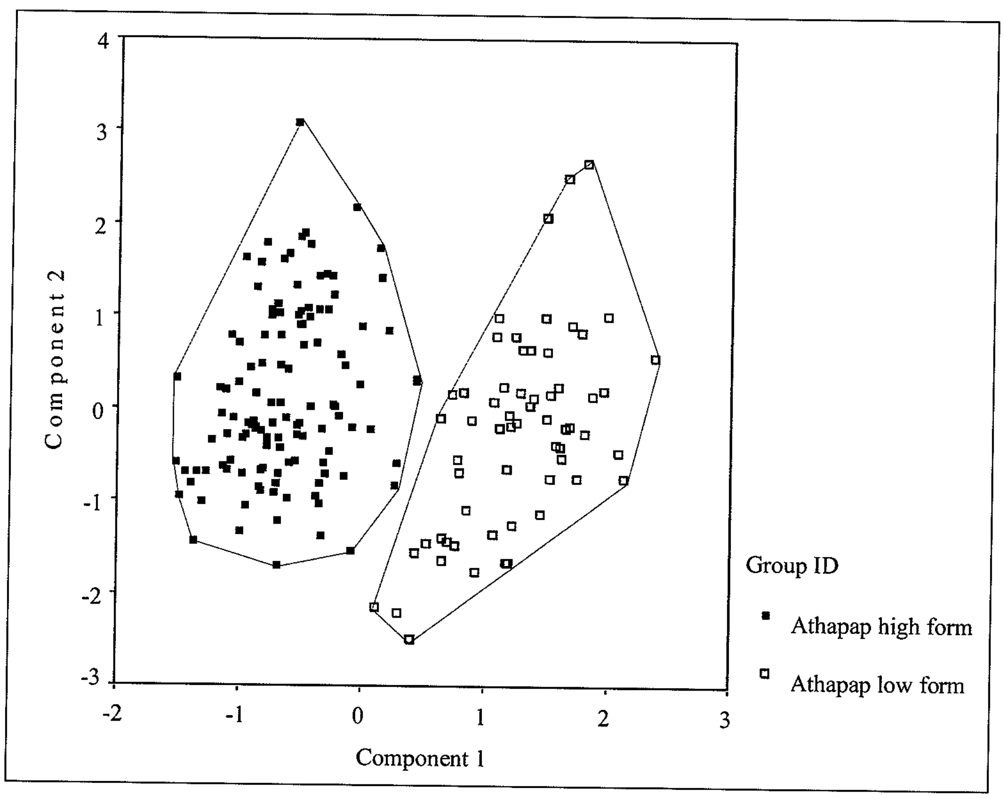


Figure 3.7. PCA plots for ciscoes from Big Athapapuskow based upon meristic and morphometric characters adjusted by ratios. Variable loadings are described in the text. Form was assigned *a posteriori* using key character criteria outlined in the text.

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).

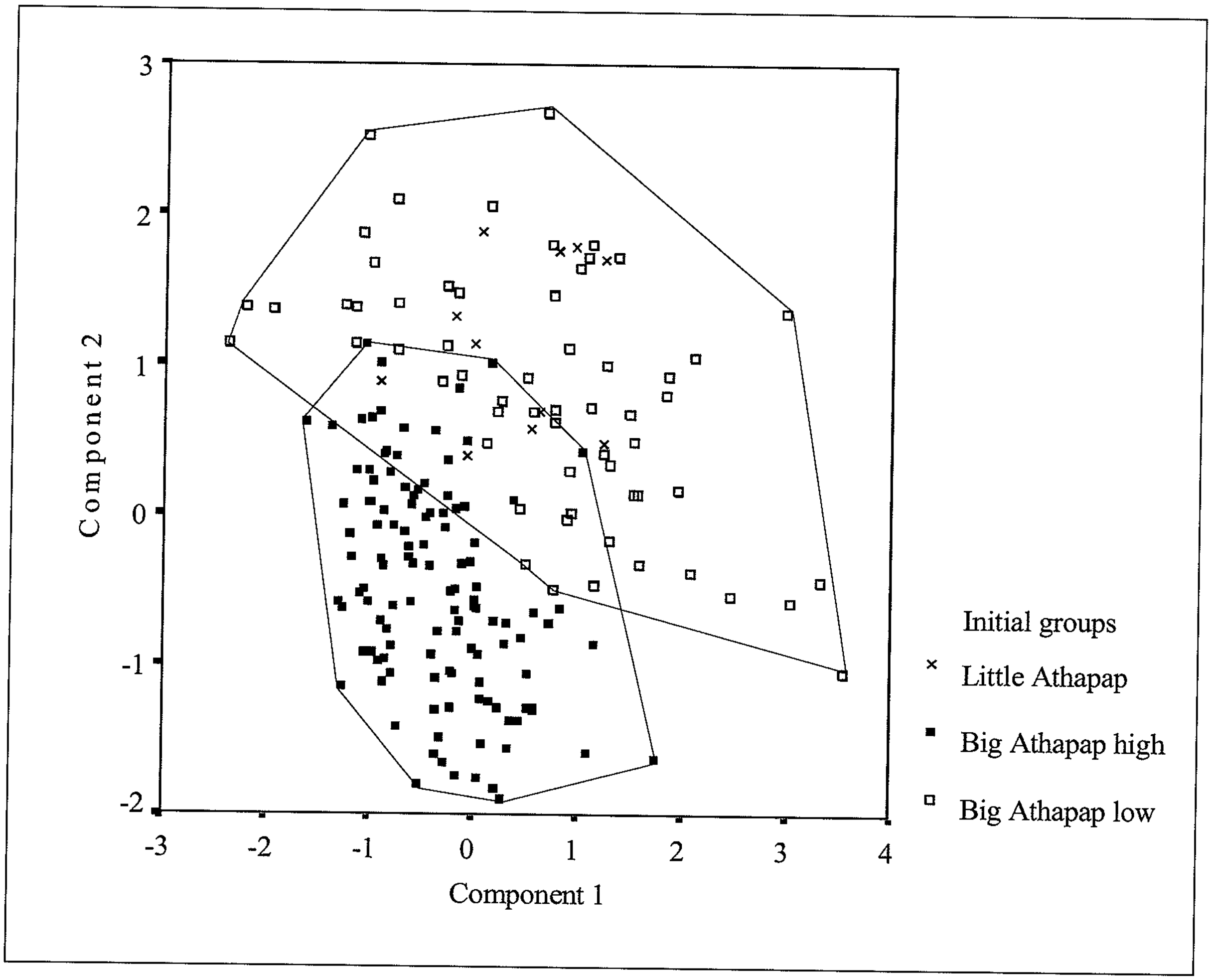


Figure 3.8. Plot of scores from PCA of all ciscoes from Lake Athapapuskow using meristic characters (not including gillraker counts) and morphometric characters adjusted by common within-group residuals.

Table 3.3. Character loadings and eigenvalues from PCA of all Lake Athapapuskow 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 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 Equality of Variance	Anova test of Equality of Means	
		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 of the ciscoes collected from Little Athapapuskow with the low form from Big Athapapuskow. However, the discriminant results suggested that five individuals originally identified as members of the low form from Big Athapapuskow grouped more closely with the Little Athapapuskow ciscoes while one individual from Little Athapapuskow should be grouped with the low form from Big Athapapuskow. In total, 95.3% of the originally grouped cases were correctly classified by this analysis supporting the presence of multiple groups (Table 3.5).

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.

Standardized Canonical Discriminant Function Coefficients

	Analysis 1	Analysis 2	
	Function 1	Function 1	Function 2
Premaxillary angle	0.25	0.25	0.01
Dorsal ray count	0.06	0.07	-0.08
Anal ray count	-0.17	-0.18	0.04
Pectoral ray count	0.16	0.15	0.05
Pelvic ray count	-0.03	-0.03	-0.03
Preorbital length	0.16	0.15	0.10
Orbital length	0.39	0.42	-0.13
Postorbital length	0.17	0.15	0.17
Trunk length	0.18	0.15	0.19
Dorsal length	0.02	0.02	-0.01
Lumbar length	0.14	0.17	-0.12
Anal length	0.10	0.04	0.34
Caudal peduncle length	0.03	0.06	-0.16
Head depth	-0.05	-0.01	-0.20
Body depth	0.07	0.14	-0.36
Caudal peduncle depth	0.43	0.42	0.15
Interorbital width	-0.64	-0.62	-0.21
Maxillary length	0.18	0.19	-0.01
Maxillary width	-0.14	-0.13	-0.09
Pectoral length	0.18	0.12	0.34
Pelvic length	0.24	0.23	0.06
Adipose length	-0.03	-0.16	0.70
Lower arch length	0.11	0.22	-0.59
Gillraker length	-0.58	-0.61	0.09
Eigenvalues	3.58	3.81	0.59
Percent of variance	100.0	86.6	13.4
Wilks' Lambda	0.22	0.13	0.63
Significance	0.00	0.00	0.00
Canonical correlation	0.88	0.89	0.61

Classification Results

Analysis 1	Predicted Group Membership		
Initial groups	Low	High	Total
Athapap low count	68	3	71
Athapap high count	2	119	121
Athapap low percent	95.8	4.2	100
Athapap high percent	1.7	98.3	100

97.4% of original grouped cases correctly classified.

Analysis 2	Predicted Group Membership			
Initial groups	Low	High	Little	Total
Athapap low count	54	1	5	60
Athapap high count	2	119	0	121
Little Athapap count	1	0	10	11
Athapap low percent	90.0	1.7	8.3	100
Athapap high percent	1.7	98.3	0.0	100
Little Athapap percent	9.1	0.0	90.9	100

95.3% of original grouped cases correctly classified.

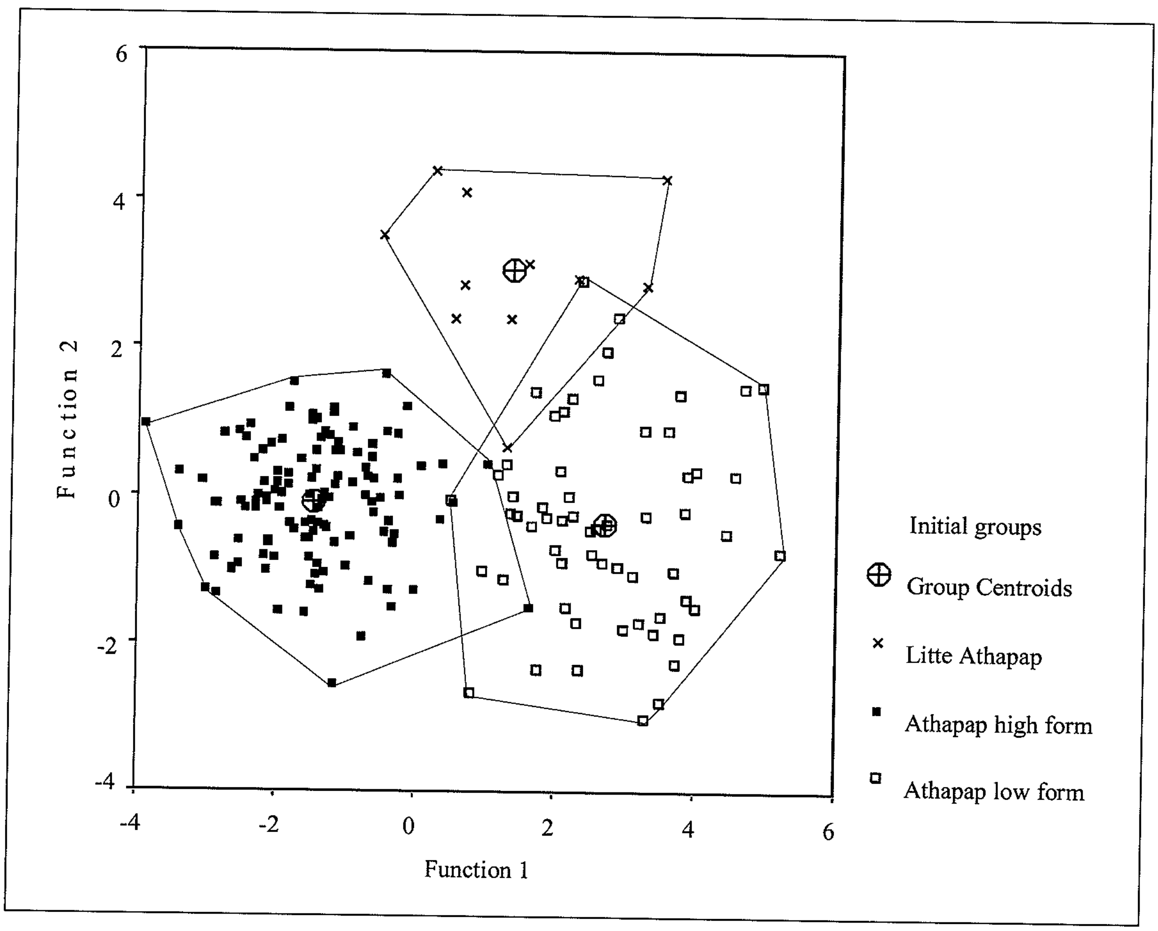


Figure 3.9. Plot of the functions calculated by a Discriminant Analysis of all Lake Athapapuskow cisco forms. All morphometric characters were adjusted by common-within-group residuals.

Summary of Lake Athapapuskow Cisco Forms

The presence of co-occurring cisco forms in Lake Athapapuskow is supported by the results of this study. Gillraker count and arrangement, jaw position, and dorsal colouration were effective initially for identifying cisco forms. The gillraker count distribution showed some overlap between forms; however, individuals in the overlap range were placed into groups effectively using dorsal colouration, jaw position, and gillraker arrangement. The PCA results also supported the presence of two cisco forms. Only one PCA resulted in complete separation (meristic characters including gillraker counts and morphometric characters adjusted by ratios Figure 3.7), all others showed minimal overlap between the two forms. The Anova and Discriminant Analysis results provided evidence supporting a low and high gillraker form being present in Lake Athapapuskow. When the individuals collected from Little Athapapuskow were considered separately from the other forms, they were found to overlap with the low gillraker form.

The following is a key to identify the two cisco forms that were collected from Lake Athapapuskow in this study. The majority of ciscoes identified as the high-gillraker form from Lake Athapapuskow were found to be immature, however, larger, mature specimens with high gillraker counts could potentially be collected from the lake.

1. Total gillraker count of 35 or fewer on first gill arch, gillrakers short and widely spaced.. Low gillraker form

Total gillraker count 40 or greater on first gill arch, gillrakers long and tightly packed ....High gillraker form

Total gillraker count 36 to 39...2

2. Premaxillary angle (see Figure 1.2 for description) usually greater than 45°, downward jaw appearance, tan to brown dorsal colouration.........Low form

   Premaxillary angle usually greater than 45°, upward jaw appearance, greenish blue to black dorsal colouration.. High form

This key is a guide based on specimens collected and examined from Lake Athapapuskow by the author. This key may not account for some of the cisco variability found within Lake Athapapuskow. See discussion for taxonomic conclusions regarding the low and high gillraker forms identified in this study.

4. RESULTS - COMPARISON OF REINDEER LAKE CISCOES

General Biology

A total of 375 ciscoes were collected from all the sets combined; the number of ciscoes collected from each site is listed in Appendix 2-2 along with location coordinates and the number of other species that were collected. Biological characteristics were examined for all individuals combined to determine if any of these characters support the presence of sympatric forms of ciscoes in Reindeer Lake. Appendix 4-1 lists the descriptive statistics for Reindeer Lake. The size range for these ciscoes was 83 to 210 mm in standard length with a mean of 156 mm and 7 to 146 g in weight with a mean of 54 g. Appendix 4-2 shows the frequency distribution for standard length with two modes apparent, one with a few individuals around 95 mm and one with a large number of ciscoes around 165 mm.

When standard length and weight were plotted together only differences related to size were apparent (Appendix 4-3). The age distribution for all ciscoes collected from Reindeer Lake had a normal distribution with most of the individuals ranging from four to 11 years of age (Appendix 4-4). The oldest individual collected was 21 years of age. The sex ratio was examined by looking at the distribution of total gillraker counts (upper and lower gillraker counts combined) versus standard length for all individuals identified by sex (Figure 4.1). When maturity was plotted along with total gillraker count and standard length the majority of individuals under 120 mm were found to be immature (Appendix 4-5). Many of the individuals with gillraker counts of 30 or less were mature females; however, mature males were also present in this range. Ciscoes with more than 30 gillrakers consisted of an even distribution of mature males and females.

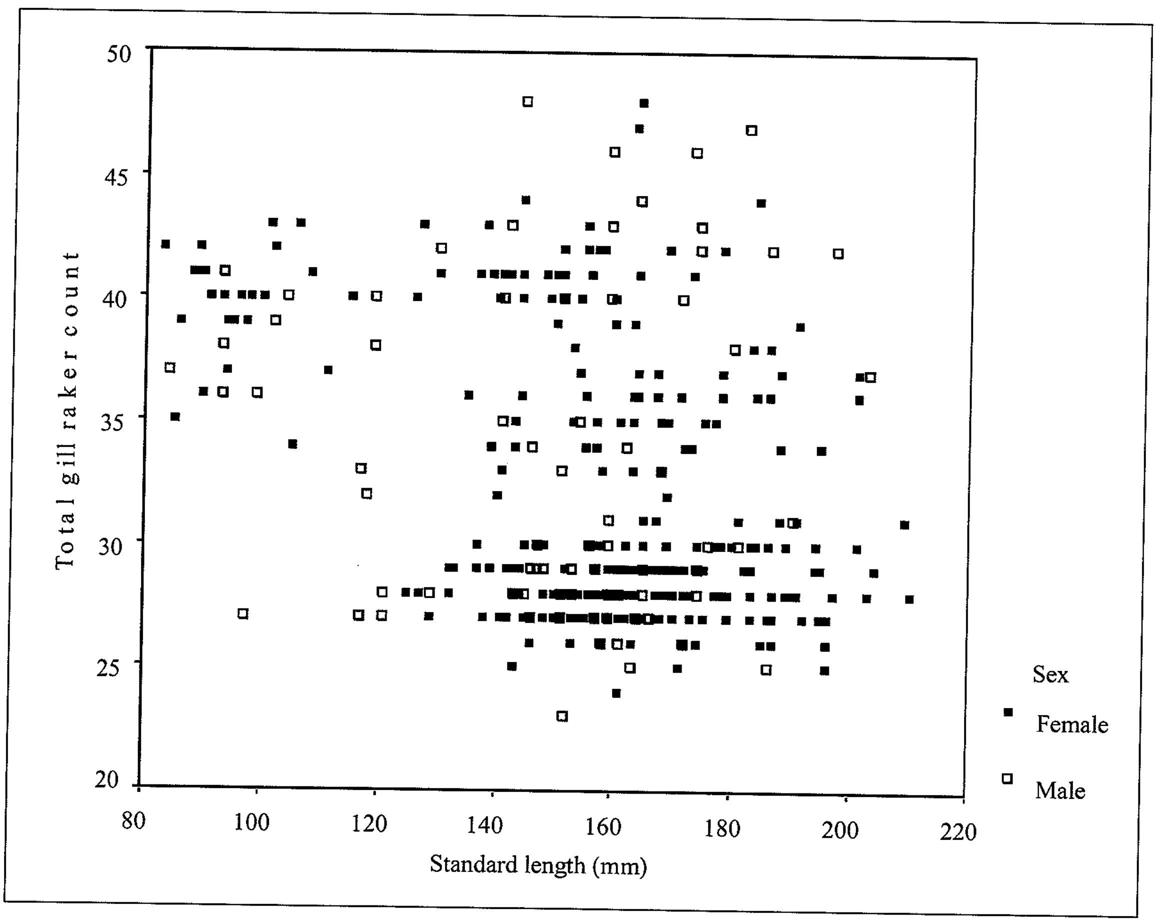


Figure 4.1. Relationship between total gillraker count and standard length for Reindeer Lake ciscoes with individuals identified by sex.

Discrimination of Cisco Forms

Gillraker count distribution was initially examined for its effectiveness in identifying cisco forms collected from Reindeer Lake. Gillraker counts suggested the presence of a high gillraker form with 39 or more, a mid gillraker form with 33 to 38, and a low gillraker form with 32 or less; however, there was no clear separation between the ranges of the values for these forms (Figure 4.2). When standard length and gillraker count were plotted along with the predicted forms, the three forms were not clearly supported (Figure 4.3). Many individuals were found to fall into the regions of overlap between the predicted forms.

Mouth morphology and orientation, general body shape, dorsal colouration, and gillraker arrangement were examined to determine if they supported the forms suggested by the gillraker counts. The majority of individuals identified as members of the low gillraker form had light dorsal colouration ranging from yellow to tan (Figure 4.4). The mid gillraker form consisted of individuals ranging from very light colouration to dark colouration with some pigmentation on the paired fins (Figure 4.4). The majority of individuals identified as members of the high gillraker form had dark dorsal colouration ranging from green to dark blue (Figure 4.4). Jaw position in the cisco groups was variable; however, in general members of the low form had equal upper and lower jaws or the upper jaws protruded slightly giving them an inferior appearance (downward jaw position). Some members of the low form and most of the mid form were found to have longer lower jaws than their upper jaws; however, their mouths also had a downward appearance. The jaw positions in the high forms were variable with the majority having longer lower jaws protruding beyond the upper jaws giving them a superior appearance (upturned jaw position). Members of the lower gillrakered form tended to have shorter, and more widely spaced gillrakers than the other two forms (Figure 4.5). The mid and high forms were found to have similar rakers of similar length; however, the higher gillrakered individuals tended to have more closely packed rakers (Figure 4.5). Dorsal colouration, jaw position, and gillraker arrangement showed some differences between groups; however, individuals with gillraker counts close to the point of separation between groups were variable. Therefore, these characters were not always effective for identifying individuals on the boundaries between the hypothesized gillraker forms.

When the gillraker count distributions for ciscoes collected from each site were examined it was found that all three forms were present at each site except for set four where only one individual with 35 gillrakers was collected (Appendix 4-6). The low gillraker group consisted of 231 individuals with a mean gillraker count of 28.2 (23-32) and a mean standard length of 163 mm (96-210). The mid gillraker group consisted of 63 individuals with a mean gillraker count of 35.5 (33-38) and a mean standard length of 153.5 mm (84-203). The high gillraker group consisted of 81 individuals with a mean gillraker count of 41.5 (39-48) and a mean standard length of 138.1 (83-197).

The descriptive statistics for the three groups for all morphometric and meristic characters are listed in appendices 4-7 to 4-9. The size-at-age for each form is presented in Appendix 4-10 revealing that the growth rate for the three forms was similar.

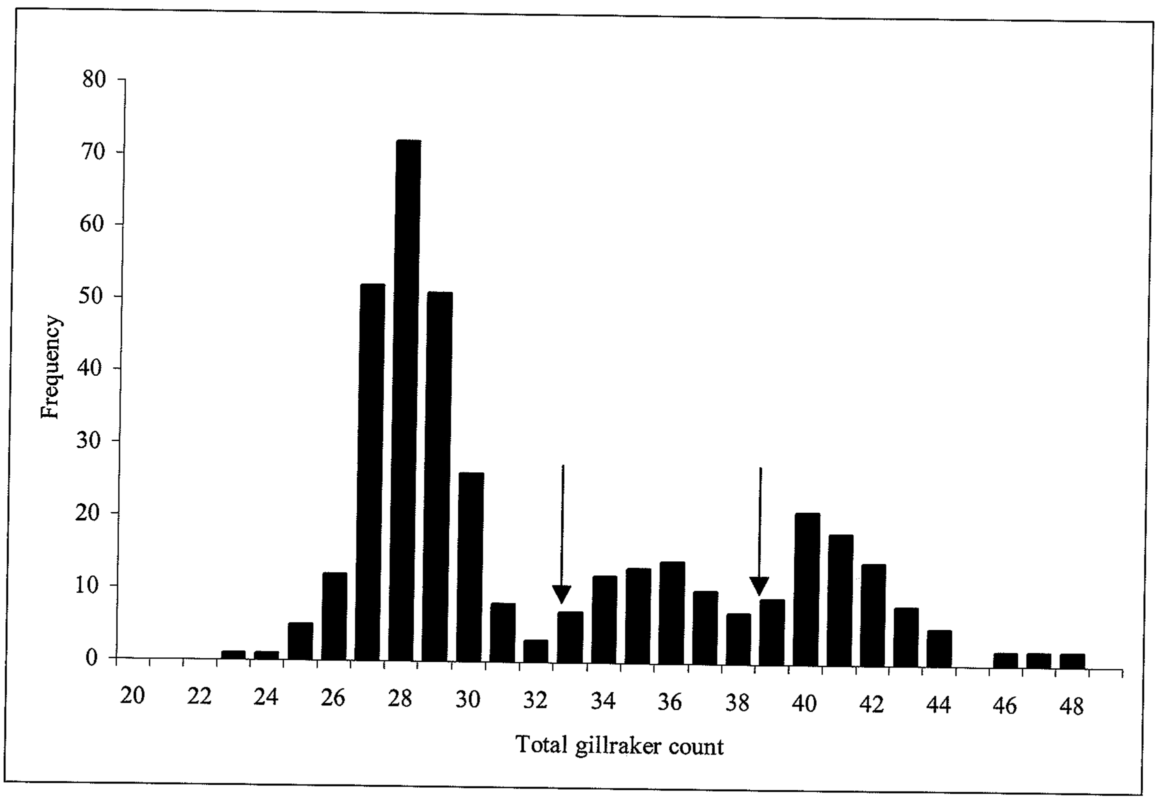


Figure 4.2. Frequency distribution of total gillraker counts for all ciscoes from Reindeer Lake. All individuals with counts of 32 or less were tentatively placed in the low group, those with 33 to 38 were placed in the mid group, and those with 39 or more were placed in the high group.

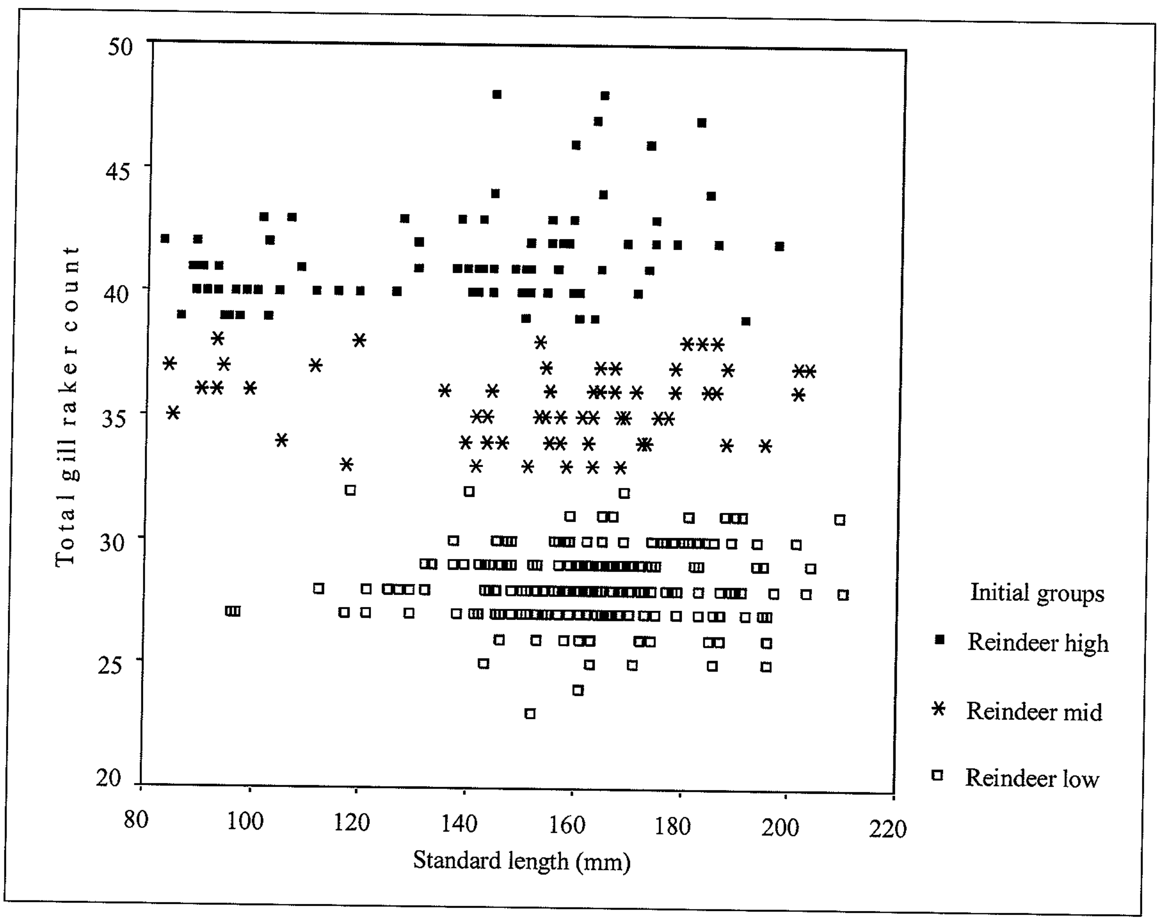


Figure 4.3. Relationship between total gillraker count and standard length for the initial groups. Hypothesized groups were based on gillraker count distributions (see text).

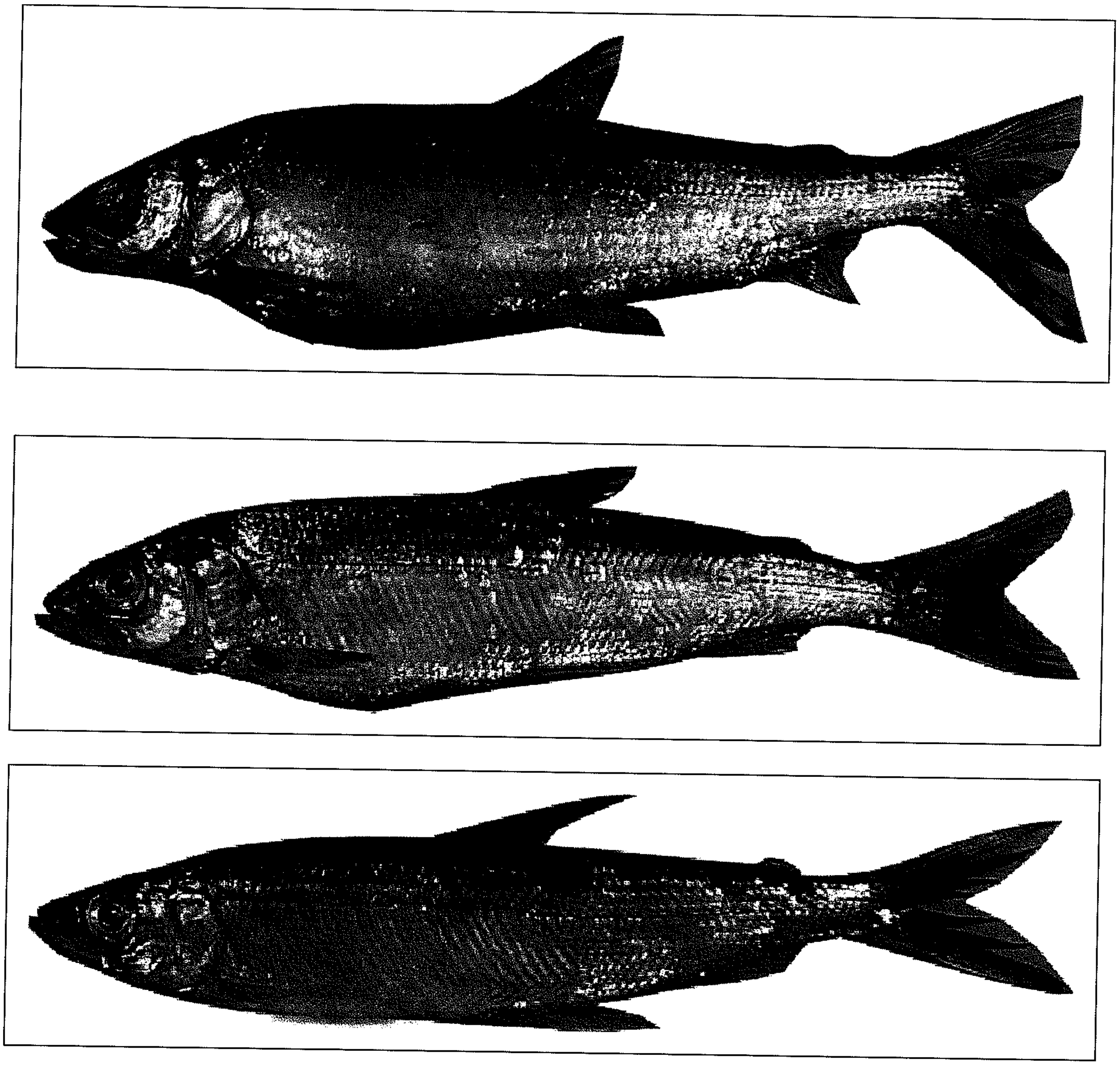


Figure 4.4. General appearance of Reindeer Lake ciscoes. The fish in the upper panel is representative of the low form and had a standard length of 196 mm and 25 gillrakers. The fish in the middle panel is representative of the mid form and had a standard length of 158 mm and 33 gillrakers. The fish 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).

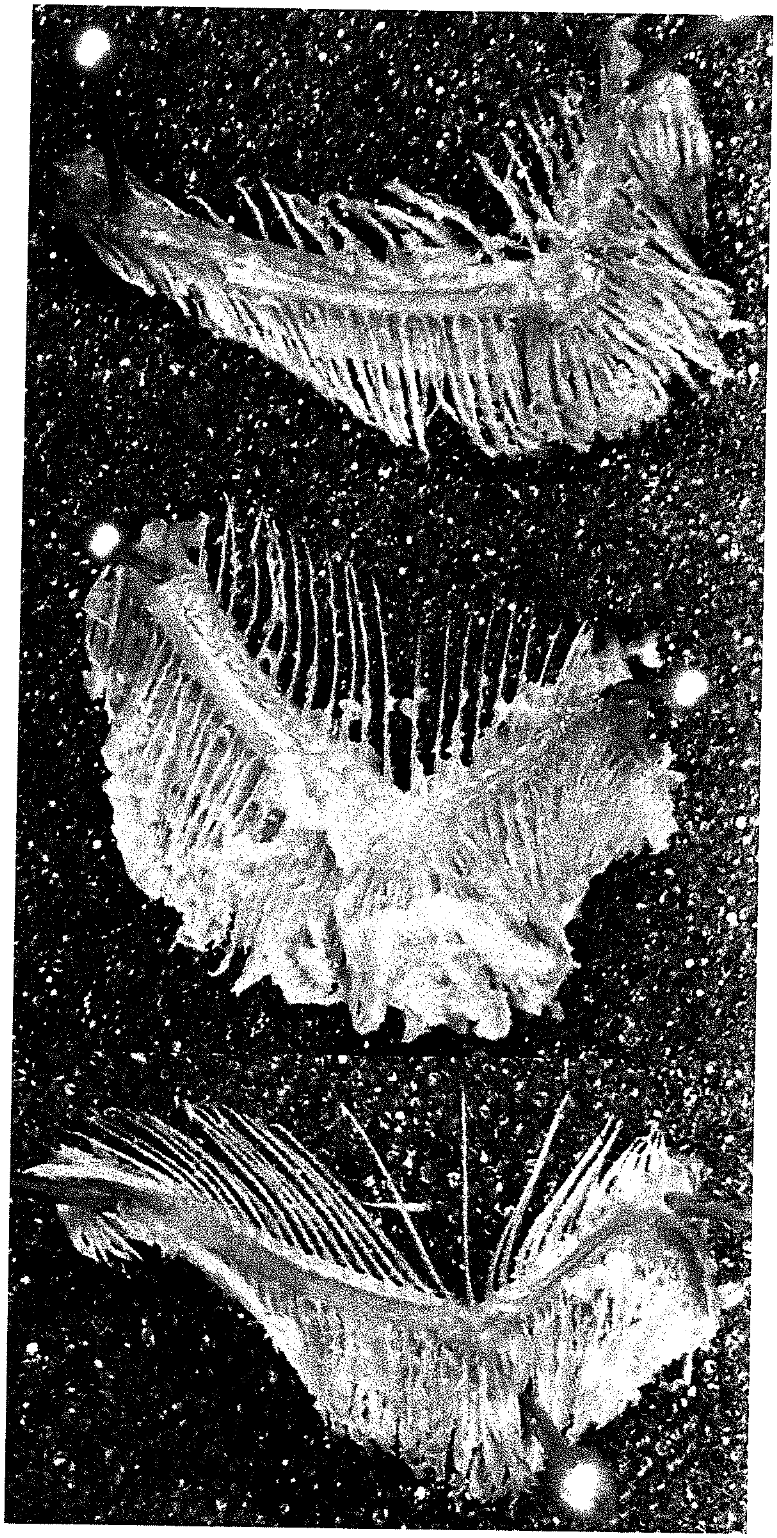


Figure 4.5. Gill arches removed from Reindeer Lake ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes, middle panel of mid-gillrakered ciscoes, and lower panel of high-gillrakered ciscoes from Reindeer Lake.

Morphological Confirmation of Differences

A series of PCAs were performed to test if the forms identified initially were supported by multivariate analysis. Because gillraker counts were not effective for identifying ciscoes that fell into the mid range between forms, the PCAs also served as a method to place these individuals into the most appropriate form. The first PCA used only meristic characters including upper and lower gillraker counts. This PCA resulted in grouping along component one but no clearly defined groups could be identified with the combination of components one and two (Appendix 4-11). The first two components explained 52 % of the total variation with upper and lower gillraker counts accounting for most of the variation positively and premaxillary angle negatively on component one (34 %). Component two (18 %) was influenced most by pectoral, pelvic and dorsal ray counts (Appendix 4-12).

A second PCA was performed using 19 morphometric characters adjusted to standardized ratios. Some separation was apparent when scores from components one and two were plotted but not complete enough to identify multiple forms (Appendix 4-13). The characters accounting for most of the variation on the first component included gillraker length, pelvic length, pectoral length, and orbital length (24 %) (Appendix 4-14). Maxillary length, lower arch length, preorbital length, and postorbital length accounted for most of the variation on component two (12.5 %) (Appendix 4-14). A PCA was also preformed using morphometric characters adjusted by standardized pooled residuals and the results were found to be similar to those using ratios.

The next PCA was performed using the meristic characters along with standardized morphometric characters adjusted to ratios (26 characters in total) (Figure 4.6). Upper and lower gillrakers were included this analysis. The results of this PCA were similar to those found when only morphometric values adjusted to ratios were used (Appendix 4-13); however, separation into groups was more apparent here (Figure 4.6). Component one provided the most separation and gillraker length, upper and lower gillraker counts, pelvic length, pectoral length, and orbital length were the most correlated characters on this component (23 %) (Table 4.1). The variation shown by component two was primarily accounted for by maxillary length, lower arch length, and postorbital length (10.5 %) (Table 4.1).

Based on these PCA results two new groups were identified and the boundaries for these are shown in Figure 4.6. Most ciscoes originally identified as members of the low or mid form were placed into a single low gillraker group. Most of the ciscoes originally identified as members of the high form and some of the mid form were placed into a high gillraker group. Nine ciscoes originally considered members of the high form were placed into the new low group and 11 ciscoes originally placed within the mid form were moved in the new high group. Another six ciscoes did not clearly fit into either group and were treated as a group of unknowns. The ciscoes originally identified as members of the high form that were moved into the low group had total gillraker counts of either 39 or 40 except for one with 42. For those individuals originally identified as members of the mid form that were moved into the high group, the gillraker counts ranged from 37 to 38.

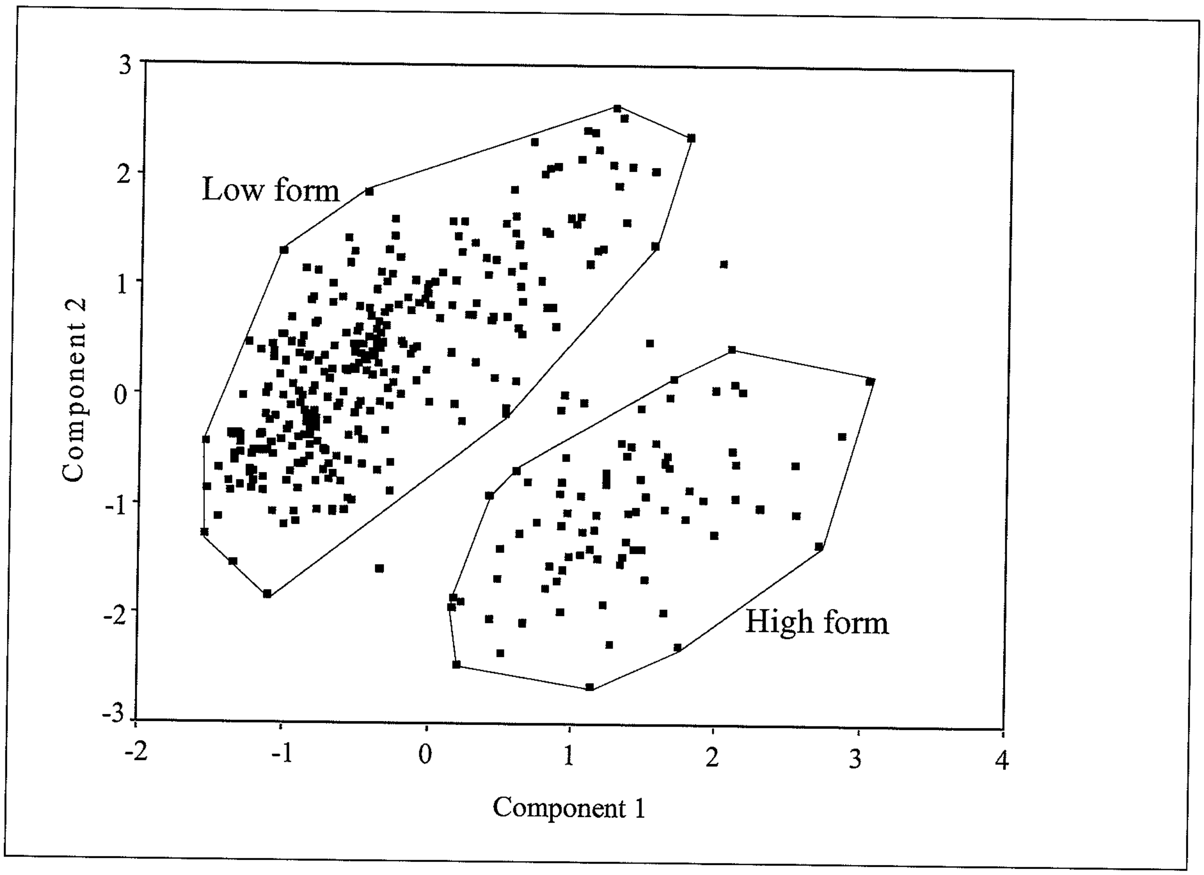


Figure 4.6. Plot of PCA scores for Reindeer Lake ciscoes using meristic and morphometric characters adjusted by ratios. Boundaries show forms suggested by the results of this analysis.

Table 4.1. Character loadings and variance explained for PCA of Reindeer Lake ciscoes using meristic and morphometric characters adjusted by ratios.

	Component	
	1	2
Preorbital length	0.16	0.55
Orbital length	0.60	0.31
Post orbital length	-0.03	0.61
Trunk length	-0.22	-0.35
Dorsal length	0.46	0.08
Lumbar length	-0.41	-0.03
Anal length	0.55	-0.31
Caudal peduncle length	-0.31	0.13
Head depth	0.57	0.41
Body depth	0.20	0.26
Caudal peduncle depth	0.58	-0.09
Interorbital width	0.55	0.35
Maxillary length	0.22	0.71
Maxillary width	0.24	-0.08
Pectoral length	0.71	-0.08
Pelvic length	0.75	-0.14
Adipose length	0.27	0.16
Lower arch length	0.13	0.65
Gillraker length	0.83	-0.11
Premaxillary angle	-0.52	0.38
Dorsal ray count	0.15	0.26
Anal ray count	0.29	-0.07
Pectoral ray count	-0.03	0.06
Pelvic ray count	-0.02	-0.05
Upper gillraker count	0.80	-0.30
Lower gillraker count	0.86	-0.23
Eigenvalues	5.92	2.74
Percent of Variance	22.77	10.54
Cumulative Percent	22.77	33.31

The final PCA for Reindeer Lake did not include upper and lower gillraker counts as they were used to initially identify the forms. The other meristic characters were not found to be effective for distinguishing between forms so they were also not included in this analysis. The groups suggested by the exploratory PCA using meristic characters and morphometric characters adjusted by ratios were used to determine the common-within-group residual values for the morphometric characters. These new characters were subsequently used in place of the original 19 morphometric characters in this analysis. The results of this PCA support the previous findings that two forms are present within the ciscoes collected from Reindeer Lake (Appendix 4-15). Although the separation was not complete between the two groups, there were only a few individuals that caused them to overlap in multivariate space. These results are significant because they show that even though gillraker counts were not included in the analysis the presence of two forms was supported. Component one accounted for 25 % of the variation in the data and gillraker length, pelvic length, and pectoral length were heavily correlated with this component (Appendix 4-16). Component two accounted for 14 % of the variance and maxillary length, lower arch length, and preorbital length were the highest loadings characters on this component (Appendix 4-16).

The above principal components analyses consistently supported two cisco forms being present within the specimens collected from Reindeer Lake. The differences between the two forms are only supported by the first one or two components in the analyses, the remaining components account for variation in characters that provide little or no information towards differentiating the groups. The initial forms identified by gillraker count distribution, along with dorsal colouration, general body shape, jaw position, and gillraker arrangement resulted in some overlap when compared to the PCA results.

Hypothesis Testing of Form Differences

The next step was examine whether the two forms suggested by the previous analyses were supported by statistical tests such as ANOVA and DA.

The results of the ANOVA test of mean differences for each character between the Reindeer Lake forms and the Levene's test of homogeneity of variance are presented in Table 4.2. Gillraker counts were not included in the analysis but the remaining 24 meristic and morphometric characters were included. Only three (head depth, pectoral fin length, and pelvic fin length) of the 26 variables were found to be significant for the Levene's test (Table 4.2, $P<0.01$) indicating heterogeneity in the variances for these characters. To account for this probability values were calculated for both situations where variances were assumed equal and where variances were assumed not equal (Table 4.2). Both tests yielded the same results finding significant differences between the forms for 18 characters (Table 4.2, $P<0.01$). Dorsal ray count, pectoral ray count, pelvic ray count, postorbital length, trunk length, and head depth were the only characters that were not significantly different between the forms.

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 $P<0.01$.

	Levene's Test of Equality of Variance	Anova test of Equality of Means	
		Variance Equal	Variance Not Equal
	Sig.	Sig.	Sig.
Premaxillary angle	0.75	**0.00**	**0.00**
Dorsal ray count	0.88	0.12	0.13
Anal ray count	0.84	**0.00**	**0.00**
Pectoral ray count	0.47	0.06	0.07
Pelvic ray count	0.46	0.42	0.45
Preorbital length	0.70	**0.00**	**0.00**
Orbital length	0.04	**0.00**	**0.00**
Post orbital length	0.97	0.01	0.01
Trunk length	0.24	0.01	0.01
Dorsal length	0.29	**0.00**	**0.00**
Lumbar length	0.18	**0.00**	**0.00**
Anal length	0.85	**0.00**	**0.00**
Caudal peduncle length	0.05	**0.00**	**0.00**
Head depth	**0.00**	0.05	0.01
Body depth	0.66	**0.00**	**0.00**
Caudal peduncle depth	0.30	**0.00**	**0.00**
Interorbital width	0.21	**0.00**	**0.00**
Maxillary length	0.01	**0.00**	**0.00**
Maxillary width	0.90	**0.00**	**0.00**
Pectoral length	**0.00**	**0.00**	**0.00**
Pelvic length	**0.00**	**0.00**	**0.00**
Adipose length	0.32	**0.00**	**0.00**
Lower arch length	0.61	**0.00**	**0.00**
Gillraker length	0.16	**0.00**	**0.00**

Discriminant Analysis was used as a quantitative test of all characters simultaneously to test if the two forms suggested by the PCA results were supported and to see where the individuals with uncertain groupings should be placed. Upper and lower gillrakers were not included in the character suite. Two discriminant functions were calculated explaining the variation in the data. The best discriminating characters on the first function were gillraker length and pelvic length positively and lower arch length, premaxillary angle and maxillary length negatively. For the second function the best discriminating characters were maxillary length and preorbital length positively and orbital length and premaxillary angle negatively. The plot of the two functions, with individuals identified by the groups suggested from the PCA, resulted in a large number of individuals being classified as uncertain (Figure 4.7 upper and Table 4.3). The functions were also plotted using the predicted group memberships from the discriminant analysis (Figure 4.7 lower). This plot showed the two main groups along with those individuals that were identified as having uncertain group membership. These results support the presence of two forms within the Reindeer Lake ciscoes collected ($P<0.001$, df=24); however, some individuals could not be placed in either group with confidence. The classification results found that 94.7 % of the original grouped cases suggested by exploratory PCA were correctly classified by DA. Those not classified correctly included five individuals originally placed within the low form that were placed in the uncertain group by DA, three individuals originally identified as members of the high form that were placed with the low group, and one individual originally considered uncertain was placed with the high group (Table 4.3).

Table 4.3. Discriminant Analysis results for Reindeer Lake ciscoes using meristic characters and morphometric characters adjusted by residuals.

Standardized Canonical Discriminant Function Coefficients	Function 1	Function 2
Premaxillary angle	-0.32	-0.38
Dorsal ray count	-0.20	-0.06
Anal ray count	-0.04	-0.27
Pectoral ray count	-0.16	-0.10
Pelvic ray count	0.08	-0.18
Preorbital length	-0.15	0.43
Orbital length	0.07	-0.61
Postorbital length	-0.06	0.10
Trunk length	0.15	-0.11
Dorsal length	0.01	0.31
Lumbar length	0.02	0.09
Anal length	0.30	0.21
Caudal peduncle length	0.00	0.25
Head depth	-0.03	-0.29
Body depth	-0.01	0.14
Caudal peduncle depth	0.17	0.08
Interorbital width	0.03	0.14
Maxillary length	-0.31	0.56
Maxillary width	0.04	-0.17
Pectoral length	0.11	0.04
Pelvic length	0.39	0.25
Adipose length	0.00	0.04
Lower arch length	-0.35	0.04
Gillraker length	0.72	-0.25
Eigenvalue	4.09	0.07
Percent of Variance	98.40	1.60
Cumulative Percent	98.40	100.00
Canonical Correlation	0.90	0.25

Classification Results

Groups suggested by PCA		Predicted Group Membership: Low	High	Uncertain	Total
Count	Reindeer low	283	0	5	288
	Reindeer high	3	66	11	80
	Uncertain	0	1	5	6
%	Reindeer low	98.26	0.00	1.74	100
	Reindeer high	3.75	82.50	13.75	100
	Uncertain	0.00	16.67	83.33	100

94.7% of original grouped cases correctly classified.

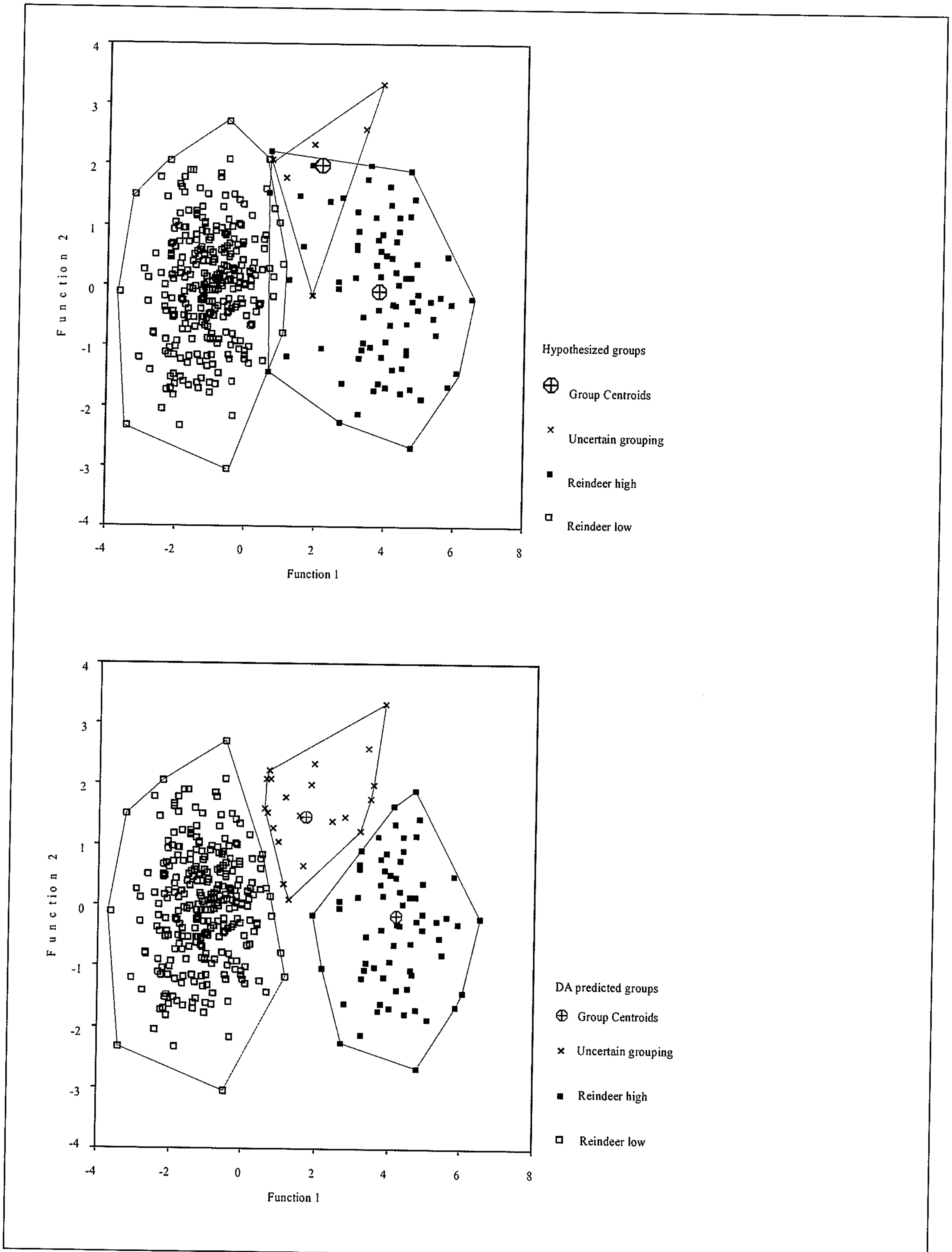


Figure 4.7. Discriminant function plots for Reindeer Lake ciscoes. Individuals identified by exploratory PCA are shown in the upper panel and new groups predicted by Discriminant Analysis are shown in the lower panel.

Summary of Reindeer Lake Cisco Forms

The presence of sympatric cisco forms in Reindeer Lake was supported by the results of this study. Gillraker count and arrangement, jaw position, and dorsal colouration were used initially to identify three potential cisco forms; however, some individuals in the region of overlap were not effectively identified by these characters alone. The PCA results supported the presence of only two cisco forms and also served as a method for placing some of the uncertain individuals into the most appropriate forms. The majority of the individuals originally identified as members of the mid-gillraker form were grouped with the low-gillraker form based on the PCA results. The Anova and DA results provided evidence supporting a low- and high-gillraker form being present with some individuals in the mid range remaining of uncertain group membership.

Three cisco forms were collected from Reindeer Lake in this study; however, the low and mid forms were found to group together by some of the tests. Based on these results both the mid and low forms were combined into a single low form.

1. Total gillraker count of 36 or fewer on first gill arch, gillrakers short and widely spaced.. Low gillraker form

   Total gillraker count 40 or greater on first gill arch, gillrakers long and tightly packed ....High gillraker form

   Total gillraker count 37 to 39...2
2. Premaxillary angle usually greater than 45°, downward jaw appearance, tan to brown dorsal colouration. ....Low form

Premaxillary angle usually greater than 45°, upward jaw appearance, greenish blue to black dorsal colouration .... High form

This key is a guide based on specimens collected and examined from Reindeer Lake by the author. This key may not account for some of the cisco variability found within the lake. See discussion for taxonomic conclusions regarding the low and high gillraker forms identified in this study.

5. RESULTS - COMPARISON OF GEORGE LAKE CISCOES

General Biology

In 2000 74 ciscoes were collected and in 2001 65 ciscoes were collected from George Lake (Appendix 2-3). Location coordinates and the other species collected in the sets are listed in Appendix 2-3. Biological characteristics were examined for all individuals combined to determine if any of these characters support the presence of sympatric forms of ciscoes in George Lake. Appendix 5-1 lists the descriptive statistics for all George Lake ciscoes. The size range for the 109 individuals analyzed was 81 to 183 mm in standard length with a mean of 123.7 mm and 7 to 92 g in weight with a mean of 32.4 g. Appendix 5-2 shows the frequency distribution for standard length and two modes were apparent, one around 90 mm and another around 155 mm.

When standard length and weight were plotted together along with capture location, no difference other than size was apparent (Appendix 5-3). The age distribution for all ciscoes collected from George Lake consists of individuals ranging in age from 1 to 20 with the majority of individuals ranging from 1 to 2 years of age (Appendix 5-4). The sex ratio was examined by looking at the distribution of total gillraker counts versus standard length for all individuals identified by sex (Figure 5.1). The plot suggested that two forms were present, one consisting of individuals with higher gillraker counts and standard lengths less than 100 and another with lower gillraker counts and larger standard lengths. The forms contained approximately equal numbers of males and females ruling out sex bias as a basis for the differences between the forms. When sexual maturity was plotted on the graph of total gillraker counts versus standard length it showed that the majority of individuals with a standard length of 120 mm or less were immature and those above 120 mm were mature (Appendix 5-5). The majority of high-gillrakered individuals were less than 100 mm and immature. Immaturity could also be ruled out as a basis for the differences between forms because gillraker counts do not decrease as ciscoes mature.

A preliminary examination of the general biology of all ciscoes collected from George Lake suggests the presence of two sympatric forms. One form consists of mostly small ciscoes with high gillraker counts and the other consists of small and large individuals with lower gillraker counts.

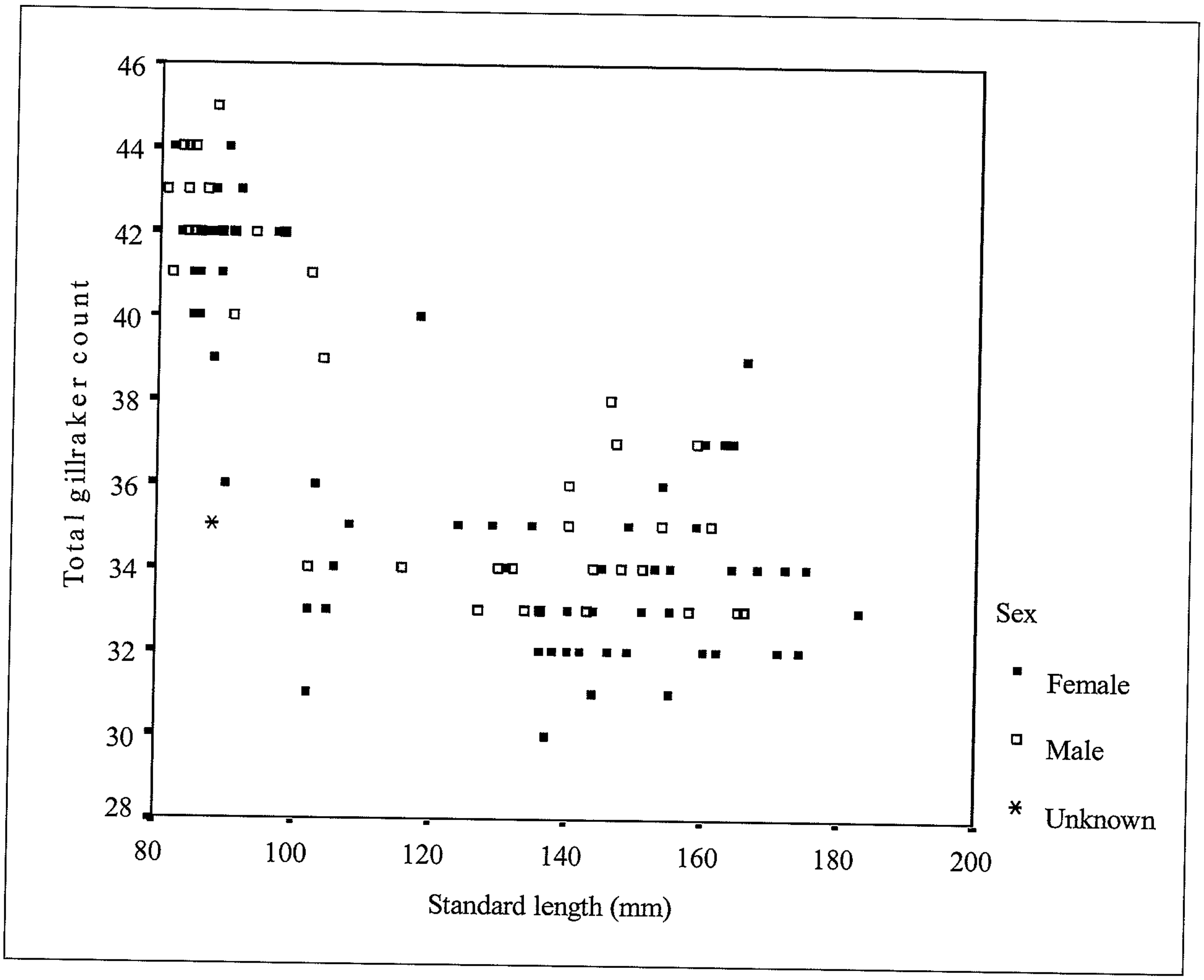


Figure 5.1. Relationship between total gillraker count and standard length for George Lake ciscoes with sex identified.

Discrimination of Cisco Forms

Discrimination of George Lake sympatric cisco forms was initially examined based on the distribution of gillraker counts and by a combination of gillraker count and standard length (figures. 5.2 and 5.3). A bimodal distribution was apparent from the gillraker frequency distribution; however, the ranges overlapped between 38 and 39 gillrakers. The counts ranged from 30 to 45 for all individuals with modes around 34 and 42. Gillraker arrangement, dorsal colouration, general body shape, and mouth morphology and orientation were also examined to see if they were effective for distinguishing between the two forms suggested by gillraker count distribution. The gillrakers tended to be shorter and more widely spaced in members of the low form than the high form (Figure 5.4). The low-gillraker form had lighter dorsal colouration than the high form ranging from yellow to tan. The high form ranged in colour from green to dark blue. Jaw position was variable between the two forms; however, the low form in general had equal upper and lower jaws or the upper jaws protruded slightly. Jaw position in the high form was usually equal or the lower jaws were longer than the upper. Based on the above key characters, the low-gillraker form consisted of individuals with gillraker counts of 38 or less (with the exception of one individual, which had 39 gillrakers), light dorsal colouration and slightly longer upper jaw than lower (Figure 5.5). The high-gillraker form consisted of ciscoes with 39 or more gillrakers, dark dorsal colouration, and even or slightly longer lower jaw (Figure 5.5).

The low-gillraker form consisted of individuals with a mean gillraker count of 33.9 (30-39) and a mean standard length of 143 mm (88-183) (Table 5.1). The high-gillraker form consisted of individuals with a mean gillraker count of 42 (39-45) and a mean standard length of 89 (81-118) (Table 5.2). The descriptive statistics of the two forms from George Lake for all morphometric and meristic characters are listed in Tables 5.1 and 5.2. The size-at-age for each form is plotted in Appendix 5-6. A difference was apparent between the two forms; however, the difference is most likely due to the lack of larger-sized individuals within the high-gillrakered form.

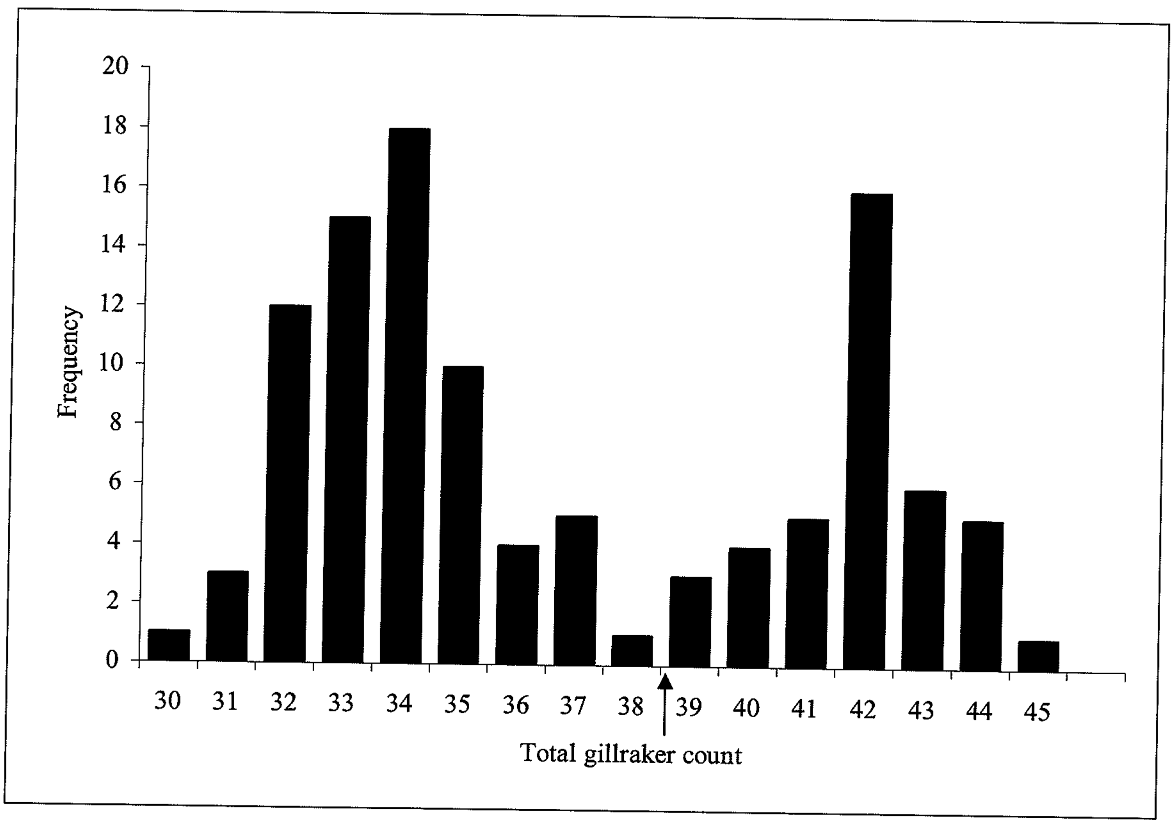


Figure 5.2. Frequency distribution of total gillraker counts for all ciscoes from George Lake. All individuals with counts of 38 or less were placed in the low form along with one individual with 39 gillrakers. All but one individual with 39 or more were placed in the high form.

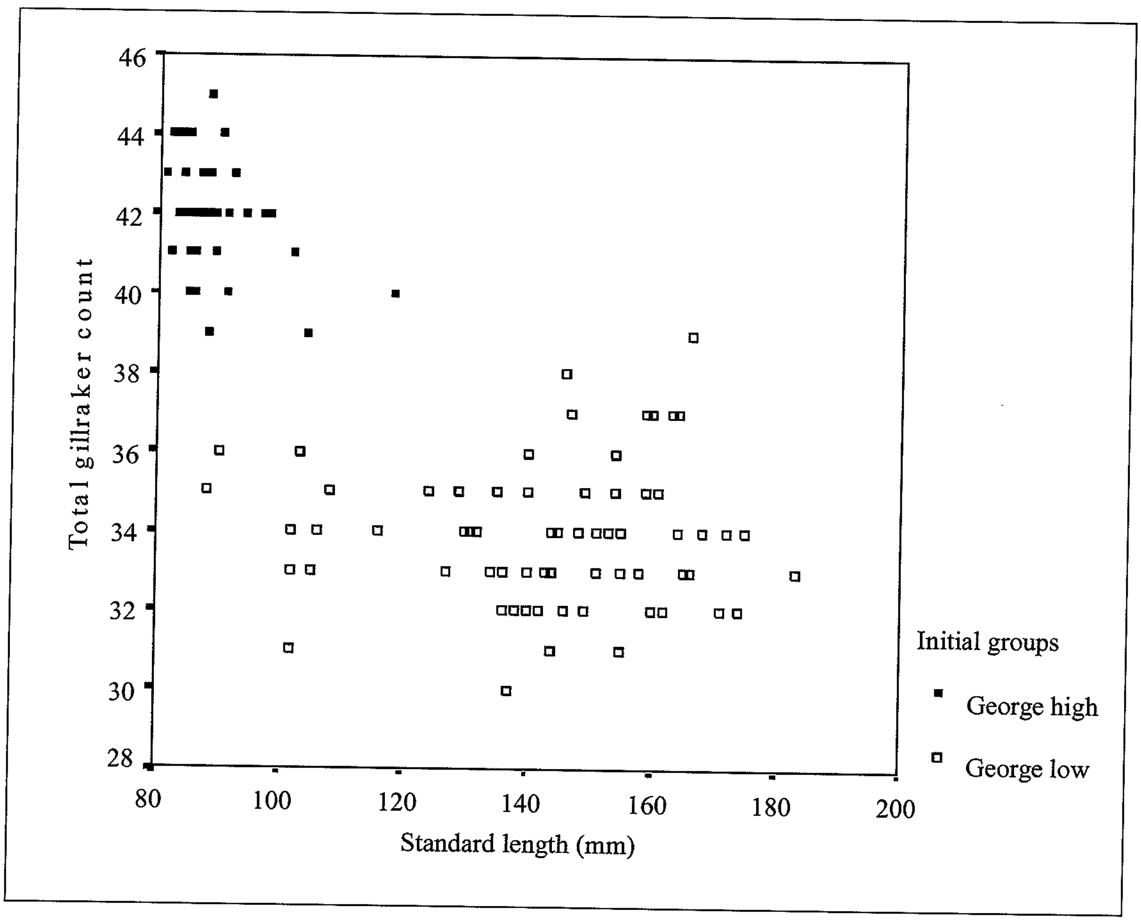


Figure 5.3. Relationship between gillraker count and standard length for George Lake ciscoes with individuals identified by initial forms.

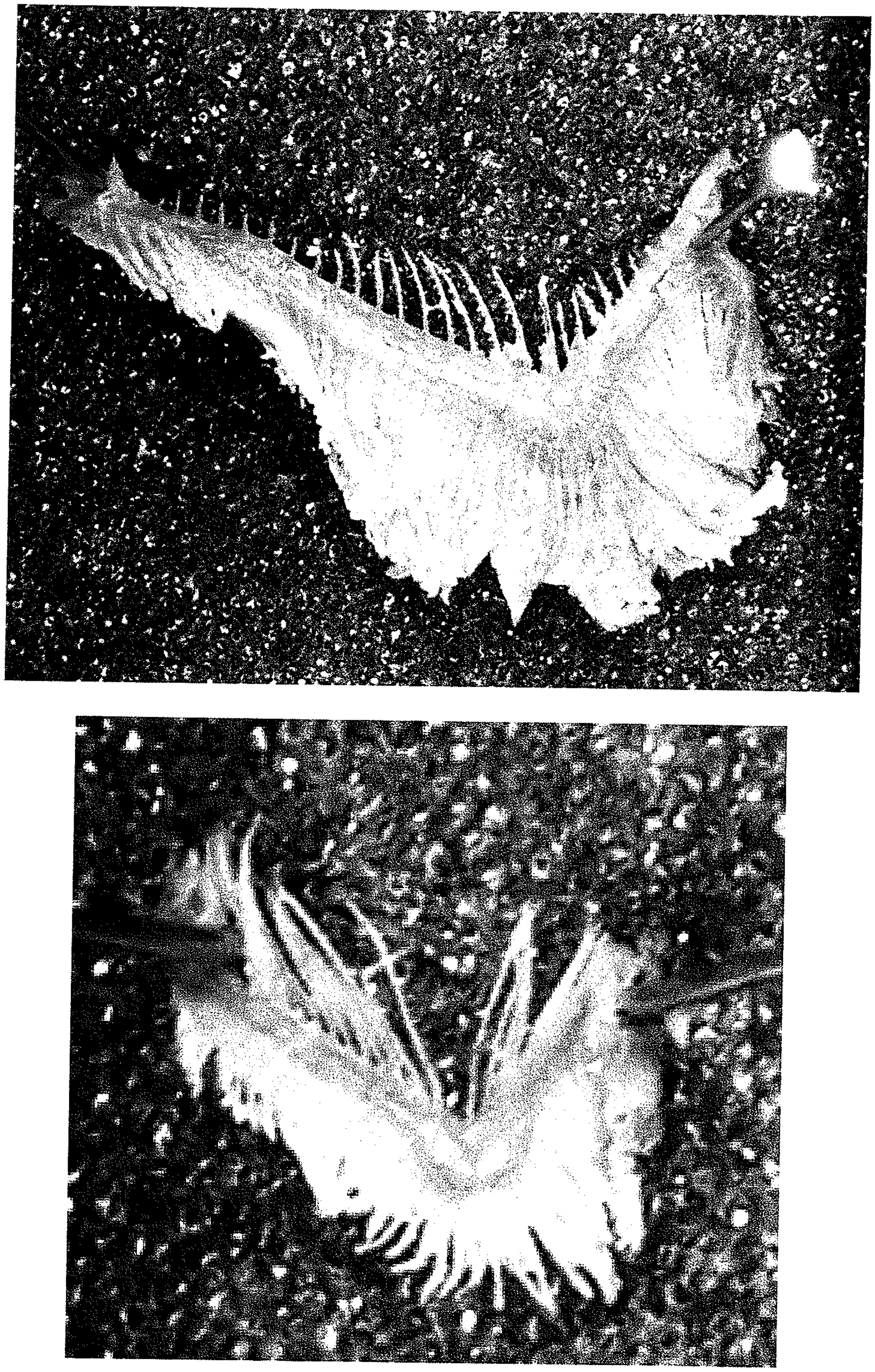


Figure 5.4. Gill arches removed from George Lake ciscoes. Upper panel shows typical gillraker structure of low-gillrakered ciscoes and lower panel of high-gillrakered ciscoes from George Lake.

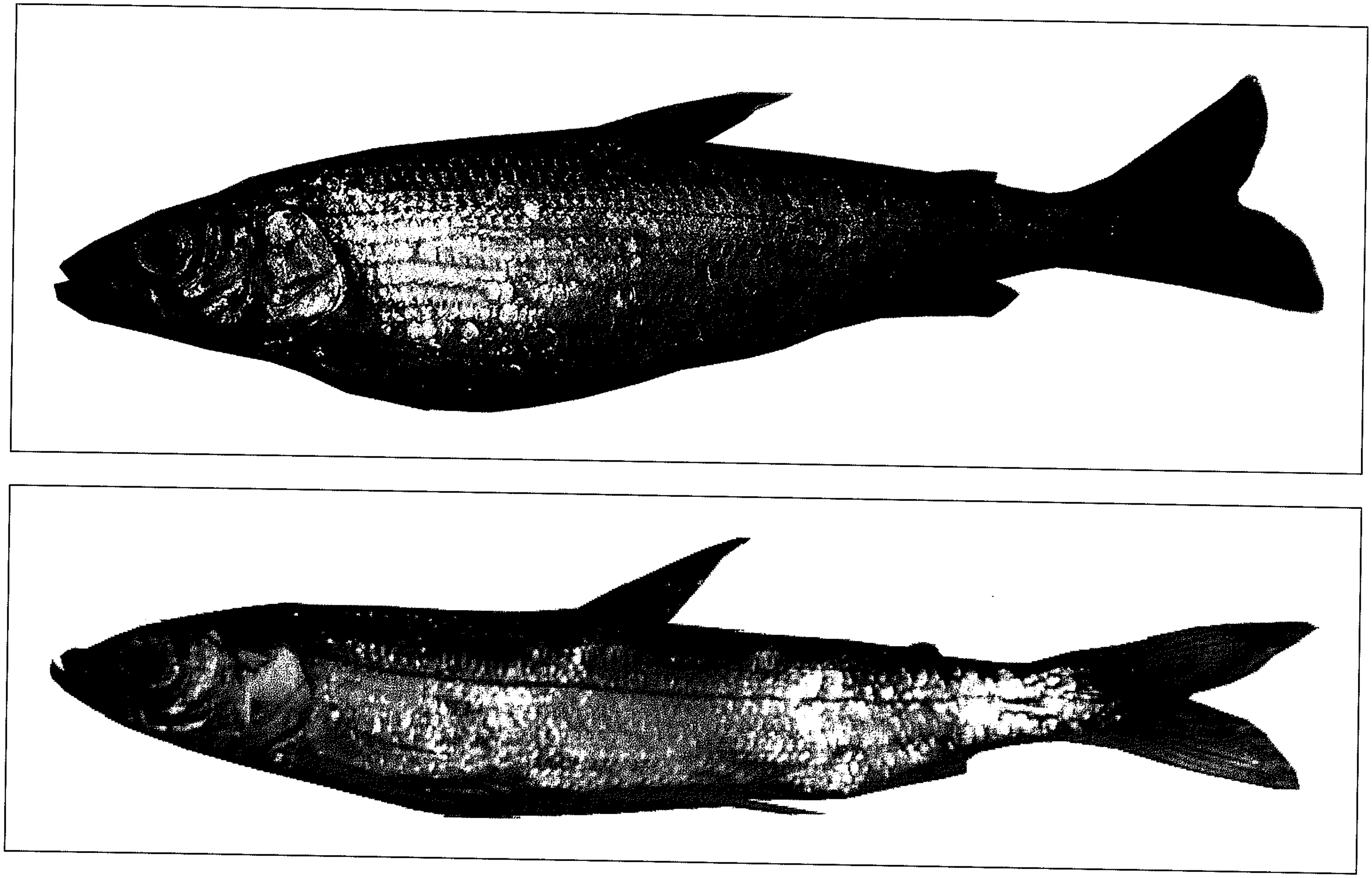


Figure 5.5. General appearance of George Lake ciscoes. The upper panel shows a member of the low form and had a standard length of 160 mm and 32 gillrakers. The lower panel shows a member of the high form had a standard length of 102 mm and 41 gillrakers. (Note: previously frozen specimens).

Table 5.1. Descriptive statistics for George Lake ciscoes placed in the low-gillraker form.

	N	Minimum	Maximum	Mean
Total gillraker count	70	30	39	33.8
Upper gillraker count	70	9	15	11.3
Lower gillraker count	70	20	26	22.5
Premaxillary angle	70	40	60	49.3
Dorsal ray count	70	9	12	11.0
Anal ray count	70	11	14	12.1
Pectoral ray count	70	13	16	15.2
Pelvic ray count	70	9	12	10.8
Age	70	1	20	8.0
Weight	70	10	92	44.9
Standard length	70	88.0	183.0	143.0
Fork length	69	98.0	203.0	159.8
Gillraker length	70	1.7	4.8	3.0
Lower arch length	70	10.5	21.2	16.1
Preorbital length	70	5.3	12.4	9.2
Orbital length	70	6.0	12.0	9.8
Post orbital length	70	10.8	23.6	18.0
Trunk length	70	18.4	47.3	35.1
Dorsal length	70	8.9	19.4	14.5
Lumbar length	70	12.8	34.4	24.5
Anal length	70	9.5	19.8	14.6
Caudal peduncle length	70	11.6	22.5	17.2
Head depth	70	9.6	21.7	16.5
Body depth	70	14.8	45.2	33.4
Caudal peduncle depth	70	6.5	13.1	10.4
Interorbital width	70	4.2	9.6	7.7
Maxillary length	70	7.7	17.4	13.1
Maxillary width	70	2.2	5.8	3.8
Pectoral length	70	14.4	32.6	24.9
Pelvic length	70	13.7	33.5	24.8
Adipose length	70	5.1	14.7	9.1

Table 5.2. Descriptive statistics for George Lake ciscoes placed in the high-gillraker form.

	N	Minimum	Maximum	Mean
Total gillraker count	39	39	45	41.8
Upper gillraker count	39	13	17	14.6
Lower gillraker count	39	22	30	27.3
Premaxillary angle	39	35	50	41.8
Dorsal ray count	39	10	12	10.5
Anal ray count	38	11	13	11.7
Pectoral ray count	39	15	17	15.5
Pelvic ray count	39	10	12	10.7
Age	39	1	18	1.7
Weight	39	7	76	12.9
Standard length	39	81.0	164.0	92.4
Fork length	35	88.0	184.0	101.4
Gillraker length	39	2.4	5.4	3.7
Lower arch length	39	8.0	19.1	10.4
Preorbital length	39	4.8	11.2	5.9
Orbital length	39	4.6	11.1	5.8
Post orbital length	39	8.6	22.5	10.9
Trunk length	39	18.6	43.5	22.3
Dorsal length	39	6.2	17.7	8.7
Lumbar length	39	11.4	30.3	15.3
Anal length	39	8.4	16.2	10.4
Caudal peduncle length	39	8.4	19.1	11.8
Head depth	39	8.8	19.5	10.4
Body depth	39	12.5	44.5	17.2
Caudal peduncle depth	39	5.1	12.2	6.3
Interorbital width	39	3.9	8.9	5.0
Maxillary length	39	5.3	15.7	7.3
Maxillary width	39	1.7	4.9	2.3
Pectoral length	39	11.5	29.7	14.9
Pelvic length	39	10.9	29.5	14.6
Adipose length	39	2.2	10.0	5.5

Morphological Confirmation of Differences

A series of PCAs were performed to examine whether the forms identified initially from George Lake by gillraker counts and then by other key characters were confirmed by multivariate analysis. The first PCA included six meristic characters along with premaxillary angle. This PCA demonstrated almost complete separation between the high and low forms; however, two ciscoes initially identified as members of the low group were found to be morphologically closer to members of the high group (Appendix 5-7). These fish both had total gillraker counts of 37 and premaxillary angles of 45 degrees. Based on this PCA these two fish were tentatively placed into the high form. The first two components explained 55 % of the total variation with upper and lower gillraker counts accounting for most of the variation positively and premaxillary angle negatively on component one (35.5%) (Appendix 5-8). Component two (19.6 %) was influenced most by pectoral, anal, and dorsal ray counts (Appendix 5-8).

The next PCA was performed on 19 morphometric characters adjusted to standardized ratios. The first two components showed separation between the high and low forms; however, there were some individuals originally considered to be members of the low form that were closer in distance to the high form (Appendix 5-9). Maxillary length, body depth, pelvic length, gillraker length (negative loading), and pectoral length were the highest loading characters on component one, the total amount of variation accounted for by component one was 30.4 % (Appendix 5-10). Lower arch length and preorbital length were the highest correlated characters on the second component and the variance accounted for was 16 % (Appendix 5-10).

A PCA was performed using meristic characters combined with the standardized morphometric characters adjusted by ratios (26 characters in total). Upper and lower gillrakers were included in this analysis. Component one provided the most separation between the low and high forms; however, two individuals from the low-gillraker form did not fit into either form and another was closer in distance to the high form (Figure 5.6). The variation displayed by component one (29 %) was primarily accounted for by a contrast between body depth and pelvic fin length against lower and upper gillraker counts, and gillraker length (Table 5.3). The highest loading variables on component two (9 %) were preorbital length and lower arch length.

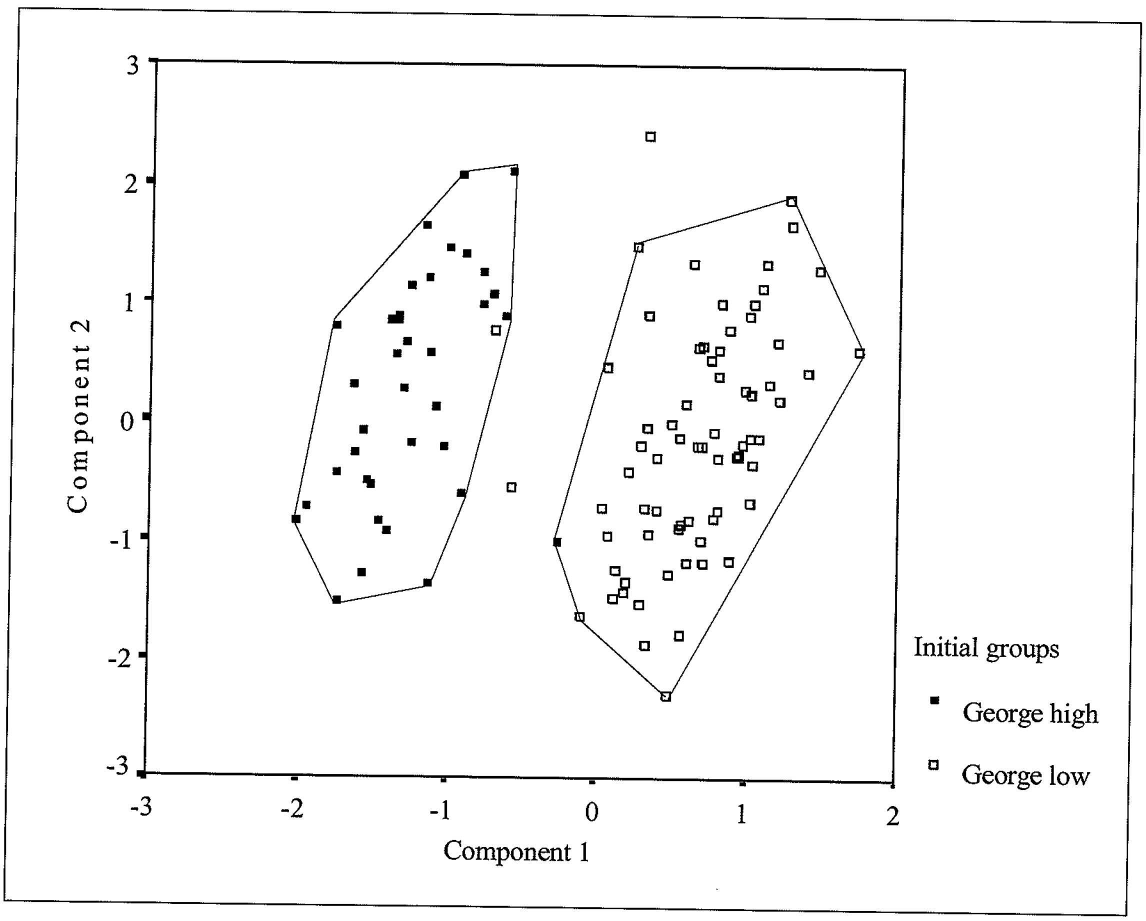


Figure 5.6. Plot of PCA scores for George Lake ciscoes using meristic characters and morphometric characters adjusted by ratios. Forms were assigned *a posteriori* as outlined in the text. Boundaries indicate Forms suggested by this PCA.

Table 5.3. Character loadings and variance explained for PCA of George Lake ciscoes using meristic characters and morphometric characters adjusted by ratios.

	Component	
	1	2
Preorbital length	0.26	0.70
Orbital length	0.66	0.31
Post orbital length	0.64	0.11
Trunk length	0.08	-0.55
Dorsal length	0.36	0.28
Lumbar length	0.29	-0.11
Anal length	-0.66	0.26
Caudal peduncle length	-0.41	0.38
Head depth	0.49	0.28
Body depth	0.82	-0.27
Caudal peduncle depth	0.59	0.33
Interorbital width	0.10	0.10
Maxillary length	0.79	0.17
Maxillary width	0.38	0.03
Pectoral length	0.67	0.15
Pelvic length	0.77	0.09
Adipose length	0.24	0.10
Lower arch length	0.17	0.68
Gillraker length	-0.84	0.28
Premaxillary angle	0.59	-0.19
Dorsal ray count	0.40	0.03
Anal ray count	0.21	-0.28
Pectoral ray count	-0.16	0.00
Pelvic ray count	0.20	0.19
Upper gillraker count	-0.82	0.20
Lower gillraker count	-0.83	0.26
Eigenvalues	7.58	2.33
Percent of Variance	29.14	8.96
Cumulative Percent	29.14	38.10

The final PCA for George Lake was performed using 19 morphometric characters adjusted by common-within-group residuals. The results of the PCA supported two forms being present; however, two individuals identified originally as members of the low gillraker form did not group closely with either form (Appendix 5-11). Component one provided the most separation between forms when plotted with component two while components three and four provide no separation. Component one accounted for 30.4 % of the variation in the data, the highest positively loading variables were orbital length, maxillary length, preorbital, lower arch length, head depth, pectoral length, orbital length, postorbital length, premaxillary angle, and dorsal length and the highest negatively loading variables were gillraker length and interorbital width (Appendix 5-12). Component two accounted for only 9.8 % of the variance, anal length and preorbital length were the highest loading variables on this component (Appendix 5-12).

Hypothesis Testing of Form Differences

The next step was examine whether the two forms suggested by the previous analyses were supported by statistical tests such as ANOVA and DA.

The results of the ANOVA test of mean differences of each character for the George Lake forms and the Levene's test of homogeneity of variance are presented in Table 5.4. All 26 meristic and morphometric characters were included in the analysis; however, common-within-group adjusted residuals were used as the morphometric characters. A total of 11 out of the 26 variables were found to be significant for the Levene's test violating the assumption of homogeneity of variance for the ANOVA (Table 5.4, $P<0.05$). To account for this, probability values were calculated for both situations where variances were assumed to be equal and not equal between forms (Table 5.4). A large number of significant differences (17 at $P<0.05$) were found between the two forms for both sets of probabilities. Only PRC, VRC, TTL, LUL, BDD, CPD, and ADL were found to not be significantly different between the low- and high-gillraker forms (see Figure 2.5 for variable descriptions).

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 $P<0.05$

	Levene's Test of Equality of Variance	ANOVA test of Equality of Means	
		Variance Equal	Variance Not Equal
	Sig.	Sig.	Sig.
Premaxillary angle	0.828	**0.000**	**0.000**
Dorsal ray count	0.609	**0.000**	**0.000**
Anal ray count	0.522	**0.010**	**0.007**
Pectoral ray count	0.280	0.084	0.091
Pelvic ray count	**0.008**	0.217	0.248
Preorbital length	**0.000**	**0.000**	**0.000**
Orbital length	0.527	**0.000**	**0.000**
Post orbital length	0.066	**0.000**	**0.000**
Trunk length	**0.002**	0.184	0.125
Dorsal length	**0.019**	**0.000**	**0.000**
Lumbar length	0.060	0.730	0.702
Anal length	**0.000**	**0.000**	**0.000**
Caudal peduncle length	0.879	**0.000**	**0.000**
Head depth	0.145	**0.000**	**0.000**
Body depth	**0.009**	0.133	0.083
Caudal peduncle depth	0.635	0.250	0.263
Interorbital width	0.698	**0.000**	**0.000**
Maxillary length	0.841	**0.000**	**0.000**
Maxillary width	**0.007**	**0.014**	**0.004**
Pectoral length	**0.001**	**0.000**	**0.000**
Pelvic length	**0.005**	**0.000**	**0.000**
Adipose length	0.757	0.898	0.901
Gillraker length	**0.000**	**0.000**	**0.000**
Lower arch length	**0.016**	**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. Upper and lower gillrakers were not included in the character suite because they were used to identify the initial forms. A single discriminant function was calculated. The correlation of each character to the function is presented in Table 5.5; the highest loading characters were gillraker length, dorsal length, lower arch length, and interorbital width. The discriminant scores from the analysis are shown in Appendix 5-13. The classification results show that 100 % of the original grouped cases were correctly classified by discriminant analysis (Table 5.5).

Table 5.5. Discriminant Analysis results for George Lake cisco forms.

Standardized Canonical Discriminant Function Coefficients	Function 1
Premaxillary angle	0.20
Dorsal ray count	-0.03
Anal ray count	0.06
Pectoral ray count	-0.05
Pelvic ray count	0.02
Preorbital length	0.09
Orbital length	0.38
Postorbital length	0.29
Trunk length	0.35
Dorsal length	0.37
Lumbar length	0.07
Anal length	0.45
Caudal peduncle length	-0.17
Head depth	0.30
Body depth	-0.20
Caudal peduncle depth	-0.11
Interorbital width	-0.40
Maxillary length	0.07
Maxillary width	0.13
Pectoral length	0.03
Pelvic length	-0.07
Adipose length	0.03
Lower arch length	0.25
Gillraker length	-0.70
Eigenvalue	15.73
Percent of Variance	100
Cumulative Percent	100
Canonical Correlation	0.97

Classification Results

	Predicted Group Membership		
Initial groups	Low	High	Total
George lake low	70	1	71
George Lake high	0	37	37

99.1% of original grouped cases correctly classified.

Summary of George Lake Cisco Forms

The presence of sympatric cisco forms in George Lake was supported by the results of this study. Gillraker count and arrangement, jaw position, and dorsal colouration were effective initially for identifying cisco forms. The gillraker count distribution showed minimal overlap between forms; however, individuals in the overlap range were placed into forms effectively using dorsal colouration, jaw position, and gillraker arrangement. The PCA results also supported the presence of two cisco forms. The ANOVA and DA results provided evidence supporting a low- and high-gillraker form being present in George Lake.

The following is a key to identify the two cisco forms that were collected from George Lake in this study. The majority of ciscoes identified as the high-gillraker form from were found to be immature, however, larger, mature specimens with high gillraker counts could potentially be collected from the lake.

1. Total gillraker count of 36 or fewer on first gill arch, gillrakers short and widely spaced... Low gillraker form

   Total gillraker count 40 or greater on first gill arch, gillrakers long and tightly packed ....High gillraker form

   Total gillraker count 37 to 39...2
2. Premaxillary angle usually greater than 45°, downward jaw appearance, tan to brown dorsal colouration. ....Low form

Premaxillary angle usually greater than 45°, upward jaw appearance, greenish blue to black dorsal colouration .... High form

This key is a guide based on specimens collected and examined from George Lake by the author. This key may not account for some of the cisco variability found within George Lake. See discussion for taxonomic conclusions regarding the low and high gillraker forms identified in this study.

6. RESULTS - COMPARISON OF CLEARWATER LAKE CISCOES

General Biology

The number of ciscoes collected for each set is listed in Appendix 2-4 as well as other species collected and the location of each set. Appendix 6-1 lists the descriptive statistics for all Clearwater Lake ciscoes. The size range for the 69 individuals analyzed was 77 to 141 mm in standard length with a mean of 92.7 mm and 7 to 37 g in weight with a mean of 11.7 g. Appendix 6-2 shows the frequency distribution for standard length, one mode was apparent around 90 mm. When standard length and weight were plotted together along with capture location, no difference other than size was apparent (Appendix 6-3). The age distribution for all ciscoes collected from Clearwater Lake consisted of individuals ranging in age from 1 to 7 with the majority of individuals ranging from 1 to 4 years of age (Appendix 6-4). The sex ratio was examined by looking at the distribution of total gillraker count versus standard length for all individuals identified by sex (Figure 6.1). The specimens collected consisted of approximately equal numbers of males and females all within the same size range. When sexual maturity was plotted on the graph of total gillraker counts versus standard length it showed that the majority of individuals with a standard length of 100 mm or less were immature and those above 100 mm were mature (Appendix 6-5).

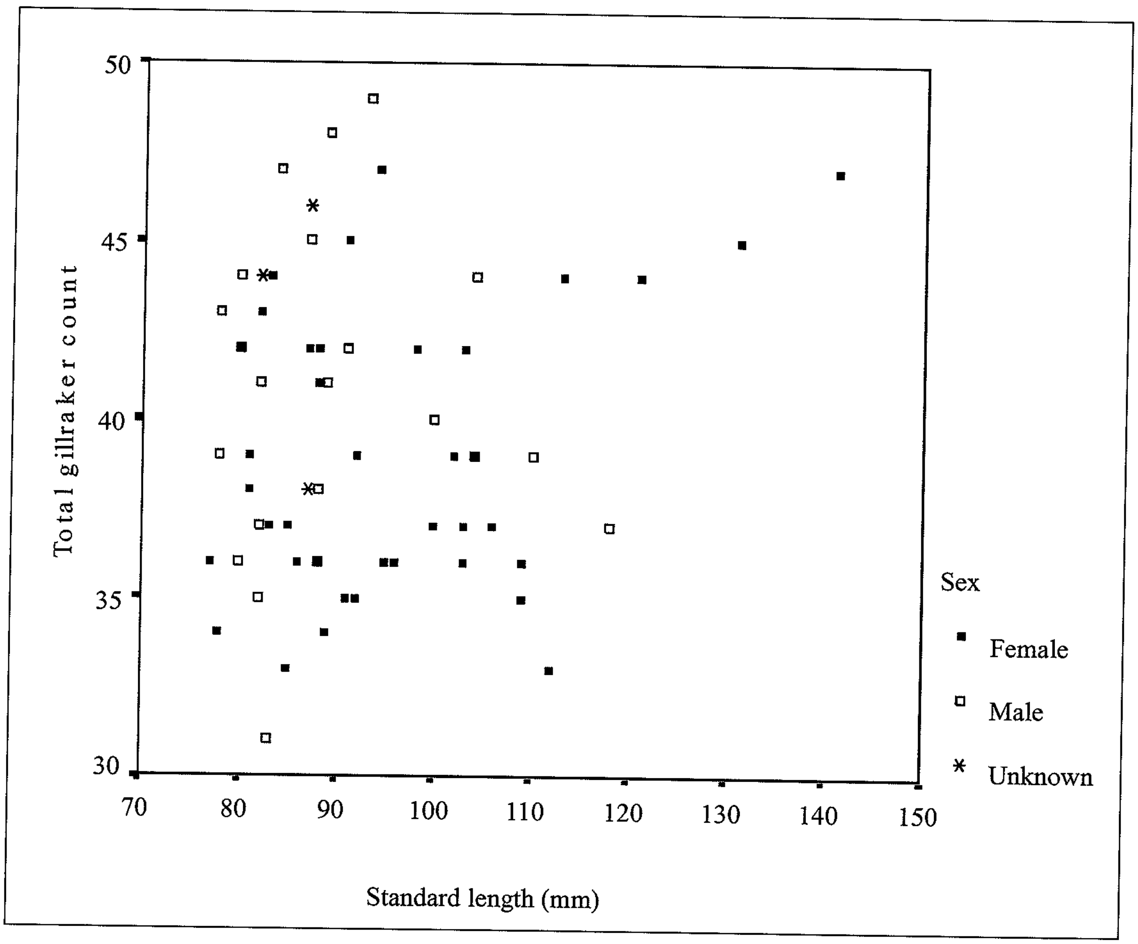


Figure 6.1. Relationship between standard length and gillraker count for Clearwater Lake with individuals identified by sex.

Discrimination of Cisco Forms

Discrimination of sympatric cisco forms was examined initially using gillraker count and arrangement (figures 6.2 and 6.3). There was some evidence of multiple forms being present based on gillraker count distribution with bimodality being found between 39 and 41 gillrakers with only one individual having 40 (Figure 6.2). Gillraker count distributions were examined for each collection site (Appendix 6-6). Gillraker arrangement varied among the ciscoes from Clearwater Lake with some individuals having shorter and more widely spaced gillrakers while others had longer, more tightly packed gillrakers (Figure 6.3). Other qualitative differences such as general body shape, dorsal colouration, and mouth morphology and orientation were examined for evidence of multiple forms being present. The general appearance of the Clearwater Lake ciscoes is shown in Figure 6.4. Some differences in dorsal colouration and head morphology were present between a few individuals; however, unlike the situation described for the other lakes, these differences were not consistent enough to easily define groups. Because groups could not be determined reliably using qualitative characters, the initial analysis included all ciscoes from Clearwater Lake combined into one group.

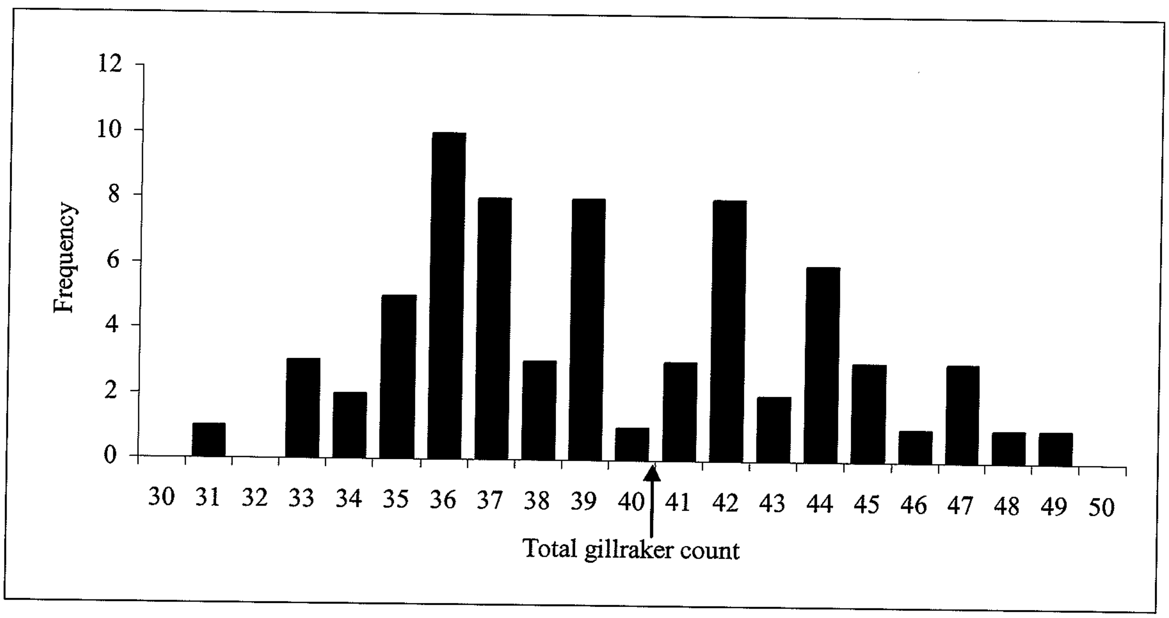


Figure 6.2. Frequency distribution of total gillraker counts for all ciscoes from Clearwater Lake.

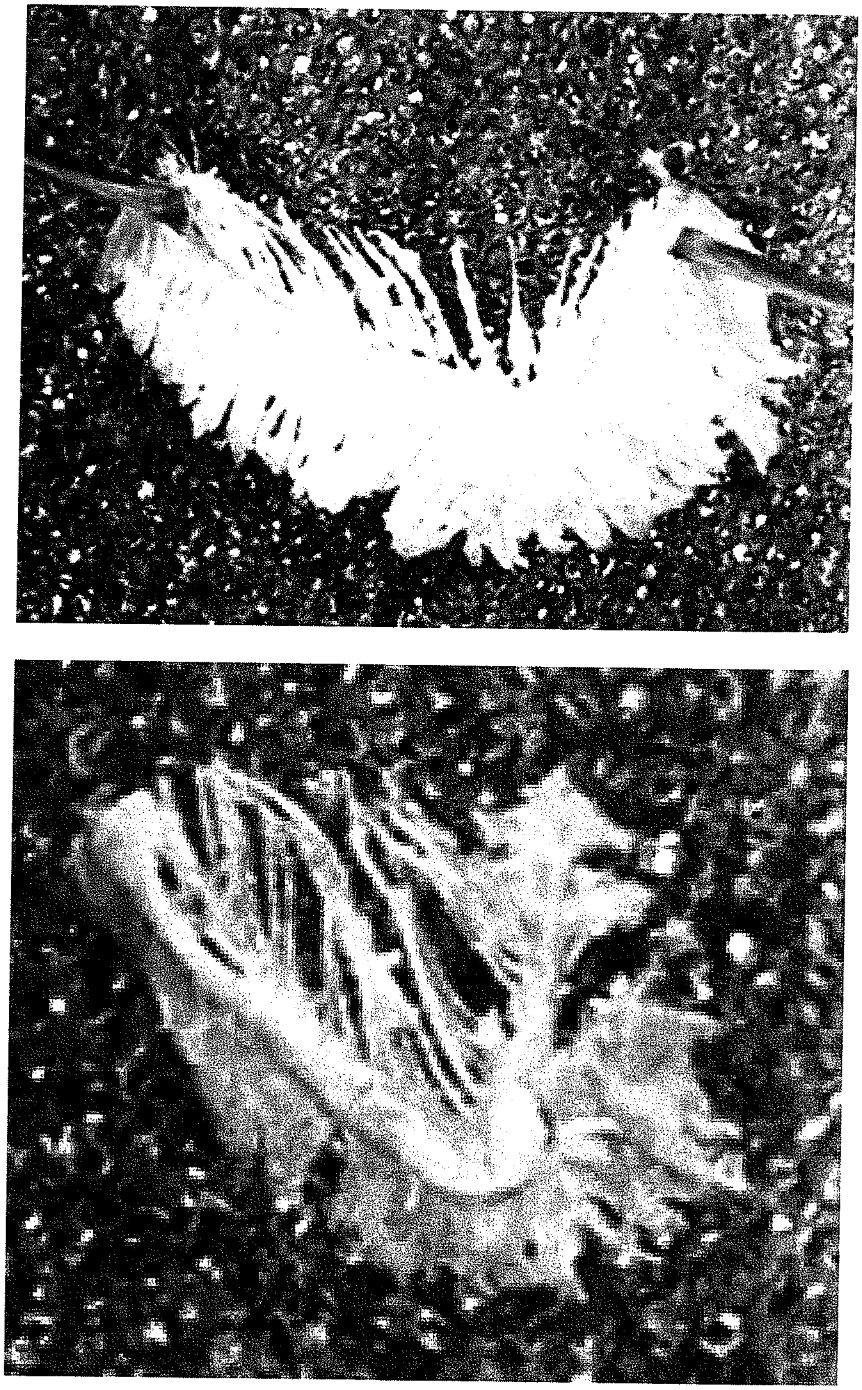


Figure 6.3. Gill arches excised from Clearwater Lake ciscoes. Upper panel shows typical gillraker structure of cisco with lower gillraker count and lower panel of cisco with higher gillraker count.

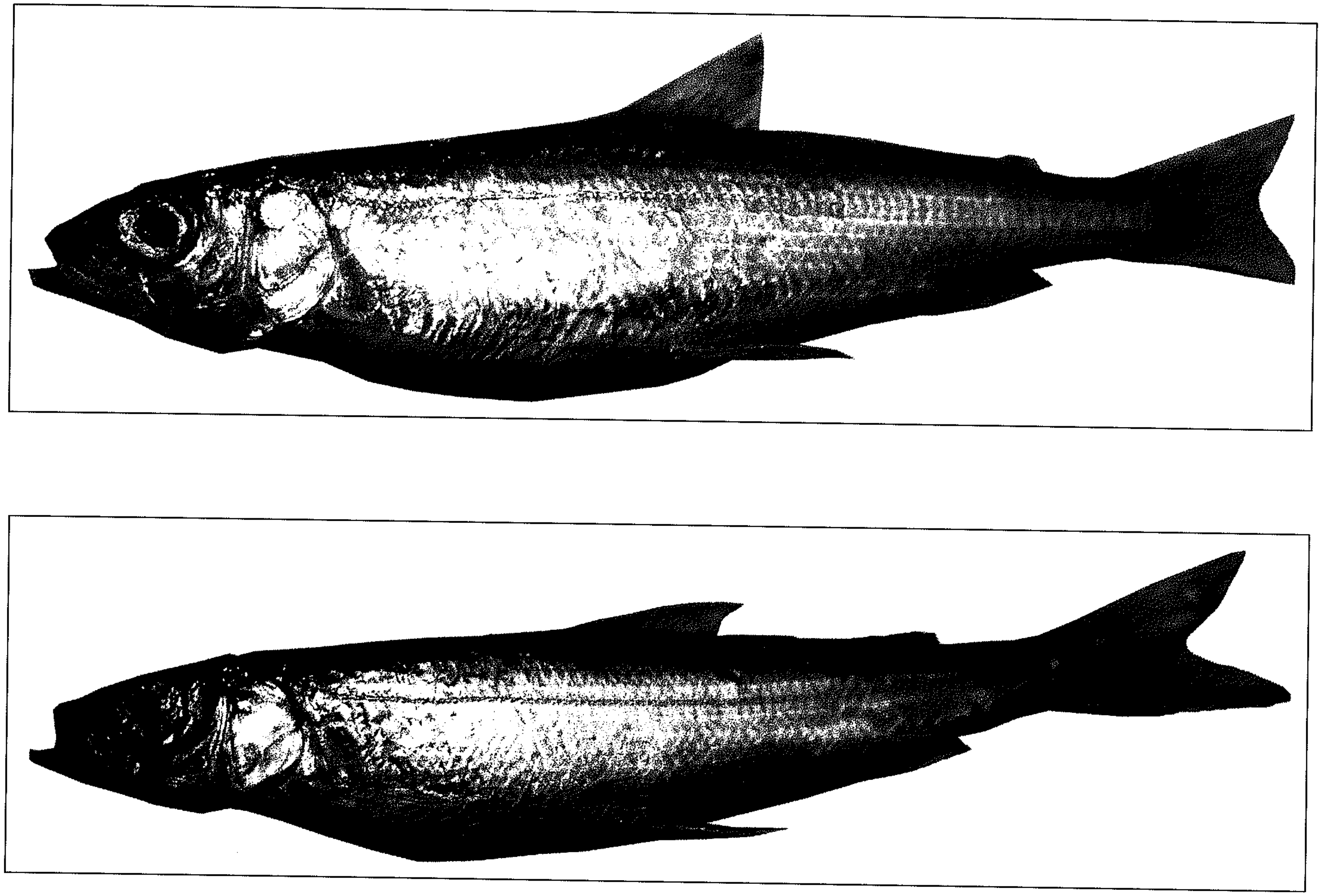


Figure 6.4. General appearance of Clearwater Lake ciscoes. The cisco in upper panel had a standard length of 113 mm and 36 gillrakers and was representative of the low form. The cisco in lower panel had a standard length of 91 mm and 42 gillrakers and was representative of the high form. (Note: previously frozen specimens).

Morphological Examination of Differences

An initial PCA was performed using the meristic characters along with premaxillary angle. This analysis was used as an exploratory method to determine if the meristic variables provided any evidence of multiple forms being present in the Clearwater Lake ciscoes. This PCA resulted in two potential forms being suggested (Figure 6.5). The first two components explained nearly 63% of the total variation and upper and lower gillraker counts accounted for most of the variation negatively and pectoral and dorsal ray counts accounted for most of the variation positively on component one (44.2 %). Component two (18.8 %) was influenced most by anal ray count and lower gillraker count (Table 6.1). One group consisted of all individuals with 40 or greater gillraker counts and the other group contained all individuals with 39 or fewer, with the exception of one fish. This cisco had a gillraker count of 39; however, it was found to group more closely with individuals with counts of 40 or more based on this PCA. An examination of the external appearance of this fish did not provide a clear indication of which form it should be placed into for further analysis.

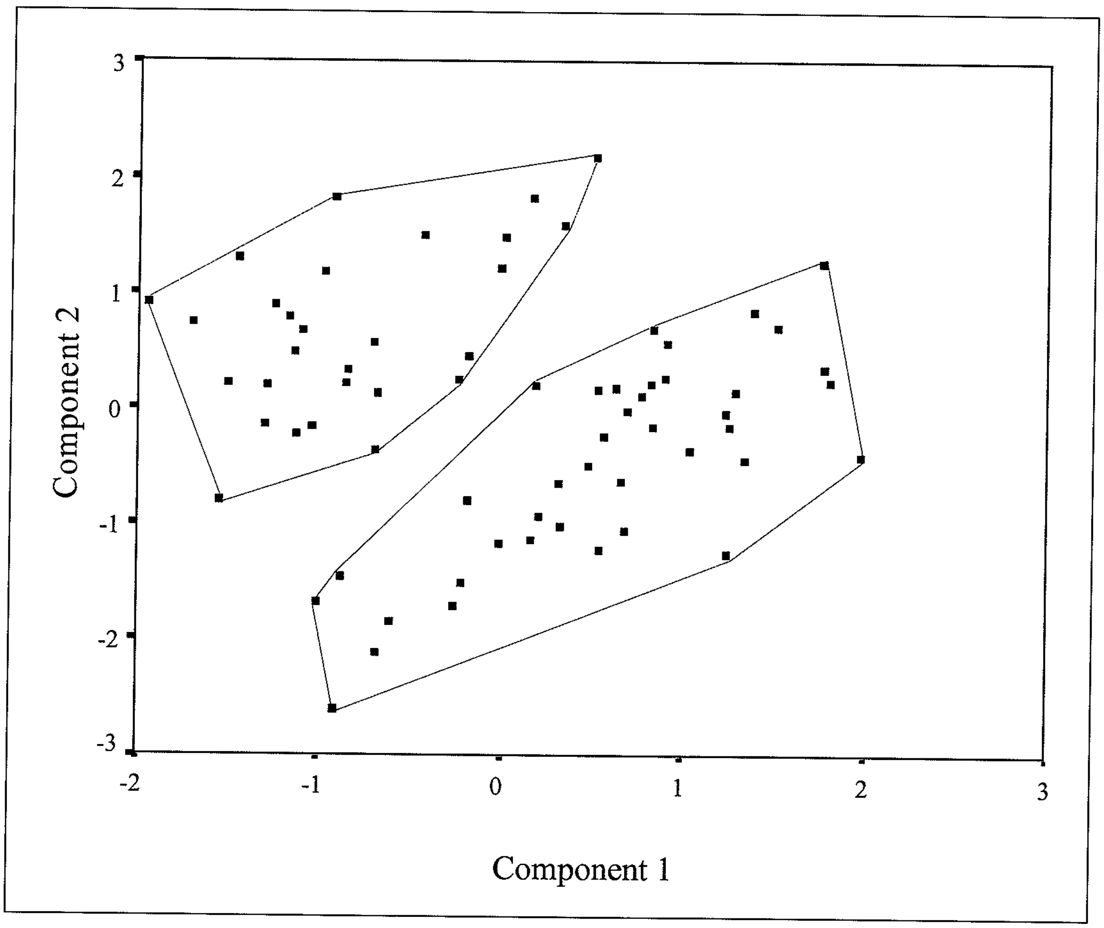


Figure 6.5. Plot scores on components 1 and 2 from PCA of ciscoes from Clearwater Lake using meristic characters including premaxillary angle. Two potential forms are suggested by the combined separation on components 1 and 2.

Table 6.1. Character loadings and variance explained by a PCA of Clearwater Lake ciscoes based upon meristic characters and premaxillary angle.

	Component 1	Component 2
Premaxillary angle	0.535	-0.483
Dorsal ray count	0.676	0.342
Anal ray count	0.469	0.550
Pectoral ray count	0.758	0.242
Pelvic ray count	0.592	0.441
Upper gillraker count	-0.811	0.337
Lower gillraker count	-0.741	0.542
Eigenvalues	3.09	1.31
Percent of Variance	44.20	18.76
Cumulative Percent	44.20	62.95

A PCA was performed on 19 morphometric characters adjusted to standardized ratios as described earlier. This PCA served as an exploratory analysis and as a means of testing the forms suggested by the PCA using meristic characters (predominantly gillraker counts). The forms suggested by the meristic PCA are referred to as Clearwater low and Clearwater high in subsequent discussions. When the scores from the first two components were plotted complete separation was present; however, the forms suggested by this PCA were different from those suggested by the meristic PCA. Component one revealed a large amount of separation between individuals with low gillraker counts and also grouped some individuals with low gillraker counts together with those with higher counts (Appendix 6-7). The highest loading variables on component one were dorsal length, preorbital length, maxillary length, body depth, and pectoral length (Appendix 6-8). Component two provided some separation between those individuals with high and low gillraker counts that were previously grouped together by component one. Although overlap was evident for component two, ciscoes with low-gillraker counts tented to score from zero to +2 while those with high-gillraker counts tended to score between zero and -2. The highest loading variables on component two were orbital length, head depth, lower arch length, and postorbital length (Appendix 6-8). The total amount of variation accounted for by component one was nearly 30 % and for component two it was 15.5 % (Appendix 6-8).

Individuals were identified by both sex and maturity *a posteriori* (results not shown) to examine any potential influence these factors may have had. Neither factor appeared to contribute to the distribution of the groups found by either of the PCAs. A PCA was also performed using both meristic and morphometric characters (adjusted by ratios); however, the results did not provide any information beyond that which was presented by the PCAs using only meristic or morphometric characters. Therefore, the results of the combined PCA are not presented here.

To remove the effects of body size, morphometric characters were adjusted using the common-within-groups method as described earlier. In order to do so, prior knowledge about suspected grouping structure is applied to the data set to determine the within-group variation. Because the PCA using meristic characters showed separation between individuals with low and high gillrakers and total gillraker count has historically been the key character used for identifying ciscoes, the groups suggested by this PCA were used to calculate the adjusted morphometric characters. These new morphometric characters were used in subsequent analyses.

The final PCA for Clearwater Lake was performed using the new adjusted morphometric values and premaxillary angle. Gillraker counts were not included because they were used to determine the common-within-group residuals for the 19 morphometric characters. The remaining meristic characters were not included in the analysis. Principal component one was a contrast between high positive loadings for dorsal length, preorbital length, maxillary length, and body depth and negative loadings for interorbital width and trunk length (Table 6.2). This component accounted for 28 % of the total variation. Principal component two was a contrast between high positive loadings for orbital length, lower arch length, head depth, and postorbital length and negative loadings for gillraker length and preorbital length (Table 6.2). Component two accounted for 16 % of the total variation. When the component scores were plotted and gillraker forms identified the results were similar to those found by the PCA using ratio-adjusted morphometric characters. Principal component one revealed separation between individuals with low-gillraker counts and grouped some individuals with low-gillraker counts along with those with high-gillraker counts (Figure 6.6). Component two; however, despite showing a large amount of overlap did provide some support for the initial groupings based primarily on gillraker count. The majority of ciscoes with low gillraker counts tended to score between -0.5 and +2 while the majority with high gillraker counts tended to score between zero and -2 (Figure 6.6, upper panel). Component two was plotted along with total gillraker count values to verify this (Figure 6.6, lower panel).

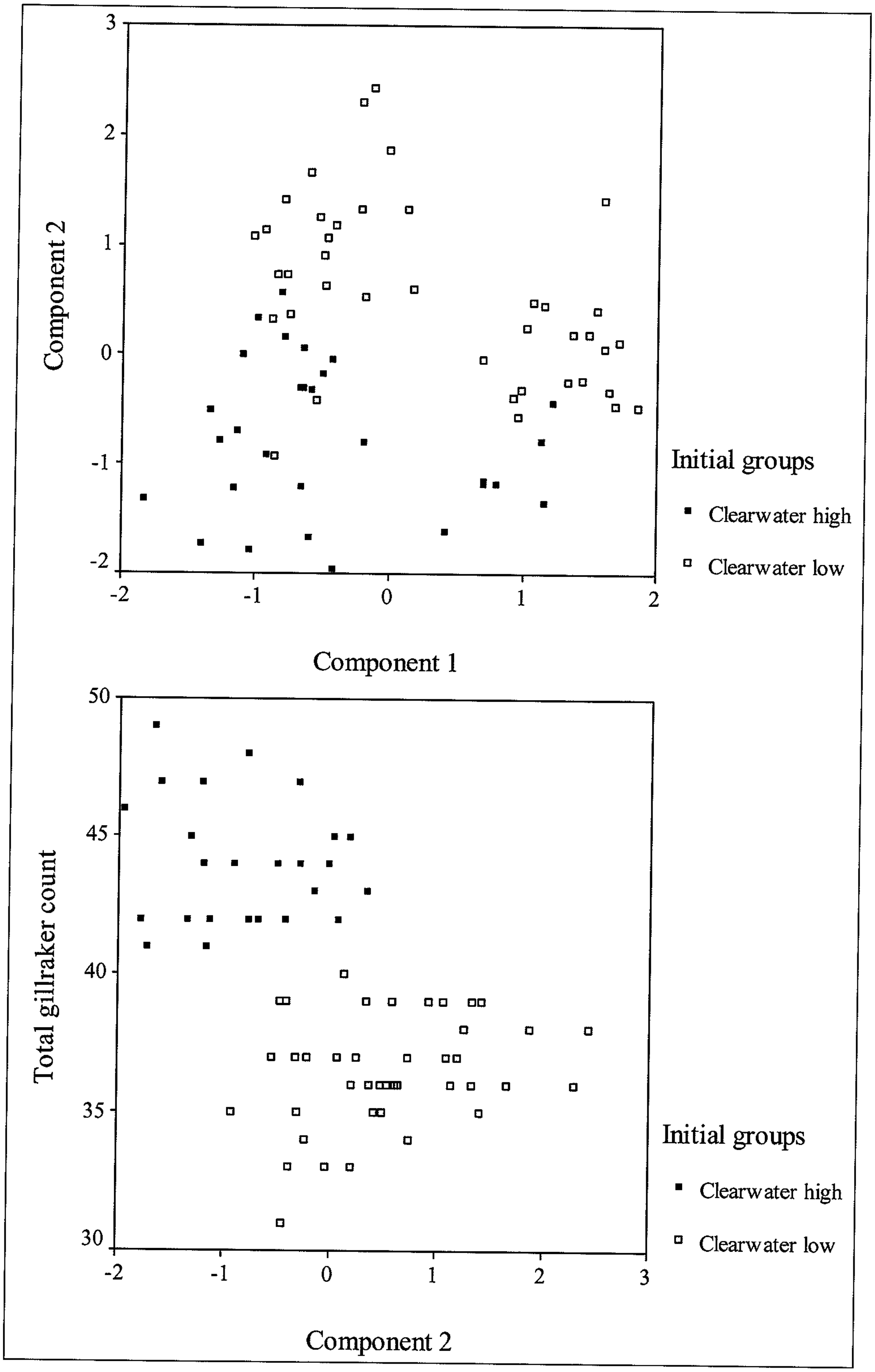


Figure 6.6. Plots of scores for the first two Principal Components using morphometric characters adjusted by common-within-group residuals (upper panel). Lower panel displays scores from Component 2 with total gillraker count. Forms were designated *a posteriori.*

Table 6.2. Character loadings and variance explained by PCA of Clearwater Lake ciscoes for morphometric characters adjusted with common-within-group residuals.

	Component	
	1	2
Premaxillary angle	0.38	0.55
Preorbital length	0.78	-0.34
Orbital length	-0.38	0.80
Postorbital length	-0.27	0.56
Trunk length	-0.40	0.16
Dorsal length	0.82	0.05
Lumbar length	-0.01	-0.08
Anal length	0.58	-0.07
Caudal peduncle length	-0.24	-0.21
Head depth	0.31	0.66
Body depth	0.72	0.38
Caudal peduncle depth	0.61	-0.18
Interorbital width	-0.58	0.45
Maxillary length	0.76	0.10
Maxillary width	0.38	0.01
Pectoral length	0.65	-0.04
Pelvic length	0.67	0.16
Adipose length	0.55	-0.07
Lower arch length	0.11	0.72
Gillraker length	-0.38	-0.55
Eigenvalues	5.57	3.13
Percent of Variance	27.85	15.63
Cumulative Percent	27.85	43.48

Hypothesis Testing of Form Differences

The next step was to examine whether the two forms suggested by the previous analyses were supported by statistical tests such as ANOVA and DA.

The results of the ANOVA testing mean differences of individual characters between Clearwater Lake forms (based on meristic PCA results) and the Levene's test of homogeneity of variance are presented in Table 6.3. All 26 meristic and morphometric characters were included in the analysis; however, common within-group adjusted residuals were used as the morphometric characters to adjust for the effects of body size. A total of seven of the 26 characters were found to be significant for the Levene's test of equality of variances (Table 6.3, $P<0.05$). Because some characters were found to violate the assumption of equality of variance required for the ANOVA, probability values were calculated for both situations where variances are assumed to be equal and not equal (Table 6.3). A total of 14 significant differences ($P<0.05$) were found between the two forms when equality of variance was assumed and 15 were found when equality was not assumed (Table 6.3). These results supported the presence of two forms within the Clearwater Lake ciscoes examined.

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*.

	Levene's test of Equality of Variance	Analysis of Variance	
		Variance Equal	Variance Not Equal
	Sig.	Sig.	Sig.
Premaxillary angle	0.068	**0.000**	**0.000**
Dorsal ray count	0.912	**0.013**	**0.009**
Anal ray count	0.189	0.654	0.636
Pectoral ray count	0.606	**0.002**	**0.001**
Pelvic ray count	0.288	0.242	0.242
Upper gillraker count	0.845	**0.000**	**0.000**
Lower gillraker count	0.572	**0.000**	**0.000**
Preorbital length	0.067	0.504	0.486
Orbital length	0.051	**0.003**	**0.002**
Post orbital length	0.873	0.088	0.095
Trunk length	**0.038**	0.174	0.213
Dorsal length	0.107	**0.005**	**0.003**
Lumbar length	0.100	0.404	0.428
Anal length	0.500	0.506	0.514
Caudal peduncle length	0.881	**0.002**	**0.002**
Head depth	0.431	**0.000**	**0.000**
Body depth	0.703	**0.000**	**0.000**
Caudal peduncle depth	0.692	0.931	0.930
Interorbital width	0.388	0.623	0.614
Maxillary length	**0.042**	**0.001**	**0.000**
Maxillary width	**0.035**	0.603	0.578
Pectoral length	0.443	0.912	0.914
Pelvic length	**0.025**	**0.022**	**0.035**
Adipose length	**0.002**	0.055	**0.036**
Gillraker length	**0.000**	**0.000**	**0.000**
Lower arch length	**0.000**	**0.000**	**0.000**

Discriminant Analysis (DA) was used as a quantitative test of all characters simultaneously to examine the hypothesis of equality of group means. Upper and lower gillrakers were not included in the character suite for this analysis because they were used to identify the forms tested here. A single discriminant function was calculated and the analysis indicated that the two forms were significantly different ($P<0.0001$, df=24). The correlation of each character to the function is presented in Table 6.4. The best discriminating characters were lower arch length, gillraker length, pectoral length, maxillary length, head depth, and premaxillary angle. A plot of the discriminant scores showed separation supporting the presence of two forms (Figure 6.7). *A posteriori* classification results showed that 97.1 % of the original grouped cases were correctly classified by the DA (Table 6.4). Only one member of each form was misclassified. Although the evidence supports the rejection of the null hypothesis that the two forms are the same, it should be noted that the statistical significance of this test is diminished due to the lack of homogeneity of variance for several of the characters.

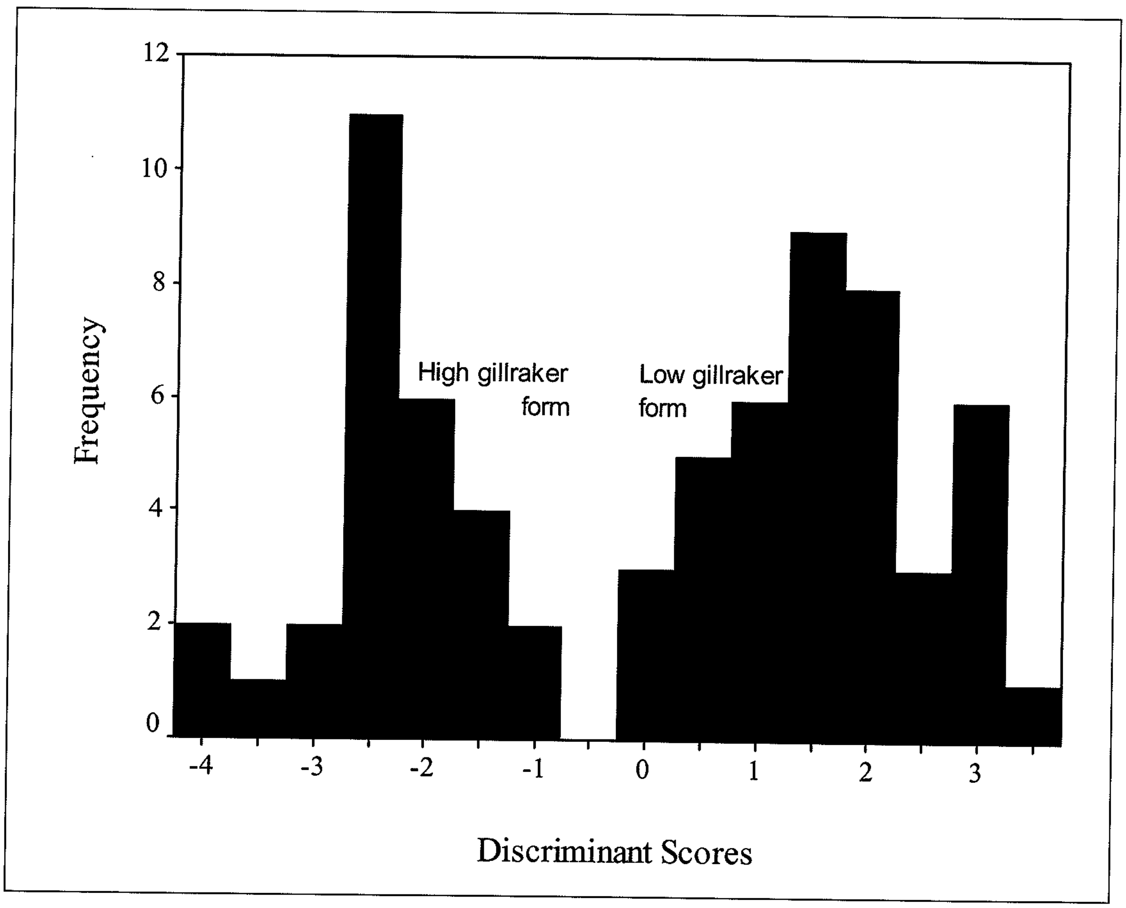


Figure 6.7. Frequency plot of discriminant scores from DA of Clearwater Lake ciscoes using morphometric characters adjusted by common-within-group residuals.

Table 6.4. Discriminant Analysis results for Clearwater Lake cisco forms using morphometric characters adjusted by common-within-groups residuals.

Standardized Canonical Discriminant Function Coefficients

	Function 1
Premaxillary angle	0.52
Dorsal ray count	0.21
Anal ray count	-0.15
Pectoral ray count	0.10
Pelvic ray count	0.07
Preorbital length	-0.17
Orbital length	-0.07
Postorbital length	0.36
Trunk length	-0.25
Dorsal length	0.07
Lumbar length	-0.36
Anal length	-0.22
Caudal peduncle length	-0.50
Head depth	0.57
Body depth	0.19
Caudal peduncle depth	-0.14
Interorbital width	-0.12
Maxillary length	0.57
Maxillary width	-0.43
Pectoral length	-0.66
Pelvic length	0.08
Adipose length	0.47
Lower arch length	1.02
Gillraker length	0.73
Eigenvalue	3.62
Percent of Variance	100
Cumulative Percent	100
Canonical Correlation	0.89

Classification Results

	Predicted Group Membership		
Initial groups	Low	High	Total
Clearwater low	40	1	41
Clearwater high	1	27	28

97.1% of original grouped cases correctly classified.

Summary of Clearwater Lake Cisco Forms

The presence of sympatric cisco forms in Clearwater Lake is supported by the results of this study. Gillraker count and arrangement, jaw position, and dorsal colouration were not as effective initially for identifying cisco forms in Clearwater Lake as they were for the other lakes included in this study. The gillraker count distribution showed overlap between forms and individuals in the overlap range could not all be placed into forms effectively using other characters including dorsal colouration, jaw position, and gillraker arrangement. The meristic PCA results suggested the presence of two cisco forms. These forms were only partially supported by the PCA using ratio-adjusted morphometric characters. The PCA using common-within-group adjusted morphometric characters did support the forms identified by the meristic PCA. The Anova and DA results supported the presence of multiple forms in Clearwater Lake.

Two cisco forms were collected from Clearwater Lake in this study, a low gillraker form and a high gillraker form. The majority of ciscoes were found to be immature, however, larger, mature specimens of either form could potentially be collected from the lake.

1. Total gillraker count of 37 or fewer on first gill arch, gillrakers short and widely spaced.. Low gillraker form

   Total gillraker count 41 or greater on first gill arch, gillrakers long and tightly packed ....High gillraker form

   Total gillraker count 38 to 40..2

2. Premaxillary angle usually greater than 45°, downward jaw appearance, tan to brown dorsal colouration. .... Low form

   Premaxillary angle usually greater than 45°, upward jaw appearance, greenish blue to black dorsal colouration .... High form

This key is a guide based on specimens collected and examined from Clearwater Lake by the author. This key may not account for some of the cisco variability found within Clearwater Lake. See discussion for taxonomic conclusions regarding the low and high gillraker forms identified in this study.

7. RESULTS - EXAMINATION OF BETWEEN-LAKE CISCO VARIATION

The cisco forms identified in the previous sections of this study were examined here for similarities and differences in characters across all lakes. The key questions addressed here were: 1) are the low and high gillraker forms identified from each lake equivalent to similar forms across all the lakes, and 2) what is the possible taxonomic identity of those forms? To address the first question the values of several taxonomically key characters were compared across all forms. The mean values for all characters were then compared between all forms using an Anova. Forms were compared multivariately using several different analyses including PCA, DA, and Cluster Analysis (CA). The latter question was addressed by comparing key characters from the forms identified in this study to known *C. zenithicus* specimens collected from Lake Superior in 1996 and Lake Nipigon in 1973, and to values for *C. zenithicus* reported in the literature.

Comparison of Key Characters

The initial comparison of the cisco forms was done using several key characters that have frequently been used to discriminate between *C. zenithicus* and *C. artedi* (Dymond 1943, Clarke 1973, Scott and Crossman 1973, Houston 1988, Steinhilber et al. 2002, Todd and Steinhilber 2002, Todd 2003). These included qualitative characters such as dorsal colouration, jaw position, and gillraker arrangement, along with quantitative characters including total gillraker count, gillraker length (in this case middle gillraker length), lower gill arch length, upper jaw or maxillary length, and premaxillary angle (Table 7.1). Several other morphometric characters that have been shown to differ between *C.*

zenithicus and *C. artedi*, although not as consistently, were compared including body depth, dorsal fin base length, head depth, eye diameter, and snout length (Table 7.2). The morphometric character values used in this comparison were ratios of the character against the standard length of the individuals to adjust for the differences in body size.

The gillraker ranges for the low forms identified in this study were found to overlap between lakes; but two of the low forms, Lake Athapapuskow and Reindeer Lake, had extremely low gillraker counts for some individuals. Lake Athapapuskow in particular was found to have a wide range in total gillraker counts (20 to 37) for the low form and 36 to 47 for the high form. The mean values for the low forms (and mid form from Reindeer Lake) were similar for some lakes but different between some others. Lake Athapapuskow and Reindeer Lake low forms had values of 28 while George Lake, Clearwater Lake, and Reindeer Lake mid forms had values ranging from 34 to 36.5. All of the high forms were found to have similar gillraker count ranges and mean values ranging from 39 to 49 for most locations except for Lake Athapapuskow where the high form ranged from 36 to 47. The middle gillraker length was found to be fairly consistent among the low and mid forms with the low forms from George and Reindeer lakes having the lowest mean values of the group and none of the forms having values above 3.8. The high forms from each lake were found to have higher mean gillraker length values. The Lake Athapapuskow, George Lake, and Reindeer Lake high forms ranged between 4.2 and 4.4 while the high form from Clearwater Lake had a value of 6.7. Gillraker arrangement tended to be a consistent qualitative character when comparing within forms. The low forms were found to have shorter and more widely spaced gillrakers than the high forms; however, variability in gillraker length within forms was present even within the same water body. The high forms had longer, more tightly spaced gillrakers.

Some similarities within forms were apparent based on an examination of qualitative characters. The low forms (including the Reindeer mid form) across all lakes tended to have lighter dorsal colouration than the high forms, usually ranging in colour from yellow to tan for the low forms and greenish blue to black for the high forms. Jaw position also tended to be consistent within forms across all lakes. In the low forms, the jaw position tended to be inferior giving a downward appearance to their mouths. The lower jaws were usually slightly shorter than or equal to the upper jaws for most members of the low form, with the exception of some individuals from Reindeer Lake, which had slightly longer lower jaws but still maintained a downward appearance to the jaws. The majority of the high forms from all lakes tended to have longer lower jaws than upper jaws giving their mouths a superior or upward appearance.

Other characters compared between these forms in Table 7.1 were more variable. Lower arch lengths were found to be slightly larger for the low forms when compared to their sympatric high forms; however, when all forms were compared the values for some low forms were found to be less than those for some high forms from different water bodies (Table 7.1). The mean maxillary length values were higher for all but one of the low forms (Clearwater low) while premaxillary angle mean values were larger for all of the low forms (Table 7.1).

Mean body depth values were higher for the low forms with the exception of the Reindeer high form, which was similar in depth to the low and mid forms from the same lake and to the low form from Clearwater Lake (Table 7.2). With the exception of the low form from Clearwater Lake, the snout length mean values tended to be greater for the low forms (Table 7.2). The mean values for the other key characters compared between the forms for all lakes were not found to be consistent within the forms (Table 7.2).

Table 7.1. Comparison of key character values for cisco forms identified in this study including known *C. zenithicus* specimens from Lake Superior and Lake Nipigon.

	Total gillraker count			**Middle gillraker length**[1]		**Lower arch length**[1]		**Maxillary length**[1]		**Premaxillary angle**	
	range	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**
Athapap. low (n = 71)	20 - 37	28.8	3.84	3.2	0.47	11.1	1.35	8.8	0.73	48.4	5.84
Clearwater low (n = 41)	31 - 40	36.5	2.03	3.7	1.57	11.8	1.82	8.4	0.98	52.9	6.12
George low (n = 70)	30 - 39	33.9	1.77	2.2	0.49	11.3	1.13	9.2	0.62	49.4	5.10
Reindeer low (n = 228)	23 - 32	28.2	1.76	2.5	0.52	12.0	0.80	8.8	0.77	51.3	5.66
Reindeer mid (n = 73)	33 - 38	35.5	2.92	3.8	0.57	12.9	1.10	9.9	0.78	46.8	6.26
Superior (n = 30)	38 - 44	40.7	1.51	3.5	0.55	10.4	0.66	9.2	0.48	50.5	6.34
Nipigon (n = 8)	33 - 37	34.9	1.46	3.7	0.19	10.0	0.77	9.0	0.49	55.0	10.00
Athapap. high (n = 121)	36 - 47	40.1	1.98	4.4	0.63	9.8	0.93	8.2	0.63	42.4	5.96
Clearwater high (n = 28)	41 - 49	43.9	2.24	6.7	3.70	8.9	3.61	7.9	0.83	44.1	4.72
George high (n = 39)	39 - 45	41.8	1.40	4.3	0.56	11.2	0.95	7.8	0.99	41.8	4.51
Reindeer high (n = 74)	39 - 48	41.5	2.34	4.2	0.56	11.6	1.39	8.7	0.67	40.2	6.05

[1]Values represented are ratios of character measurement with standard length.
st. dev. = standard deviation.

Table 7.2. Comparison of character values for cisco forms identified in this study including known *C. zenithicus* specimens from Lake Superior and Lake Nipigon.

	Body depth[1]		Dorsal fin base length[1]		Head depth[1]		Eye diameter[1]		Snout length[1]	
	mean	st. dev.	mean	st. dev.	mean	st. dev.	mean	st. dev.	mean	st. dev.
Athapap. low (n = 71)	24.1	1.93	10.7	1.23	11.7	0.89	6.5	0.45	7.1	0.42
Clearwater low (n = 41)	20.4	2.29	10.4	1.70	12.3	0.88	8.6	1.13	5.2	1.07
George low (n = 70)	23.2	2.05	10.2	0.86	11.6	0.69	6.9	0.49	6.4	0.62
Reindeer low (n = 228)	20.4	1.61	9.7	0.82	10.4	0.75	6.4	0.51	6.9	0.51
Reindeer mid (n = 73)	20.5	1.72	10.2	0.89	11.8	0.99	6.8	0.48	7.3	0.63
Superior (n = 30)	23.4	1.56	10.7	0.57	10.8	0.70	7.2	9.59	6.3	0.48
Nipigon (n = 8)	26.7	2.10	10.5	0.78	11.2	0.41	4.9	0.36	6.1	0.28
Athapap. high (n = 121)	19.7	1.72	11.3	1.23	11.6	0.79	6.4	0.53	6.9	0.48
Clearwater high (n = 28)	18.0	2.08	9.4	1.40	11.4	0.92	7.9	0.77	5.1	0.85
George high (n = 39)	17.8	1.76	9.4	0.88	11.2	0.82	6.9	1.12	5.5	1.39
Reindeer high (n = 74)	20.5	2.67	10.4	1.15	11.1	0.79	6.9	0.59	6.8	0.68

[1]Values represented are ratios of character measurement with standard length.
st. dev. = standard deviation.

Multivariate Test of Equality of Cisco Forms

The next step in the comparison of forms between lakes was to examine if parallel forms exist. This question was addressed by examining whether like-forms were equivalent to one another in multivariate space (i.e., all low forms overlap with one another and all high forms overlap with one another. To examine this, two PCA's were performed, one using all characters including upper and lower gillrakers, and one using morphometric characters adjusted by common-within-group residuals.

The first PCA resulted in considerable overlap of similar forms when the scores for components one and two were plotted (Figure 7.1). All of the low forms tended to occupy the same multivariate space with only a few individuals overlapping with some of the high forms. All of the high forms also tended to occupy the same multivariate space, with near complete separation from the low forms. The majority of individuals identified as Reindeer mid forms grouped closer to the low forms; however, several others grouped more closely with the high forms. The characters that accounted for most of the variance on component one (15 %) were upper and lower gillraker counts, gillraker length, pectoral and pelvic fin lengths, and premaxillary angle which was negatively loaded (Table 7.3). The characters with the highest loadings on component two (13 %) were maxillary length, body depth, postorbital length, lower arch length, and premaxillary angle positively, and upper and lower gillraker count, and gillraker length negatively (Table 7.3). None of the other components contributed to the identification of forms.

The multivariate pattern displayed by this analysis reflected that seen when each lake was examined individually. The low forms identified from each lake were found to group more closely to each other than to their sympatric high forms in multivariate space. The PCA results found that the low forms tended to have low gillraker counts, short gillraker lengths, large premaxillary angles, long maxillaries, and deep bodies (Figure 7.1, Table 7.3). The high forms alternatively tended to have high gillraker counts, long gillrakers, small premaxillary angles, short maxillaries, and shallow bodies (Figure 7.1, Table 7.3). The mid form from Reindeer Lake was noted as having longer paired fins than the other forms, and the influence of these characters on component one likely accounted for most of the separation between the mid form and the low forms (Figure 7.1, Table 7.3).

Table 7.3. Character loadings and variance explained by PCA on all cisco forms using meristic and morphometric characters adjusted by ratios.

	Component				
	1	2	3	4	5
Premaxillary angle	-0.46	0.46	0.12	0.08	-0.02
Dorsal ray count	0.11	0.25	0.29	0.46	0.13
Anal ray count	0.21	-0.01	0.41	0.39	0.12
Pectoral ray count	-0.01	0.11	0.31	0.41	0.10
Pelvic ray count	0.04	0.02	0.37	0.36	-0.05
Upper gillraker count	0.64	-0.56	-0.02	0.01	0.19
Lower gillraker count	0.69	-0.54	-0.09	-0.03	0.12
Preorbital length	0.21	0.47	-0.13	-0.17	-0.31
Orbital length	0.42	0.20	-0.37	0.28	0.31
Post orbital length	0.01	0.58	-0.21	0.17	0.02
Trunk length	-0.29	-0.05	0.10	-0.46	0.28
Dorsal length	0.46	0.19	0.25	0.05	-0.44
Lumbar length	-0.42	0.12	-0.02	-0.11	0.55
Anal length	0.51	-0.06	0.37	-0.06	-0.41
Caudal peduncle length	-0.18	-0.07	-0.24	-0.06	-0.40
Head depth	0.47	0.36	-0.42	0.10	0.10
Body depth	0.02	0.63	0.28	-0.25	0.17
Caudal peduncle depth	0.43	0.34	0.12	-0.45	-0.04
Interorbital width	0.45	0.14	-0.41	-0.07	0.04
Maxillary length	0.23	0.63	-0.24	0.15	-0.11
Maxillary width	0.24	0.06	-0.12	-0.09	-0.13
Pectoral length	0.55	0.32	0.32	-0.19	0.27
Pelvic length	0.52	0.32	0.33	-0.24	0.27
Adipose length	0.19	0.35	0.18	-0.17	-0.11
Lower arch length	0.12	0.52	-0.34	0.21	0.07
Gillraker length	0.68	-0.46	-0.10	0.05	0.09
Eigenvalues	3.97	3.42	1.84	1.52	1.42
Percent of Variance	15.25	13.15	7.09	5.86	5.46
Cumulative Percent	15.25	28.40	35.49	41.34	46.81

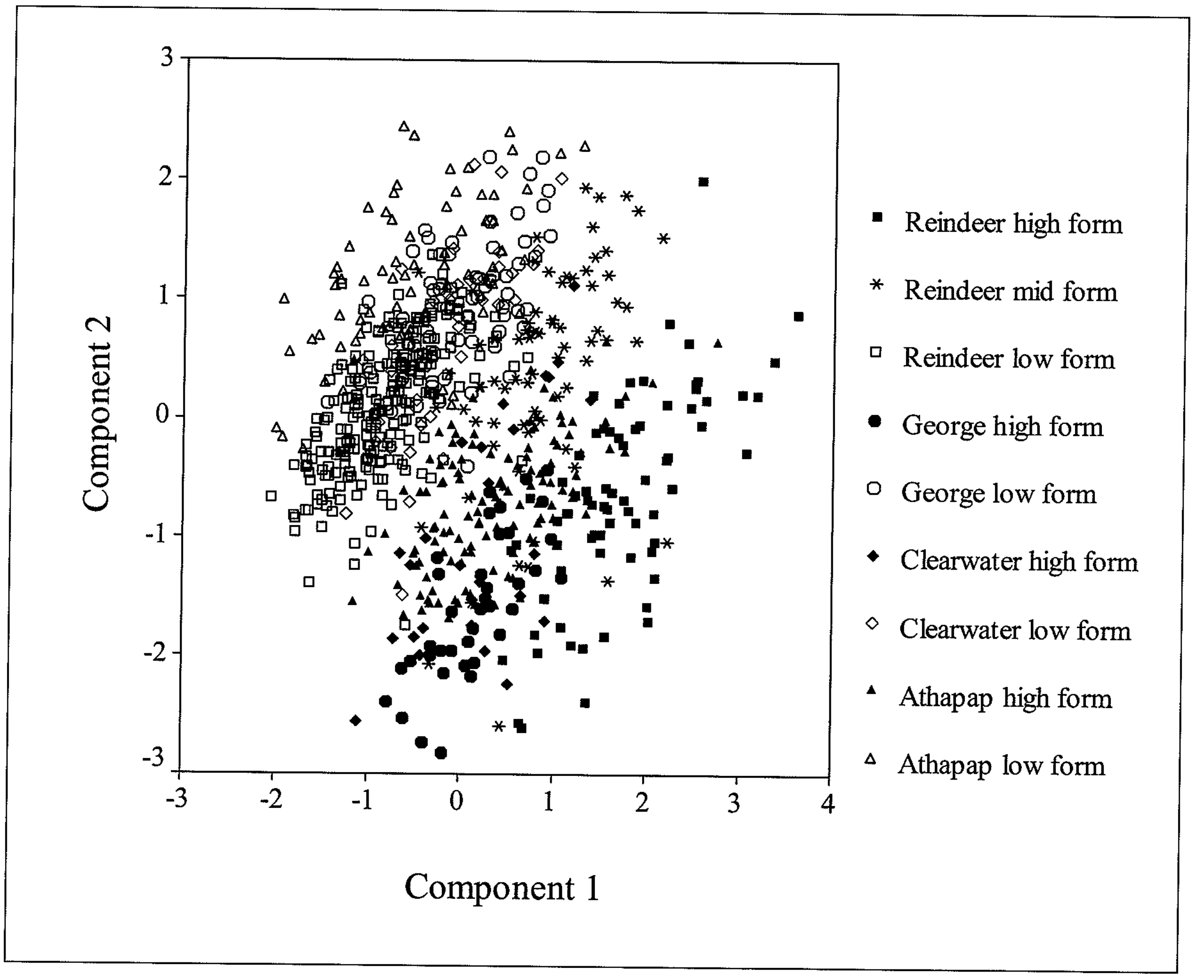


Figure 7.1. Plot of scores from PCA of all cisco forms using meristic characters and morphometric characters adjusted by ratios. Forms were designated *a posteriori.*

The next PCA was performed using only morphometric characters adjusted by the common-within-group residual method. Gillraker counts were not included in this analysis because they were integral for the identification of the forms, which were used to calculate the common-within-group residuals for this analysis.

This PCA resulted in some overlap of similar forms when the scores for components one and two were plotted; however, there was more overlap between the high and low forms for this analysis than in the previous PCA (Figure 7.2). Most of the low forms (including the Reindeer mid form) tended to occupy the same multivariate space along component one with the majority of individuals having scores ranging from – 0.5 to 1.5 (Figure 7.2). Most of the high forms were found to range between – 2 and – 0.5 along component one with the exception of the Clearwater Lake high form which ranged from – 2 to –4 (Figure 7.2). It is interesting to note also that the Reindeer Lake high form overlapped considerably with some of members of the low forms from George Lake and Lake Athapapuskow (Figure 7.2). Component one accounted for almost 21 % of the total variance within the data set (Table 7.4). The characters that contributed most to this component were maxillary length, lower arch length, and preorbital length positively and gillraker length and trunk length negatively (Table 7.4). Component two accounted for more variation within like-forms than between unlike-forms (Table 7.4). This component accounted for 15 % of the variation in the data set and the characters with the highest loadings were caudal peduncle depth, interorbital width, body depth, pelvic length, and head depth (Table 7.4). Component three provided slightly better within-form association than component two did when plotted (Figure 7.2). This component accounted for 8 % of the variation with lumbar length and orbital length having the highest positive loadings, and anal length and dorsal length the high negative loadings (Table 7.4).

The low forms identified from each lake were found to group more closely to each other than to their sympatric high forms along component one but the overlap between low and high forms was greater for this analysis (Figure 7.2). The low forms (including the Reindeer mid form) were found to have long maxillaries, long gill arches, long snouts (preorbital length), and short gillrakers (Figure 7.2, Table 7.4). The high forms tended to have short maxillaries, short gill arches, short snouts, and long gillrakers (Figure 7.2, Table 7.4).

Table 7.4. Character loadings and variance explained by PCA on all cisco forms using morphometric characters adjusted by common-within-group residuals.

	Component				
	1	2	3	4	5
Preorbital length	0.74	-0.19	-0.23	0.06	0.07
Orbital length	0.28	-0.29	0.49	-0.32	0.22
Post orbital length	0.58	-0.05	0.13	0.04	0.36
Trunk length	-0.45	0.27	0.11	-0.15	-0.14
Dorsal length	0.22	0.37	-0.38	-0.58	-0.04
Lumbar length	-0.18	-0.17	0.64	0.24	-0.04
Anal length	0.45	0.32	-0.52	0.07	-0.27
Caudal peduncle length	0.16	-0.29	-0.19	0.68	0.11
Head depth	0.30	0.43	0.09	-0.27	0.56
Body depth	0.12	0.66	0.19	-0.05	-0.05
Caudal peduncle depth	0.03	0.75	0.17	0.11	0.00
Interorbital width	-0.22	0.68	-0.05	0.12	0.47
Maxillary length	0.81	-0.20	0.00	0.04	0.18
Maxillary width	0.14	0.36	-0.01	0.46	0.29
Pectoral length	0.62	0.27	0.28	0.05	-0.38
Pelvic length	0.44	0.50	0.32	0.10	-0.43
Adipose length	0.38	0.31	-0.08	0.30	-0.15
Lower arch length	0.79	-0.27	0.06	-0.14	0.05
Gillraker length	-0.56	0.18	-0.12	0.14	0.16
Eigenvalues	3.95	2.89	1.48	1.44	1.33
Percent of Variance	20.80	15.23	7.78	7.58	6.98
Cumulative Percent	20.80	36.04	43.81	51.39	58.37

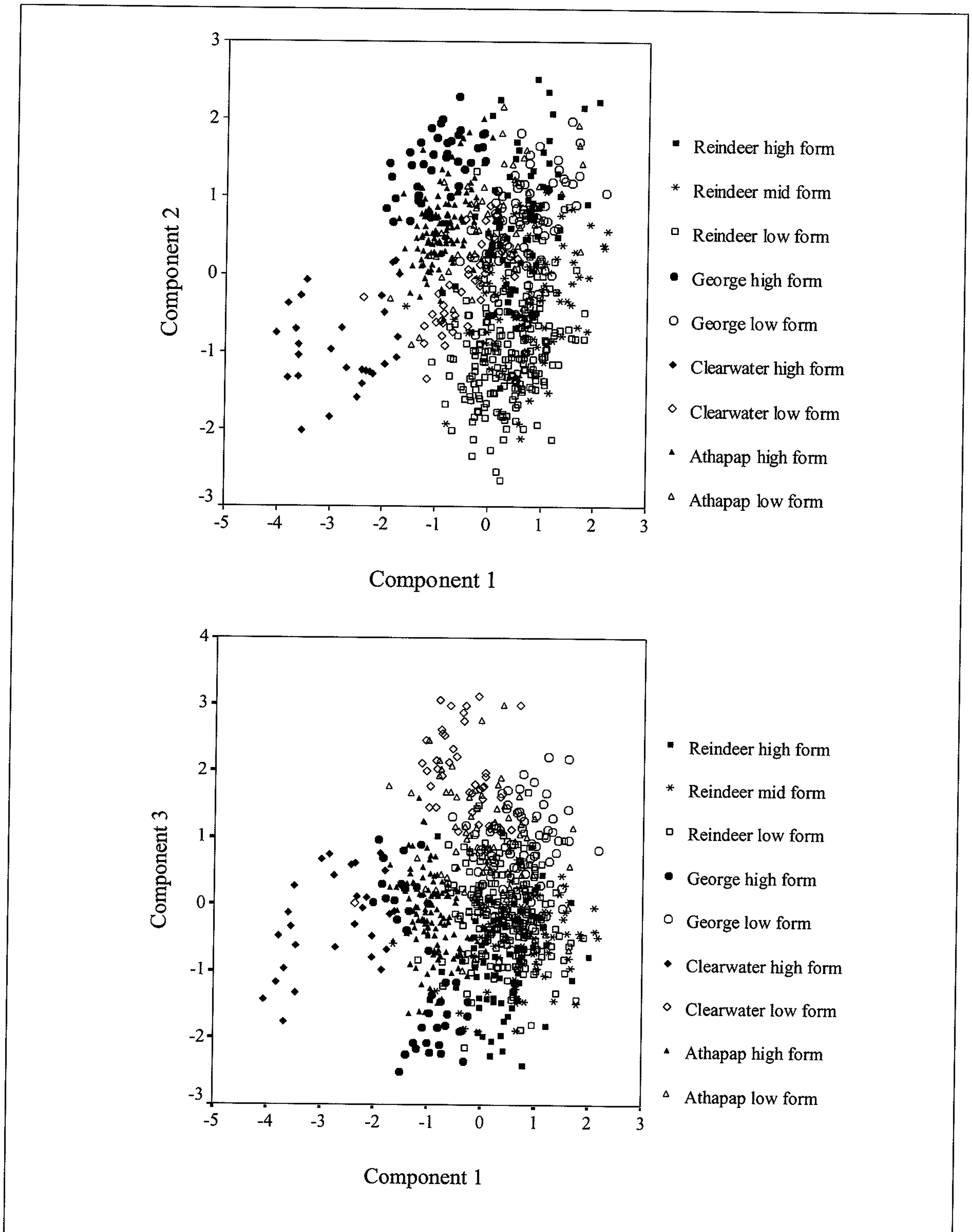


Figure 7.2. Plot of scores from PCA of Manitoba cisco forms using morphometric characters adjusted by common-within-group residuals. Upper panel shows components one and two, lower panel one and three.

The next step in testing whether parallel forms exist between lakes was to perform an ANOVA. This method tests the statistical validity of the forms previously identified. An ANOVA has certain assumptions that must be met in order for the test to statistically valid. One of these assumptions is that the variances are homogeneous. This was tested using Levene's test of homogeneity of variance and most characters failed, indicating heterogeneity (Appendix 7-1). The sample sizes of the forms being compared in this study were imbalanced causing this heteroescasdicity. To account for this a robust *a posteriori* test of pairwise differences was used to determine which characters differ and how many in total differ between forms. The Games-Howell test was used because it is a liberal pairwise comparison test that assumes that the variances are not equal.

With the exception of pectoral ray count, all characters were found to be significantly different for the overall ANOVA indicating only that differences exist between the forms (Appendix 7-1). However, the assumptions of the ANOVA were violated so the results of the post hoc test assuming inequality of variances should be more informative. The mean differences of the pairwise comparison are presented in Appendix 7-2 with the bold values indicating that they are statistically significant ($P<0.05$). Most of the fin ray counts were found to be similar across low and high forms. Upper and lower gillraker counts were significantly different between most forms including some similar forms from different lakes. Premaxillary angle, orbital length, and preorbital length were found to be consistent between similar forms while other characters including body depth, maxillary length, lower arch length, and gillraker length were significantly different for most forms including some similar forms from different lakes (Appendix 7-2). A summary of the total number of significant mean differences between all forms is presented in Figure 7.3. These results support in most instances that the groups present within the same lake are more different from each other than they are from similar forms in different lakes. The Lake Athapapuskow low form was found to have fewer mean differences with the George Lake, Clearwater Lake, and Reindeer Lake low and mid forms than with the sympatric Lake Athapapuskow high form. However, some low forms were found to have fewer mean differences with some high forms from different lakes than with some of the low forms from different lakes.

	Athapap low	Athapap high	Clearwater low	Clearwater high	George low	George high	Reindeer low	Reindeer mid
Athapap high form	15							
Clearwater low form	10	13						
Clearwater high form	18	16	19					
George low form	10	14	13	20				
George high form	17	14	16	11	18			
Reindeer low form	14	17	10	18	11	18		
Reindeer mid form	14	11	18	18	15	20	11	
Reindeer high form	11	16	14	19	11	17	18	16

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 significant between cisco forms across all lakes ($P<0.05$).

The final test of the statistical validity of the forms identified in this study was a Discriminant Analysis using all morphometric characters (adjusted by common-within-group residuals) and premaxillary angle. Upper and lower gillraker counts were not included in this analysis because they were the classification characters used to calculate the adjusted morphometric characters. A DA uses pre-determined groups and multiple characters to calculate discriminant functions that maximize the separation among the groups relative to the within-group variation (Reyment et al. 1984). A DA, like the Anova, has certain assumptions that should be met. One of these is variance homogeneity, which this data set was found to violate as previously noted in the Anova section above. Because of this violation the interpretability of the results presented here for the DA is reduced.

The functions calculated by the DA are presented in Table 7.5 (only the first five are presented here). Function one account for 44 % of the variation between forms while function two only accounted for 16 % and function three 15 % (Table 7.5). When these functions were plotted it was found that most of the low forms had similar discriminant scores along the first function ranging from 0 to 4 (Figure 7.4). Likewise, the high forms had similar discriminant scores along this function ranging from –6 to –1; however, some individuals identified as Clearwater Lake high form were found to have even lower scores ranging from –10 to –8 (Figure 7.4). Function two accounted for more variation within similar forms than between dissimilar forms; however, much of the variability was probably due to the Clearwater Lake high form. This form was found to group separately from most of the other forms (Figure 7.4).

The classification results found that 89.9 % of the originally identified cases were correctly classified (Table 7.6). Most of the individuals considered incorrectly classified were low forms from one lake being more closely associated with low forms from a different lake. Few individuals were found to be incorrectly classified when forms from within the same lake were compared, supporting the initial identification of forms during the individual lake analyses (Table 7.6). The only exception was for Reindeer Lake where several individuals identified as low forms were found to classify more closely with the mid form and visa versa (Table 7.6). The individual analysis of Reindeer Lake ciscoes reflected this problem with identification as some characters supported a low, mid, and high form being present in the lake while other characters only supported a low and high form.

Table 7.5. Coefficients for Discriminant Analysis of all cisco forms using premaxillary angle and morphometric characters adjusted by common-within-group residuals.

	Standardized Canonical Discriminant Function Coefficients				
	Function				
	1	2	3	4	5
Premaxillary angle	0.21	-0.14	-0.21	-0.09	-0.32
Preorbital length	0.25	-0.16	0.29	-0.23	0.10
Orbital length	0.21	-0.25	-0.45	0.66	-0.02
Postorbital length	0.16	0.14	-0.06	-0.02	-0.18
Trunk length	0.09	0.14	-0.18	0.01	0.23
Dorsal length	0.12	-0.15	-0.44	-0.36	0.51
Lumbar length	0.17	-0.01	0.07	-0.01	0.02
Anal length	0.10	0.19	0.33	0.22	0.22
Caudal peduncle length	0.16	-0.20	0.50	0.13	-0.20
Head depth	-0.06	0.11	-0.20	-0.17	0.28
Body depth	-0.08	0.36	-0.06	-0.12	-0.38
Caudal peduncle depth	-0.02	0.23	-0.06	0.41	0.06
Interorbital width	-0.48	0.14	0.27	-0.32	-0.06
Maxillary length	0.28	0.01	0.22	-0.11	-0.07
Maxillary width	-0.05	-0.05	0.20	0.08	-0.12
Pectoral length	0.22	-0.05	0.09	0.35	0.28
Pelvic length	-0.27	0.50	0.07	0.20	0.01
Adipose length	-0.10	0.22	-0.01	0.10	-0.09
Lower arch length	0.30	-0.05	0.11	-0.07	0.43
Gillraker length	-0.53	-0.51	0.22	0.14	0.33
Eigenvalue	5.34	1.95	1.78	1.25	1.03
Percent of Variance	44.0	16.0	14.7	10.3	8.5
Cumulative Percent	44.0	60.0	74.6	84.9	93.5
Canonical Correlation	0.92	0.81	0.80	0.75	0.71

Table 7.6. Classification results from Discriminant Analysis of all cisco forms using premaxillary angle and morphometric characters adjusted by common-within-group residuals.

		Predicted Group Membership									
	Initial groups	Athapap low form	Athapap high form	Clearwater low form	Clearwater high form	George low form	George high form	Reindeer low form	Reindeer mid form	Reindeer high form	Total
Count	Athapap low form	59	1	0	0	5	0	0	6	0	71
	Athapap high form	2	118	0	0	0	0	0	1	0	121
	Clearwater low form	5	0	35	1	0	0	0	0	0	41
	Clearwater high form	0	1	1	25	0	0	1	0	0	28
	George low form	4	0	0	0	62	0	1	1	2	70
	George high form	0	0	0	0	0	39	0	0	0	39
	Reindeer low form	6	0	0	0	9	0	202	8	3	228
	Reindeer mid form	2	1	0	0	1	0	4	63	2	73
	Reindeer high form	4	2	0	0	1	0	0	0	67	74
Percent	Athapap low form	83.1	1.4	0.0	0.0	7.0	0.0	0.0	8.5	0.0	100.0
	Athapap high form	1.7	97.5	0.0	0.0	0.0	0.0	0.0	0.8	0.0	100.0
	Clearwater low form	12.2	0.0	85.4	2.4	0.0	0.0	0.0	0.0	0.0	100.0
	Clearwater high form	0.0	3.6	3.6	89.3	0.0	0.0	3.6	0.0	0.0	100.0
	George low form	5.7	0.0	0.0	0.0	88.6	0.0	1.4	1.4	2.9	100.0
	George high form	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Reindeer low form	2.6	0.0	0.0	0.0	3.9	0.0	88.6	3.5	1.3	100.0
	Reindeer mid form	2.7	1.4	0.0	0.0	1.4	0.0	5.5	86.3	2.7	100.0
	Reindeer high form	5.4	2.7	0.0	0.0	1.4	0.0	0.0	0.0	90.5	100.0

89.9% of original grouped cases correctly classified.

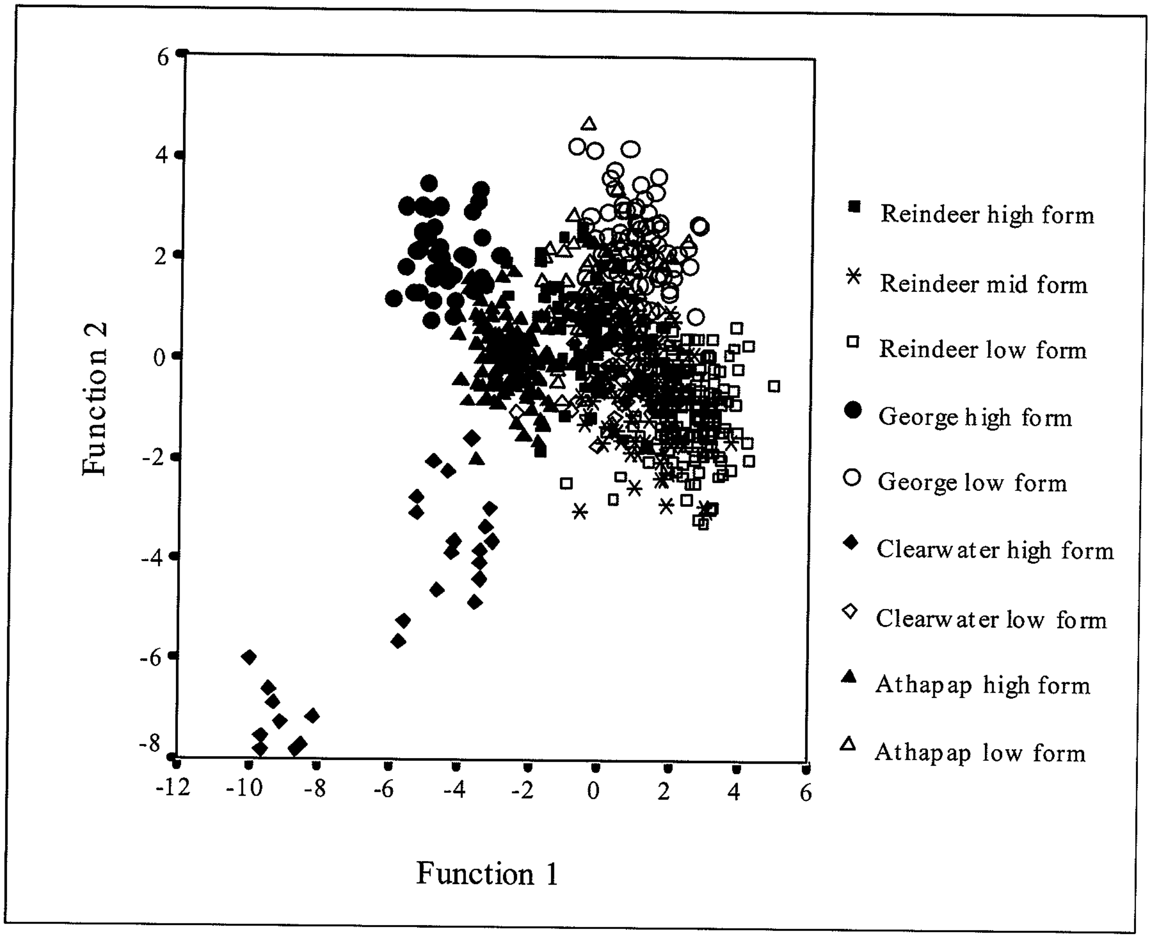


Figure 7.4. Plot of function coefficient scores from Discriminant Analysis using premaxillary angle and morphometric characters adjusted by common-within-group residuals. Forms were identified based on predicted group membership values suggested by the DA results.

Taxonomic Identity of Manitoba Cisco Forms

The forms identified in this study were compared to known *C. zenithicus* specimens collected from Lake Nipigon (n=8) and Lake Superior (n=30). The same suite of morphometric and meristic characters recorded for the Manitoba specimens was recorded from these specimens. The Lake Nipigon ciscoes were found to have similar gillraker counts to the low forms from Lake Athapapuskow, George Lake, Clearwater Lake, and Reindeer Lake including the mid form (Table 7.1). The Lake Superior specimens were found to have higher values than the low gillraker forms identified in this study (Table 7.1), however, previous studies have found that some populations of *C. zenithicus*, particularly those from Lake Superior commonly have higher gillraker counts than those reported for Lake Nipigon and other inland lakes (Todd and Steinhilber 2002, Steinhilber et al. 2002). The gillraker count ranges reported in the literature for *C. zenithicus* were found to consistently overlap with the low forms identified in this study (Table 7.7). The high forms identified in this study were found to have gillraker counts that overlapped with both *C. zenithicus* and *C. artedi* values reported in the literature; however, the upper ranges of the high forms normally fell beyond the reported range for *C. zenithicus* but well within the range for *C. artedi* (Table 7.7). Gillraker length, maxillary length, and premaxillary angle were found to be similar between the low forms (including Reindeer mid) and the known *C. zenithicus* specimens (Table 7.1).

To further examine the relationship between the known *C. zenithicus* specimens and the low gillraker forms identified in this study a PCA was performed using all meristic characters and all morphometric characters adjusted by ratios. This PCA is the same as the first PCA performed in the previous section with the exception that the Lake Nipigon and Lake Superior specimens were included in this analysis. The results for the Manitoba forms remain the same for this analysis and for ease of comparison the scores for the Manitoba cisco forms are represented as ellipses instead of individual points (Figure 7.5). The known *C. zenithicus* specimens were within both the high- and low-form ellipses; however, the majority grouped more closely with the low forms (6 of 8 for Lake Nipigon; 23 of 30 for Lake Superior). The characters accounting for most of the variation on component one (15 %) were gillraker length, upper and lower gillraker count, pectoral length, and pelvic length positively and premaxillary angle negatively (Table 7.8). The second component accounted for almost the same amount of variation as component one (13 %) and the highest correlated characters were maxillary length, body depth, postorbital length, lower arch length, preorbital length (snout length), and premaxillary angle positively and upper and lower gillraker count and gillraker length negatively (Table 7.8).

Table 7.7. Range of values for gillraker count reported by various sources for *Coregonus zenithicus* and *C. artedi* populations throughout North America.

Source	**Main Location**	***C. zenithicus***	***C. artedi***
Evermann 1909 and 1911	Great Lakes	37 - 42	37 - 55
Koelz 1929	Great Lakes	31 - 48	41 - 66
Dymond and Pritchard 1930	Western Canada	< 43 (usually 38 - 40)	41 - 62
Bajkov 1932	Lake Winnipeg, MB	31 - 44	37 - 66
Dymond 1943	Northwestern Canada	33 - 40	40 - 52
Paterson 1969	Barrow Lake, AB	37 - 41	44 - 51
Clarke 1969	Lake Athapapuskow, MB	usually less than 37	usually greater than 37
Clarke 1973	Western Canada	29 - 40 (population means)	39 - 63 (population means)
Scott and Crossman 1973	North America	32 - 46	36 - 64
Steinhilber et al. 2002	North America	30 - 46	42 - 62

Table 7.8. Character loadings and variance explained by PCA on all cisco forms using meristic characters and morphometric characters adjusted by ratios.

	Component				
	1	2	3	4	5
Premaxillary angle	-0.46	0.46	0.13	0.05	0.00
Dorsal ray count	0.10	0.25	0.32	0.44	0.17
Anal ray count	0.21	-0.02	0.43	0.36	0.15
Pectoral ray count	-0.01	0.10	0.33	0.39	0.18
Pelvic ray count	0.03	0.02	0.36	0.34	0.00
Upper gillraker count	0.63	-0.56	-0.03	0.00	0.18
Lower gillraker count	0.67	-0.55	-0.09	-0.03	0.12
Preorbital length	0.21	0.48	-0.14	-0.14	-0.32
Orbital length	0.42	0.18	-0.35	0.23	0.38
Post orbital length	0.01	0.59	-0.19	0.18	0.03
Trunk length	-0.28	-0.06	0.08	-0.47	0.21
Dorsal length	0.47	0.18	0.26	0.11	-0.42
Lumbar length	-0.41	0.10	-0.01	-0.21	0.52
Anal length	0.51	-0.06	0.36	-0.01	-0.41
Caudal peduncle length	-0.17	-0.05	-0.25	0.01	-0.38
Head depth	0.47	0.35	-0.41	0.11	0.12
Body depth	0.03	0.60	0.29	-0.27	0.16
Caudal peduncle depth	0.43	0.30	0.12	-0.45	-0.07
Interorbital width	0.44	0.14	-0.40	-0.03	0.02
Maxillary length	0.23	0.63	-0.22	0.16	-0.07
Maxillary width	0.23	0.06	-0.15	-0.06	-0.16
Pectoral length	0.55	0.31	0.29	-0.25	0.23
Pelvic length	0.53	0.31	0.29	-0.30	0.22
Adipose length	0.20	0.34	0.18	-0.15	-0.14
Lower arch length	0.12	0.52	-0.34	0.20	0.10
Gillraker length	0.66	-0.47	-0.10	0.03	0.10
Eigenvalues	3.89	3.34	1.83	1.51	1.40
Percent of Variance	14.96	12.86	7.04	5.82	5.37
Cumulative Percent	14.96	27.82	34.86	40.68	46.05

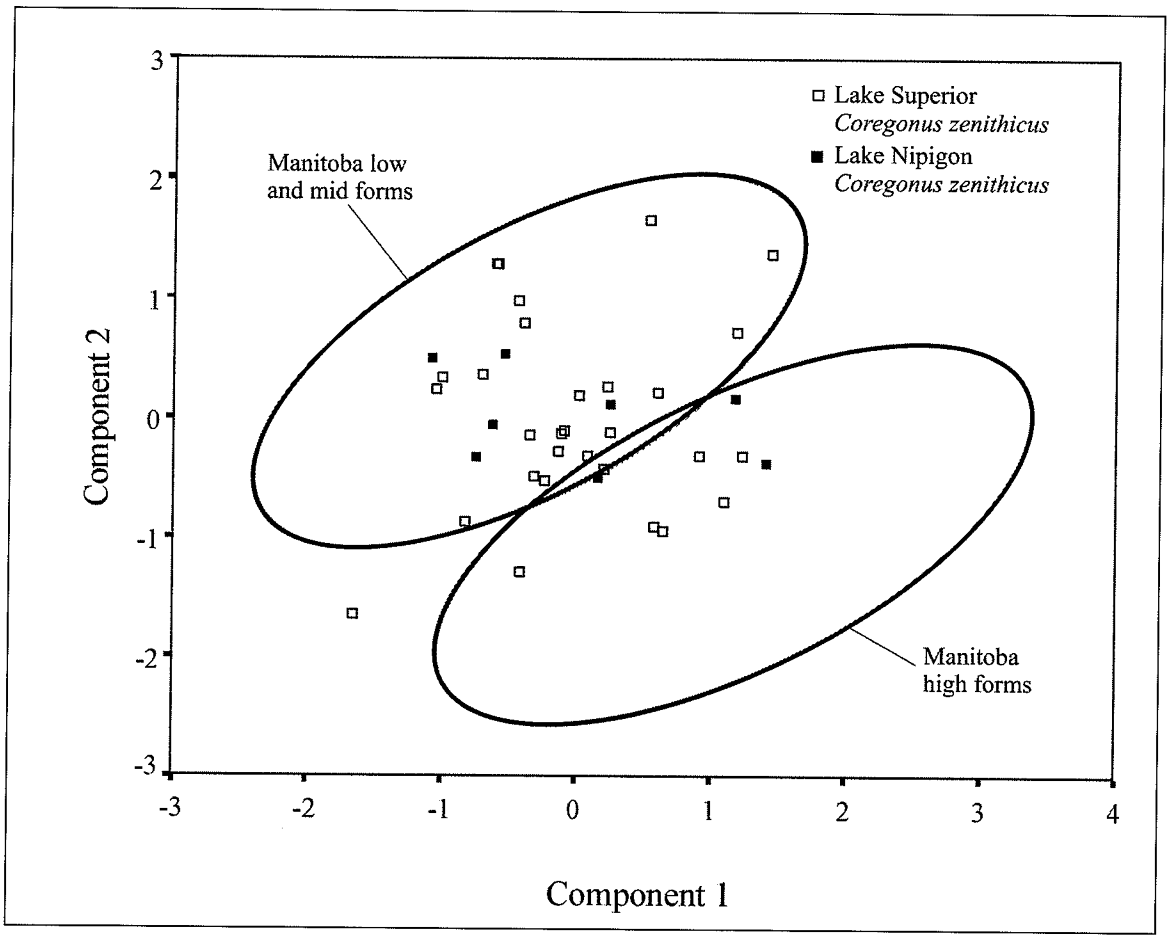


Figure 7.5. Plot of component scores for PCA of meristic and morphometric characters adjusted by ratios. Individual Lake Nipigon and Lake Superior known *Coregonus zenithicus* specimens are indicated by solid and shaded squares respectively. Ellipses include the majority of Manitoba ciscoes into their respective forms.

8. DISCUSSION

Lake Athapapuskow

The presence of multiple sympatric cisco forms from Lake Athapapuskow was first reported by Clarke (1969). In 1969 Clarke concluded that three species (*Coregonus reighardi*, *C. artedi*, and *C. hoyi*) were present in Lake Athapapuskow. In Big Athapapuskow, Clarke distinguished *C. reighardi* from *C. artedi* and *C. hoyi* by their vertical premaxillae, included lower jaws, terete bodies, and 24 to 36 short gillrakers. They were also described as having greenish colouration above the lateral line and large eyes. *Coregonus artedi* and *C. hoyi* were harder to distinguish from one another, however, he found that *C. artedi* had the highest number of gillrakers, smaller eyes, equal jaws, and immaculate pectoral fins. The *C. hoyi* group had slightly fewer gillrakers on average than *C. artedi*, larger eyes, pigmented pectoral fins, and protruding lower jaws. Clarke (1969) found that all three Lake Athapapuskow species were atypical from their Great Lakes equivalents based on several characters. He also concluded that *C. reighardi* and *C. zenithicus* were phenotypically similar throughout the Great Lakes making identification uncertain regarding the low gillraker form from Lake Athapapuskow.

In 1973 Clarke re-examined the cisco fauna of Lake Athapapuskow and concluded that the low gillraker form should be identified as *C. zenithicus*. Clarke also concluded that the specimens identified as *C. hoyi* were instead sympatric morphotypes of *C. artedi*. The gillraker count range for *C. zenithicus* was 24 to 36 (mean of 29.4) and for the two *C. artedi* forms they were 38 to 47 (mean of 42.4) and 42 to 49 (mean of 45.6). Clarke (1973) also described three cisco forms that were collected from Little Athapapuskow.

They included a low gillraker form with counts ranging from 32 to 37 (mean of 34.5), a mid gillraker form with counts ranging from 40 to 46 (mean of 42.7), and a high gillraker form with counts ranging from 48 to 54 (mean of 51.4). Although the gillraker counts were slightly different from the Big Athapapuskow forms, they were considered to represent the same species found in Big Athapapuskow.

In 1997 ciscoes were collected from Little Athapapuskow by J. Johnson and R. Fudge of Fisheries and Oceans Canada. These specimens were examined and the results were presented by Aoki and Bodaly (2003). Two cisco forms were identified by their bimodal gillraker distribution. The low gillraker form had 35 to 41 gillrakers with a mode of 38/39 while the high gillraker form had 44 to 54 gillrakers with a mode of 44/45. Individuals with 42 or 43 gillrakers were not classified due to uncertainty about their type due to their intermediate values. The low gillraker form was smaller (fork length 105-165 mm) than the high gillraker form (150-255 mm). The low gillraker form made up the majority of the catch from the deeper net (38 m) while both forms were present in the shallower net (15-26 m). These results differed from the forms identified by Clarke (1973) described above. The majority of Clarke's work was done in Big Athapapuskow with some in Little Athapapuskow throughout the summer and fall in the late 1960's. The ciscoes examined by Aoki and Bodaly were collected in September of 1997 from Little Athapapuskow only. As described above, Big and Little Athapapuskow are linked by a narrows, which may limit cisco movement throughout Lake Athapapuskow.

Two distinct taxa were considered to be present in Lake Athapapuskow based on the cisco specimens collected in this study. Gillraker count and arrangement were found to differ between the two taxa with the low form ranging from 20 to 37, short, widely spaced gillrakers. The high form ranged from 36 to 47, longer, more tightly packed gillrakers. These ranges are very similar to those found by Clarke (1973) for the low and mid forms, identified by Clark as *C. zenithicus* and *C. artedi*. The structure of the gillrakers for the respective forms identified in this study were also found to be similar to those described by Clarke (1973). There was an absence of members of the high gillraker form identified by Clarke in this study (1973). Two ciscoes were collected from Lake Athapapuskow which had gillraker counts of 47 and standard lengths of over 180 mm. The majority of individuals identified as members of the high gillraker form were less than 120 mm in standard length. The two larger high gillrakered individuals may be members of the high form identified by Clarke (1973). The lack of other large, high gillrakered individuals was likely due to sampling, possibly because they prefer shallower regions of the lake during October due to spawning (Scott and Crossman 1973).

Other key characters were also found to be useful for identifying the cisco forms and these included jaw position and dorsal colouration. For those individuals of either the low or high form that were found to be close to the overlap range for gillraker counts (36-37), these characters were effective for separating the two forms. The PCA results also supported the presence of two cisco forms. Only one PCA resulted in complete separation between forms, however, all PCA,s showed minimal overlap between them. The characters accounting for the variation between the two forms included gillraker length, maxillary length, snout length and orbital length, all characters considered to be important for distinguishing between *C. zenithicus* and *C. artedi*. The Anova and Discriminant Analysis results provided evidence supporting a low and high gillraker form being present in Lake Athapapuskow.

Reindeer Lake

In 1943, Dymond examined 13 cisco specimens from Reindeer Lake that had been collected by Dr. D. S. Rawson of the University of Saskatchewan. Dymond considered these specimens to be equivalent to *C. zenithicus* based on his previous cisco work in western Canada (Dymond and Pritchard 1930). The mean gillraker count for the Reindeer Lake specimens was 36 with 39 being the maximum count recorded (Dymond 1943). Dymond measured several morphometric characters and compared them to *C. zenithicus* specimens from Lake Winnipeg and Lake Nipigon (McPhail and Lindsey 1970). The pelvic and pectoral fin lengths of the Reindeer Lake specimens were similar to those from Lake Nipigon while both were shorter than the Lake Winnipeg specimens (Dymond 1943). In 1973, Clarke examined five ciscoes from Reindeer Lake and found they had gillraker counts ranging from 34 to 38 and a mean of 35.6. These specimens were noted to have short gillrakers, a large premaxillary angle, long upper jaw, long snout, and a large eye diameter (Clarke 1973).

The presence of sympatric cisco forms in Reindeer Lake was supported by the results of this study. Gillraker count and arrangement initially suggested that three forms may be present in the specimens collected from Reindeer Lake. One form consisted of individuals with gillraker counts ranging from 23 to 32 (mean of 28.2), another form consisted of individuals with 33 to 38 gillrakers (mean of 35.5), and the final form consisted of individuals with 39 to 48 gillrakers (mean of 41.5). Upon closer examination of the gillraker structure, jaw position, and dorsal colouration it was apparent some individuals which had gillraker counts close to overlap range between forms were placed in the wrong groups. The PCA results supported the presence of only two cisco forms and also served as a method for placing some of the uncertain individuals into the most appropriate forms. The two forms consisted of a low form ranging in gillraker counts from 23 to 38 and a high form ranging in gillraker counts from 38 to 47. The Anova and DA results provided evidence supporting a low and high form being present.

George Lake

In 1969, Gibson and Johnson examined the fish fauna of George Lake. Five ciscoes were caught at a depth of 107 feet in the upper basin of the lake and another 35 were caught at 80 feet in the mid basin, both using 1.5 inch mesh. No description of the fish was given in the report; however, they considered them to be *C. hoyi*. Their identification of the fish as *C. hoyi* was based on previous reports done by the province in the 1930's and 40's (J. Beyette, Manitoba Conservation, Lac Du Bonnet, MB, pers. comm. 2001). In Clarke's 1973 study five specimens were examined from George Lake. Clarke identified these specimens as *C. zenithicus* based on gillraker counts which ranged from 33 to 37 with a mean of 35.4. These individuals also possessed other *C. zenithicus*-like characters, such as short gillraker length, long maxillary length, large eye diameter, and large premaxillary angle. Based on these findings *C. zenithicus* was considered to be the only species present in George Lake, the only instance of this species being present in a lake without *C. artedi*. The belief that only *C. zenithicus* were present in the lake was supported by sampling conducted in August 1996 by J.D. Reist (Fisheries and Oceans Canada, Winnipeg), T.N. Todd (US Geological Survey, Ann Arbor), and R. A. Bodaly (Fisheries and Oceans Canada, Winnipeg) who collected only *C. zenithicus*-like specimens. Identification was based primarily on low gillraker counts; however, they were noted to be somewhat distinct from Great Lakes *C. zenithicus* populations morphologically (T.N. Todd, pers. comm.). Sampling was done in the deeper north basin of the lake.

The possibility of two forms being present in the George Lake was investigated in 2000 when the author was given specimens collected from George Lake by Manitoba Conservation. The gillraker counts for the 11 ciscoes ranged from 38 to 43, higher than those reported by Clarke (1973). Evidence of co-occurring cisco forms in George Lake was supported by the results of this study. One form, referred to as the low gillraker form consisted of individuals with gillraker counts ranging from 30 to 39 (mean of 33.9) and the other form, referred to as the high from consisted of individuals with counts ranging from 39 to 45 (mean of 42). Gillraker structure and arrangement, jaw position, and dorsal colouration were also found to be useful for distinguishing between the two forms, especially for the three individuals with 39 gillrakers. The PCA results also supported the presence of two cisco forms along with the ANOVA and DA results.

Clearwater Lake

In 1973, Clarke reported two specimens of cisco collected from Clearwater Lake both with gillraker counts of 33. Clarke (1973) also collected 28 ciscoes from Clearwater Lake with gillraker counts from 38 to 49. The low form was found to have shorter gillrakers than the high-gillraker form. Clarke (1973) tentatively identified the low form to be *C. zenithicus* based on the low gillraker count, large premaxillary angle, long upper jaw, large eye diameter and long snout; however, due to the small sample size they were not included in more detailed analysis. No other information was available about *C. zenithicus* or ciscoes in general regarding Clearwater Lake.

The presence of sympatric cisco forms in Clearwater Lake was supported by the gillraker counts observed in this study. The low form was identified as individuals with gillraker counts ranging from 31 to 39 and the high form consisted of individuals with gillraker counts ranging from 39 to 49. The gillraker count distribution of the high form was very similar to the range reported by Clarke (1973) for *C. artedi* in Clearwater Lake. Gillraker arrangement, jaw position, and dorsal colouration did show some differences between the two forms suggested by gillraker counts, however, not all individuals could be placed into groups based on these characters. The PCA using meristic characters supported to the two forms previously identified by gillrakers counts, however, when only morphometric characters were examined the forms were not supported. The characters accounting for much of the variation in this analysis included dorsal length, pectoral length, pelvic length, and anal length.

Comparison of Cisco Forms Between-Lakes

The gillraker ranges for the low forms identified in this study overlapped between lakes. There was some variation between lakes for this character but the majority of individuals had gillraker counts in the mid 30's. The gillraker count range for all individuals identified as low forms in this study was 20 to 40 gillrakers. The high forms between lakes were found to overlap and consisted of individuals with gillraker counts ranging from 36 to 49 with most individuals having counts in the low 40's. Gillraker structure was also found to be similar among like-forms between lakes. The low forms were found to have shorter and more widely spaced gillrakers than the high forms. Middle gillraker length was also found to be consistent among the low forms.

The low forms (including the Reindeer mid form) across all lakes tended to have lighter dorsal colouration than the high forms, ranging from yellow to tan for the low forms and greenish blue to black for the high forms. Jaw position in the low forms tended to be inferior giving a downward appearance to their mouths. The lower jaws were usually slightly shorter than or equal to the upper jaws for most members of the low form, with the exception of some individuals from Reindeer Lake, which had slightly longer lower jaws but still maintained a downward appearance to the jaws. The majority of the high forms from all lakes tended to have longer lower jaws than upper jaws giving their mouths a superior or upward appearance.

The multivariate pattern displayed by this analysis reflected that seen when each lake was examined individually. The low forms identified from each lake were found to group more closely to each other than to their sympatric high forms in multivariate space. The PCA results found that the low forms tended to have low gillraker counts, short gillraker lengths, large premaxillary angles, long maxillaries, and deep bodies. The high forms alternatively tended to have high gillraker counts, long gillrakers, small premaxillary angles, short maxillaries, and shallow bodies. The overlap of similar forms (i.e., low to low, high to high) was also supported by Discriminant Analysis. The characters accounting for most of the variation found between the forms included lower arch length, maxillary length, and preorbital length positively, and gillraker length, interorbital width, and pelvic length negatively. Based on these findings, the low forms can be characterized as having longer lower gill arches, longer maxillaries, longer snouts (preorbital length), shorter gillrakers, smaller interorbital widths, and shorter pelvic fins than the high forms.

Taxonomic Association of Cisco Forms

The low gillraker forms identified in this study were found to conform to descriptions of *C. zenithicus* reported in previous studies for several characters including gillraker counts, gillraker length, gillraker structure, maxillary length, and jaw morphology and also with *C. zenithicus* specimens collected from Lake Nipigon (Hubbs and Lagler 1964, Scott and Crossman 1973, Clarke 1973, Smith and Todd 1984, Todd and Smith 1992, Todd and Steinhilber 2002, Todd 2003, Etnier and Skelton 2003). Specimens from Lake Superior were found to have higher gillraker counts than most of the specimens included in this study. Turgeon and Bernatchez (2003) found that Lake Nipigon ciscoes (*C. artedi*, *C. zenithicus*, *C. hoyi*, and *C. nigripinnis*) grouped more closely with western cisco populations than with cisco species from Lake Superior and other Great Lakes using microsatellites. The only cisco form common between their study and this study was the low form from George Lake. The sympatric high gillraker form was not included in their analysis; however, a sample from Lake Winnipeg identified as *C. artedi* was included and was found to group closest to the George Lake specimens (Turgeon and Bernatchez 2003). These differences between two "known" populations of *C. zenithicus* (both identified by T. Todd, Ann Arbor, Michigan) exhibits the problems associated with equating these cisco forms across different lakes. Despite the morphological differences found between the Lake Superior specimens and the low forms identified in this study, the similarities between the low forms and the majority of available *C. zenithicus* descriptions suggest that the low forms identified in this study represent that species.

The high forms identified in this study have gillraker count ranges that overlap with gillraker counts reported for populations of *C. artedi* by most researchers (Koelz 1929, Hubbs and Lagler 1964, McPhail and Lindsey 1970, Scott and Crossman 1973). *Coregonus artedi* are known to vary considerably throughout their range and the high forms identified in this study fit most descriptions of this species (McPhail and Lindsey 1970, Scott and Crossman 1973, Stewart and Watkinson 2004). *Coregonus artedi* is reportedly the only other cisco species present in the study region. None of the high forms were found to have gillraker counts high enough to suggest that *C. nigripinnis* is present within any of the samples collected in this study, supporting the current arrangement of ciscoes in Manitoba.

The number of gillrakers present on the first branchial arch has been considered a relatively stable and useful character for coregonine identification. Svardsen (1950, 1957, 1965) found that mean gillraker counts of transplanted lake whitefish did not change over time spans of 22 to 80 years suggesting that it has a high genetic component. Similarly, Loch (1974) found that gillraker number did not significantly change for lake whitefish that were transplanted from Clearwater Lake, a large, deep, northern lake, to Lyons Lake, a small, shallow, southern lake, both of which are in Manitoba. Loch (1974) did find, however, that gillraker length changed in relation to an increase in benthic food eaten, which was assumed to be due to increased abrasion on the gillrakers. Gillraker counts have been reported to change somewhat under varying laboratory and environmental conditions (McCart and Anderson 1967, Lindsey 1981, Todd et al. 1981, Todd 1998). Gillraker number, length, and spacing has been found to relate to prey size and to the amount of benthic versus pelagic food particles consumed in some studies (Kliewer 1970, Loch 1974). However, other studies have found that feeding ecology does not appear to be correlated with morphology and number of gillrakers and that differences in number are more likely the result of phenotypic plasticity acting upon a stable and genetically associated character (Lindsey 1981, Amundsen et al. 2004, Næsje et al. 2004). The difference in gillraker counts between the low forms identified in this study may be due to phenotypic responses to different conditions present in each lake. These may include differences in prey size and type, differences in the abundance and distribution of competitor species, or environmental differences.

The results of the multivariate analyses suggest that the Manitoba low-gillraker cisco forms are morphologically similar to the known *C. zenithicus* specimens from Lake Superior and Lake Nipigon. The characters associated with the differentiation of the low forms from high forms in this study have historically been associated with the identification of *C. zenithicus* (Koelz 1929, Dymond 1943, Clarke 1973, Scott and Crossman 1973, Todd and Smith 1992, Steinhilber et al. 2002, Todd and Steinhilber 2002, Steward and Watkinson 2004). These characters include lower gillraker counts, shorter, more widely spaced gillrakers, longer maxillaries, larger premaxillary angles, longer snouts, deeper bodies, longer lower gill arches, lighter dorsal colouration, and inferior jaw position.

There was some disparity present in the results that did not completely support the identification of the cisco forms found in this study. The Lake Superior *C. zenithicus* specimens differed in several characters, including gillraker counts from the low forms identified in this study. There was also some overlap between members of the low and high forms in this study in some characters and variation between some of the low forms identified in this study. These differences may attributable to several factors. The time since each of these lakes was first invaded by these forms is different due to their geographic distribution. The lakes themselves also differ from each other in characters such as size, shape, depth, water temperature, co-occurring species, and prey species to name a few. Differences in these characters undoubtedly have an influence on the cisco species present within each lake and also on how they evolved (Schluter 2000). The environmental differences between the lakes have likely caused character convergence to occur at different levels within each water body (Robinson and Parsons 2002). The differences found between the low forms in this study and the Lake Superior specimens may be due to divergence from the ancestral form towards a form possessing fewer gillrakers. The ciscoes of Lake Superior have been subjected to significant changes in the last century due to overfishing, environmental changes, and invasion of non-native species. These changes may have influenced the cisco diversity within the lake and altered the species boundaries causing introgression and hybridization to occur.

Convergence of key characters among cisco species affects our ability to differentiate and identify taxa. This is mostly due to environmental variation, however, hybridization and introgression has also been suggested as a source of some variation (Smith 1964). Todd et al. (1981) noted that often the variability displayed among cisco stocks of the same species is sometimes greater than that observed between different species of ciscoes, leading them to suggest that fewer species may exist than originally thought or that, conversely, some stocks of the same species should be considered different species altogether. Although some consistent morphological differences have been found between co-occurring populations of putative *C. zenithicus* and *C. artedi* (Clarke 1973, Todd and Smith 1980, Steinhilber et al. 2002), genetic studies have failed so far to find any significant differences between their DNA (Reed et al. 1998, Turgeon et al. 1999, Steinhilber et al. 2002). Turgeon and Bernatchez (2003) found that genetic variation reflected geography more so than taxonomy for several North American cisco species including populations of *C. artedi* and *C. zenithicus*. Their evidence was interpreted to suggest that much of the differentiation seen in ciscoes is due to ecophenotypic diversification such as gillraker polymorphism and depth-related habitat preferences. It has been suggested, however, that the time since the two species diverged may be insufficient for genetic differences to be apparent (Bailey and Smith 1981, Avise and Saunders 1984, Smith and Todd 1984, Reed et al. 1998). Similarly, a lack of genetic difference may be due to the presence of a single taxon that radiated from the Great Lakes following glaciation subsequently forming species-level taxa allopatrically (Turgeon and Bernatchez 2003). Parallel evolution may have produced a deepwater-feeding low-gillraker morphotype repeatedly where suitable habitat was available. The low-gillraker morphotype would differ morphologically from the sympatric mid-water ciscoes; however, genetically it would show a high degree of relatedness (Turgeon and Bernatchez 2003). Another possibility for a lack of genetic difference could be because the portion of the genome that has been sampled so far is so small that researchers have failed to find key differences that may exist. The only way to confirm that no genetic differences exist would be to sample every possible genetic locus, a time consuming and expensive task.

Speculated Origin of Sympatric Cisco Forms

The presence of similar phenotypes among the lakes examined here suggests a common origin for the variation. This may be due to independent repeated occurrences of ecological speciation, which Schluter (1996) referred to as parallel speciation, or by the invasion of two lineages post-glacially that had previously formed species by allopatric speciation or by ecological speciation. In order to better understand which scenario is more plausible, a closer examination of the speciation processes required for each to occur is needed.

Under the first scenario, ecological speciation occurs when reproductive isolation evolves due to divergent selection on traits between populations or subpopulations existing in contrasting environments (Schluter 2001). Environment in this case refers to all elements of the habitat (e.g., temperature, resources, physical structure) as well as any interactions with other species (e.g., competition, predation) (Schluter 2001). If similar ecological conditions are present in multiple lakes then it might be expected that the process would be repeated independently producing similar phenotypes with superficially similar character suites, a process referred to as parallel speciation (Schluter 1996). Sympatric speciation has been suggested as a plausible explanation for several fish species in North American (Schluter 1996) including lake whitefish (Lindsey et al. 1970, Bernatchez et al. 1996, Chouinard et al. 1996, Pigeon et al. 1997, Lu and Bernatchez 1999).

The other scenario is the allopatric or two-species model, which is often considered to be the most plausible model for the origin of lacustrine species (Smith and Todd 1984); however, the sympatric or ecological model has recently gained more acceptance (Schluter 2001). This model requires that two closely related species exist (or existed) outside of the lake where the sympatric pair occur. These pairs have evolved reproductive isolating mechanisms that prevent interbreeding upon secondary contact between populations. These mechanisms have evolved as a result of adaptive divergence between the two lineages in their respective isolated habitats (Bush 1975). An alternative to this model is a combination of sympatric and allopatric speciation. Sympatric ecological speciation may have produced the original species pairs prior to glaciation or within glacial refugia. Both lineages then radiated out through a series of fluctuating water connections and persisted where suitable habitat conditions occurred for both forms (Smith and Todd 1984).

It has been suggested that shared character states between populations can provide evidence towards which form of speciation (sympatric or allopatric) may have occurred. If sympatric forms are present which share characters that appear to be derived and unique then sympatric speciation is considered to be the most probable hypothesis for their origin (Lindsey et al. 1970, Smith and Todd 1984). It is expected then that sympatrically derived forms should overlap more closely with one another than to allopatric populations when a large suite of morphological characters are examined simultaneously (Smith and Todd 1984, Pigeon et al. 1997, Steinhilber et al. 2002). If, however, a member of a sympatric pair is found to group more closely with one of the allopatric populations then it is likely the product of independent lineages colonizing the lakes (Smith and Todd 1984).

Under the ecological speciation model, character convergence due to similar ecological conditions would most likely be responsible for the similarities noted between the low gillraker forms identified here and for other populations of *C. zenithicus*, creating a polyphyletic group. In order to examine whether character convergence is occurring usually requires extensive and time consuming environmental manipulation studies which were beyond the scope of this project. It has been noted that sympatrically derived forms would differ most in characters related to competition and trophic status (Smith and Todd 1984, Schluter 2001). Several morphologically plastic traits in postglacial North American fishes have been found to have similar responses to either pelagic or littoral environmental conditions. Fish occurring in littoral conditions tend to have larger paired fins, more robust bodies, larger heads, deeper, more compressed caudal peduncles, subterminal mouths, and fewer, shorter, more widely spaced gillrakers than those in pelagic conditions (Schluter 1996, Robinson and Parsons 2002). These differences are in agreement with the characters commonly associated with the differentiation between *C. zenithicus* (generally benthic or littoral) and *C. artedi* (usually more pelagic) (Smith and Todd 1984).

With the exception of George Lake, all cisco forms were collected together in the same niche at the same time, usually in the deeper regions of the lakes. Clarke (1969) found that *C. artedi* in Lake Athapapuskow tended to occur in shallower waters while *C. zenithicus* occurred in deeper regions of the lake. Clarke (1969) also found that interspecific differences in feeding related to vertical distribution were present in Lake Athapapuskow ciscoes. Plankton and adult insects were found to be predominant prey items fed upon by *C. artedi*, both of which were found to be more abundant in the pelagic zone of the lake. *Coregonus zenithicus* was found to be most abundant in the littoral zone and their diet consisted predominantly of *Mysis* and other benthic prey items (Clarke 1969). Steinhilber (2000) found no significant differences in prey items between *C. zenithicus* and *C. artedi* in Barrow Lake, AB. The vertical distribution of cisco species in this lake appears to be the reverse of the situation reported for most lakes possessing both these species (Steinhilber 2000).

Ecological specialization is believed to be responsible for morphological divergence in sympatry, either through genotypic response or phenotypic plasticity (Schluter 1996). For species to have evolved in sympatry, it is expected that they inhabit very different niches with minimal overlap (Bush 1975). There appears to be evidence of niche overlap between the sympatric cisco forms identified in this study; however, the overlap did not appear to be present in George Lake and has previously been reported to be minimal in Lake Athapapuskow (Clarke 1969). It is difficult to speculate whether differences in characters related to niche specialization are the result of divergence in sympatry or whether they originated in allopatry due to the intense selective and environmental pressures upon them (Smith and Todd 1984).

The phenotypic similarity displayed within the low forms and within the high forms identified in this study suggests that they are more closely related to each other than to their co-occurring form. Phenotypic variation found within each form is most likely due to phenotypic plasticity or local adaptations, however, the possibility of sympatric speciation producing superficial resemblance between populations cannot be ruled out by these results. The repeated occurrence of these two forms outside of the Great Lakes seems to support the allopatric model but morphological and genetic distinctiveness of some populations identified as *C. zenithicus* casts doubt on whether they are indeed from the same lineage as those from the Mississippi refugium (Todd and Steinhilber 2002).

These putative-*C. zenithicus* forms may be distinct genetic lineages or they may be ecophenotypes of the *C. zenithicus* morphotype adapted to local environmental conditions. The discovery and examination of additional co-occurring cisco pairs may help address questions about their origin. Based on the results of this study the most plausible scenario for the distribution of cisco forms identified in this study remains that two lineages, *C. zenithicus* and *C. artedi*, colonized these lakes, probably through a single colonizing event that provided post-glacial links to the Mississippi Refugium. However, further direct evidence of reproductive isolation and the genetic basis for key discriminating characters as well as the discovery of informative genetic markers is needed to satisfactorily corroborate this conclusion. If, however, further examination of these sympatric pairs indicates that sympatric speciation is responsible then a re-evaluation of the nomenclature of North American ciscoes is required. In such a case, the proposal by Turgeon and Bernatchez (2003) to recognize all ciscoes from Central Canada and Northern United States (including Great Lakes endemics) as *C. artedi (sensu lato)* may be the most appropriate course of action. The diversity represented in lakes with sympatric pairs would then be addressed on a lake-by-lake basis and managed accordingly. Although the Great Lakes populations of this species are at risk of being lost, most of the populations examined in this study are considered to be stable and not at risk (Murray and Reist 2003). The one population that may be at risk is George Lake due to the small size of the water body and the potential for resource competition with rainbow smelt (*Osmerus mordax*) if it becomes present in the lake.

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Appendix 1-1 . Physical characteristics of Lake Athapapuskow (after Day 1983).

	Big Athapapuskow		Little Athapapuskow		North Basin	
Maximum depth (m)	71.7		40.3		23.0	
Mean depth (m)	16.0		14.3		8.0	
Surface area (km^2)	187.8		39.3		19.0	
Contour surface area as km^2 and percent total surface area	km^2	%	km^2	%	km^2	%
0 - 9 m	75.1	39.9	16.3	41.4	11.2	58.8
9-18 m	42.8	22.7	8.2	20.8	7.1	37.5
18 - 27 m	25.3	13.4	9.3	23.7	0.7	3.7
27 - 36 m	26.6	14.1	5.4	13.7		
36 - 46 m	10.6	5.6	0.4	0.9		
46 - 55 m	4.4	2.3				
55 - 64 m	2.4	1.3				
64 - 72 m	0.6	0.3				
Total dissolved solids (mg/l)	258		304		200	
	Depth (m)	Date	Depth (m)	Date	Depth (m)	Date
Maximum thermocline	21	Aug 26th	16	Sept 7th	14	Aug 26th
Dissolved oxygen (mg/l)	Epilimnion	Hypolimnion	Epilimnion	Hypolimnion	Epilimnion	Hypolimnion
Spring (May 26 to June 24)	11.5 - 13.5	12.0 - 13.5	11.0 - 12.5	10.5 - 12.5	10.0 - 13.5	7.0 -13.0
Summer (July 3 to Aug 8)	9.0 - 11.5	10.5 - 14	10.0 - 11.5	8.0 - 11.5	8.5 - 11.0	0 - 9.0
Fall (Aug 26 to Sept 7)	10.0	10.5	10.0	5.0 - 7.0	9.0	0 - 1.0

Appendix 1-2. Physical characteristics of Reindeer Lake (after Dean 1975).

		Water surface area (km^2) in different regions					
		North East	North West	Central	Southern	Deep Bay	Total
Depth zone (m)							
0-15		569.0	859.9	1112.1	681.7	15.0	3237.7
15-30		225.0	381.3	359.5	216.3	9.1	1191.2
30-50		36.0	299.4	269.6	81.3	10.1	696.4
50-100		1.8	32.9	44.8	25.9	21.0	126.4
100-150		-	-	-	-	22.8	22.8
150-200		-	-	-	-	18.9	18.9
200+		-	-	-	-	3.1	3.1
Total		831.8	1573.5	1786.0	1005.2	100.0	5296.5
Percent area		15.7	29.7	33.7	19.0	1.9	100.0
Percent volume		11.6	31.0	31.9	15.8	9.7	100.0
Island area (km^2)		152.6	328.1	596.2	221.4	3.6	1301.9
Oxygen Concentration (cm^3/l)							
Surface:	Maximum	-	7.7	7.8	6.0	7.7	
	Minimum	-	5.5	5.6	5.7	5.9	
Bottom:	Maximum	-	7.5	7.7	5.8	8.4	
	Minimum	-	5.8	5.9	5.5	6.6	
Total dissolved solids (ppm)							
	Range		18-46	21-34	22-36	21-28	
	Average		30.7	26.2	25.5	24.8	
Maximum thermocline (m)			24	20		20	

Appendix 1-3. Physical characteristics of George Lake (data from Gibson and Johnson 1969).

	North Basin	Mid Basin	South Basin	Total
Maximum depth (m)	45.0	24.4	10.0	45
Mean depth (m)	13.4	10.7	7.0	11.9
Surface area (km^2)	13.6	6.8	2.2	22.4
Maximum length (km)	6.6	5.8	2.3	12.2
Maximum width (km)	3.5	2.1	1.8	-
Length of Shoreline (km)	-	-	-	48.3
Volume (m^3)	17.9×10^7	71.5×10^6	15.0×10^6	26.6×10^7
Total dissolved solids (mg/l)	79	65	78	-
Dissolved oxygen (mg/l)				
Surface	8.5	8.6	-	
Bottom	8.0	3.1	3.1	
Maximum thermocline (m)	12	13	10.5	

Appendix 1-4. Physical parameters of Clearwater Lake (after Schlick 1978).

	Water surface area (km^2)	Percentage of total area
Depth interval (m)		
0-6	76.7	26.6
6-12	72.2	25.0
12-18	70.1	24.3
18-24	27.4	9.5
24-30	25.4	8.8
30-36	15.0	5.2
36+	2.0	0.7
Total	288.7	100.0
Maximum depth (m)	42.5 (140 ft)	
Mean depth (m)	13.2 (43.4 ft)	

Appendix 2-1. Collection information for sets from Lake Athapapuskow, 2000.

Set number	1	2	3	4
Date	Oct. 11	Oct. 11	Oct. 11	Oct. 12
Time set	4:35 PM	5:35 PM	6:30 PM	6:10 PM
Time checked	10:30 AM	11:50 AM	2:00 PM	9:15 AM
Duration	17.92 hrs	18.25 hrs	19.5 hrs	15.08 hrs
Location	Big Athapap	Big Athapap	Big Athapap	Little Athapap
Coordinates (dd mm.mmm)				
Northing	N 54° 31.889'	N 54° 31.845'	N 54° 33.272'	N 54° 37.184'
Westing	W 101° 46.027'	W 101° 40.796'	W 101° 39.148'	W 101° 39.451'
Water Depth				
Start of set	41.2 m (135 ft)	48.5 m (159 ft)	64.0 m (210 ft)	38.1 m (125 ft)
End of set	40.2 m (132 ft)	45.7 m (150 ft)	65.5 m (215 ft)	37.2 m (122 ft)
Number of specimens collected				
Cisco sp.	2	132*	37**	12***
Lake whitefish	81	26	4	52
Lake trout	6	13	10	11
Burbot	6	0	2	5
Deepwater sculpin	0	2	0	0

* An additional 60 ciscoes were caught but not included in the study due to poor condition.

** An additional 50 ciscoes were caught but not included in the study due to poor condition.

*** Approximately 20 ciscoes were caught but not included in the study due to poor condition.

Appendix 2-2. Collection information for sets from Reindeer Lake, 2001.

Set number	1	2	3	4	5	6	7	8
Date	7/8/2001	7/8/2001	7/9/2001	7/9/2001	7/10/2001	7/10/2001	7/11/2001	7/11/2001
Time set	1:50 PM	3:45 PM	7:50 PM	8:35 PM	1:45 PM	7:55 PM	5:55 PM	6:30 PM
Time checked	1:30 PM	4:00 PM	2:30 PM	5:30 PM	2:30 PM	11:30 AM	2:45 PM	5:15 PM
Duration	23.67hrs	24.25hrs	18.7hrs	20.9hrs	24.75hrs	15.6hrs	20.85hrs	22.6hrs
Coordinates								
N (dd°mm'ss)	57 11 14	57 13 40	57 15 48	57 13 22	57 12 48	57 04 30	57 16 00	57 15 40
W (dd°mm'ss)	102 06 09	102 23 15	102 18 52	102 13 04	102 19 22	102 14 19	102 18 56	102 19 45
Water Depth								
Start of set	52 m	61 m	65.5 m	35 m	52 m	55 m	64 m	37 m
End of set	37 m	50 m	38 m	34 m	58 m	35 m	63 m	65.5 m
Number of specimens collected								
Cisco sp.	39	60	95	1	16	62	60	42
Lake whitefish	23	39	7	29	10	9	25	27
Lake trout	0	3	5	2	1	7	4	1
Burbot	3	1	0	0	2	11	2	2
Longnose sucker	12	2	2	0	10	8	0	0
Deepwater sculpin	3	1	0	2	1	0	1	3

Appendix 2-3. Collection information for sets from George Lake.

Set number	1	2	3	4	5
Date	Sept. 21, 2000	June 27, 2001	June 27, 2001	June 28, 2001	June 28, 2001
Time set	7:15 PM	9:00 PM	9:15 PM	7:10 PM	9:30 PM
Time checked	10:00 AM	9:15 AM	9:35 AM	5:55 AM	6:15 AM
Duration	14.75 hrs	12.25 hrs	12.33 hrs	10.75 hrs	8.75 hrs
Location	North Basin	North Basin	North Basin	Mid Basin	North Basin
Coordinates (decimal lat/long)					
Northing	50.15855	50.25441	50.24531	50.22138	50.243
Easting	-95.28521	-95.49365	-95.51258	-95.50173	-95.51189
Water Depth					
Start of set	44.2 m (145 ft)	29 m (95 ft)	9.1 m (30 ft)	6.1 m (20 ft)	4.6 m (15 ft)
End of set	45.1 m (148 ft)	28.3 m (93 ft)	10.1 m (33 ft)	7.6 m (25 ft)	11.6 m (38 ft)
Number of specimens collected					
Cisco sp.	74	-	36	11	18
Lake whitefish	1	11	6	16	12
Lake trout	7	4	-	1	-
Deepwater sculpin	2	-	-	-	-
Perch	-	-	8	143	13
White sucker	-	-	-	4	-
Northern pike	-	-	-	3	-
Spottail shinner	-	-	-	9	-
Trout perch	-	-	-	-	1

Appendix 2-4. Collection information for sets from Clearwater Lake.

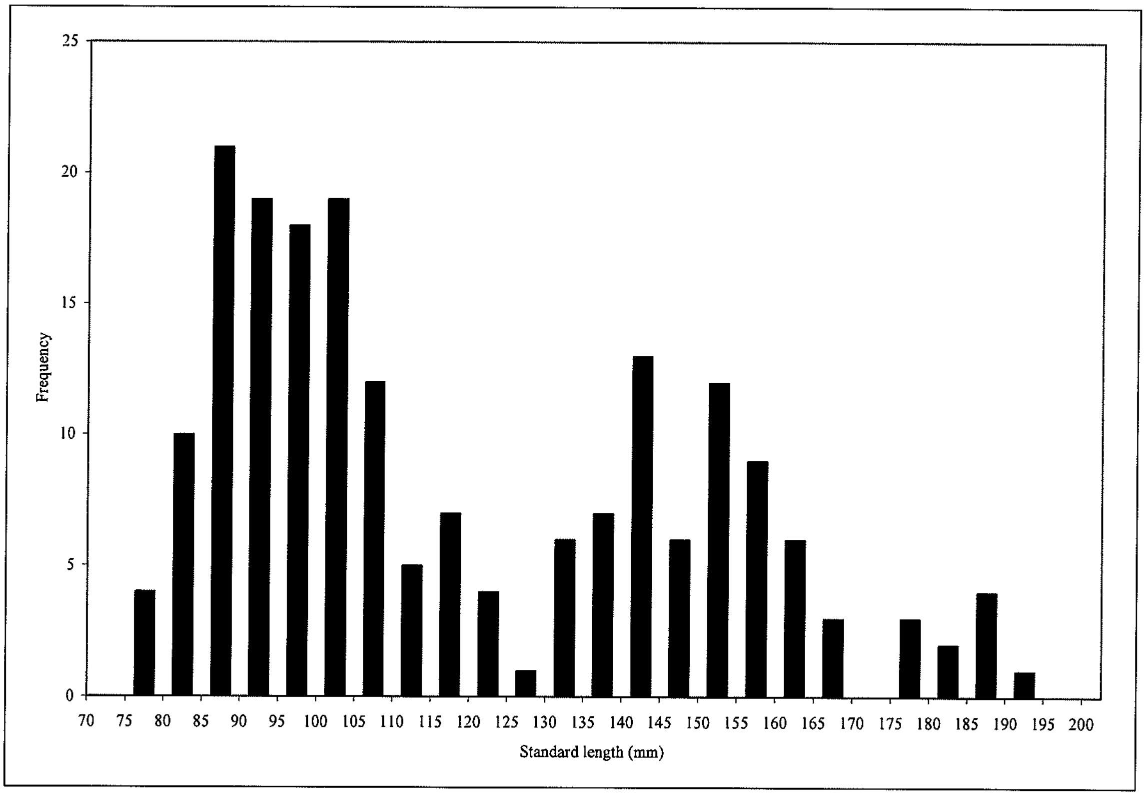
Set number	1	2	3	4	5	6
Date	Oct. 13, 2000	Oct. 13, 2000	Sept. 10, 2002	Sept. 11, 2002	Sept. 11, 2002	Sept. 11, 2002
Time set	6:05 PM	6:45 PM	8:00 PM	4:30 PM	5:15 PM	5:50 PM
Time checked	9:30 AM	11:30 AM	10:30 AM	2:30 PM	10:30 AM	10:00 AM
Duration	15.42 hrs	16.75 hrs	14.5 hrs	22 hrs	17.15 hrs	16.15 hrs
Coordinates (dd°mm.mmm')						
Northing	N 54 04.579	N 54 04.268	N 54 04.579	N 54 05.631	N 54 04.327	N 54 04.777
Westing	W 101 00.842	W 101 06.047	W 101 00.842	W 101 00.663	W 101 05.800	W 101 04.763
Water Depth						
Start of set	41.2 m (135 ft)	33.2 m (109 ft)	41.5 m (136 ft)	36.5 m (120 ft)	33 m (108 ft)	18.5 m (60 ft)
End of set	37.2 m (122 ft)	31.7 m (104 ft)	42.5 m (140 ft)	38.5 m (127 ft)	35 m (115 ft)	30 m (98 ft)
Number of specimens collected						
Cisco sp.	9	13	15	7	13	12
Lake whitefish	148	130	46	47	50	75
Lake trout	7	9	14	3	3	6
Burbot	1	6	4	3	2	4
White sucker	9	-	-	-	1	13
Deepwater sculpin	-	-	-	1	-	-

Appendix 3-1. Descriptive statistics for the combined cisco catch from Big Athapapuskow. All variables are represented by raw, untransformed values.

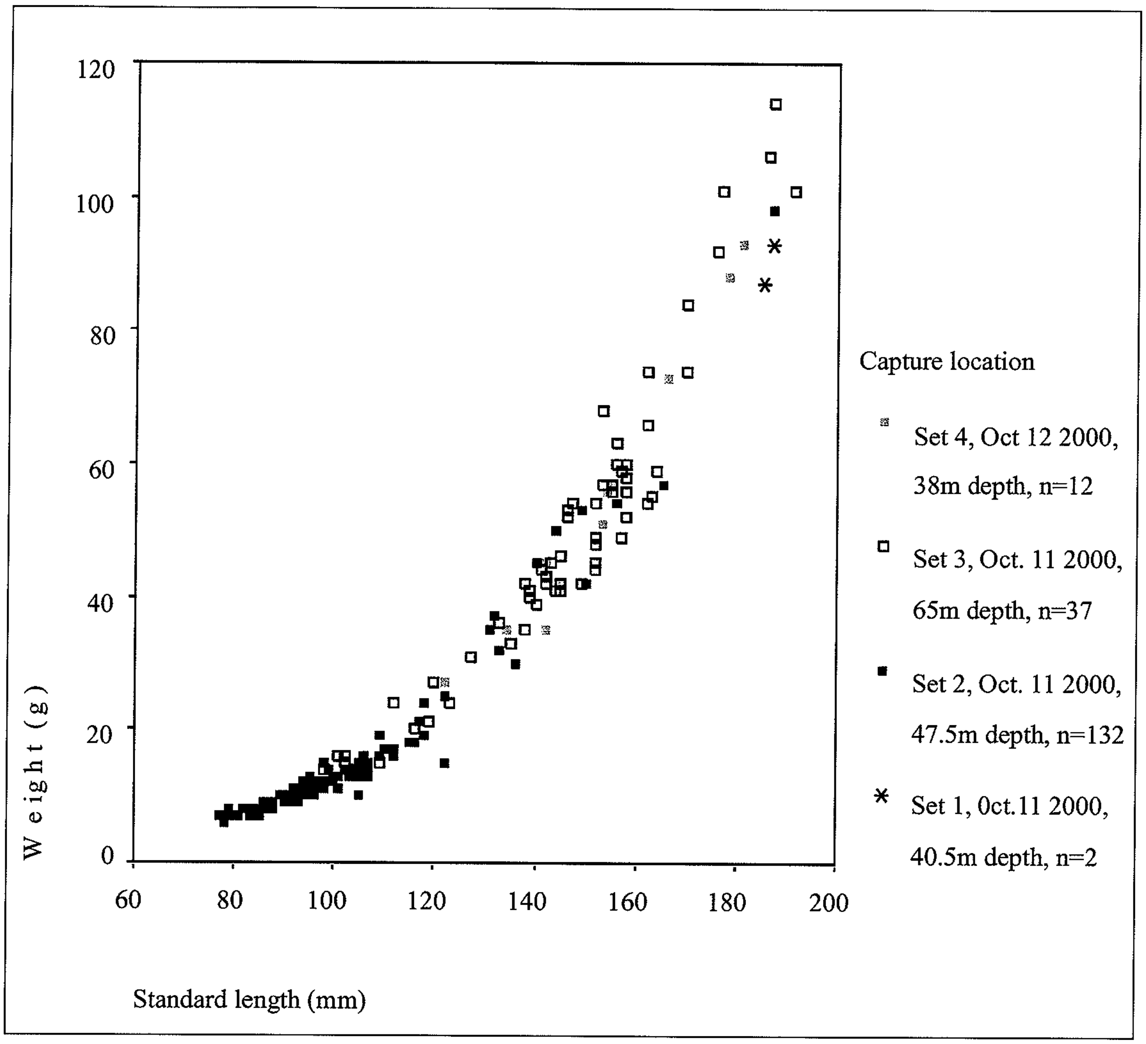
	N	Minimum	Maximum	Mean
Total gillraker count	181	20	47	35.8
Upper gillraker count	181	8	16	12.2
Lower gillraker count	181	10	32	23.6
Premaxillary angle	181	25	65	44.5
Dorsal ray count	181	8	12	10.7
Anal ray count	181	10	14	12.3
Pectoral ray count	181	11	18	16.4
Pelvic ray count	181	10	13	11.3
Age	179	1	17	4.7
Weight	181	6	114	27.5
Standard length	181	77.0	191.0	117.2
Fork length	153	85.0	216.0	132.9
Gillraker length	181	2.7	8.5	4.5
Lower arch length	181	7.0	27.9	12.2
Preorbital length	181	3.9	15.2	7.5
Orbital length	181	4.9	12.5	7.6
Post orbital length	181	8.3	25.1	13.9
Trunk length	181	15.5	52.6	28.8
Dorsal length	181	7.4	24.3	12.9
Lumbar length	181	8.4	36.0	18.8
Anal length	181	6.5	23.5	11.3
Caudal peduncle length	181	7.2	22.6	13.2
Head depth	181	8.8	24.8	13.7
Body depth	181	13.1	51.5	25.4
Caudal peduncle depth	181	5.2	14.2	8.2
Interorbital width	181	3.6	13.0	6.3
Maxillary length	181	6.6	19.3	9.9
Maxillary width	181	1.7	6.6	3.3
Pectoral length	181	11.3	31.3	18.4
Pelvic length	181	11.1	32.3	18.8
Adipose length	181	3.5	13.0	6.8

Appendix 3-1. con't. Descriptive statistics for the ciscoes collected from Little Athapapuskow. All variables are represented by raw, untransformed values.

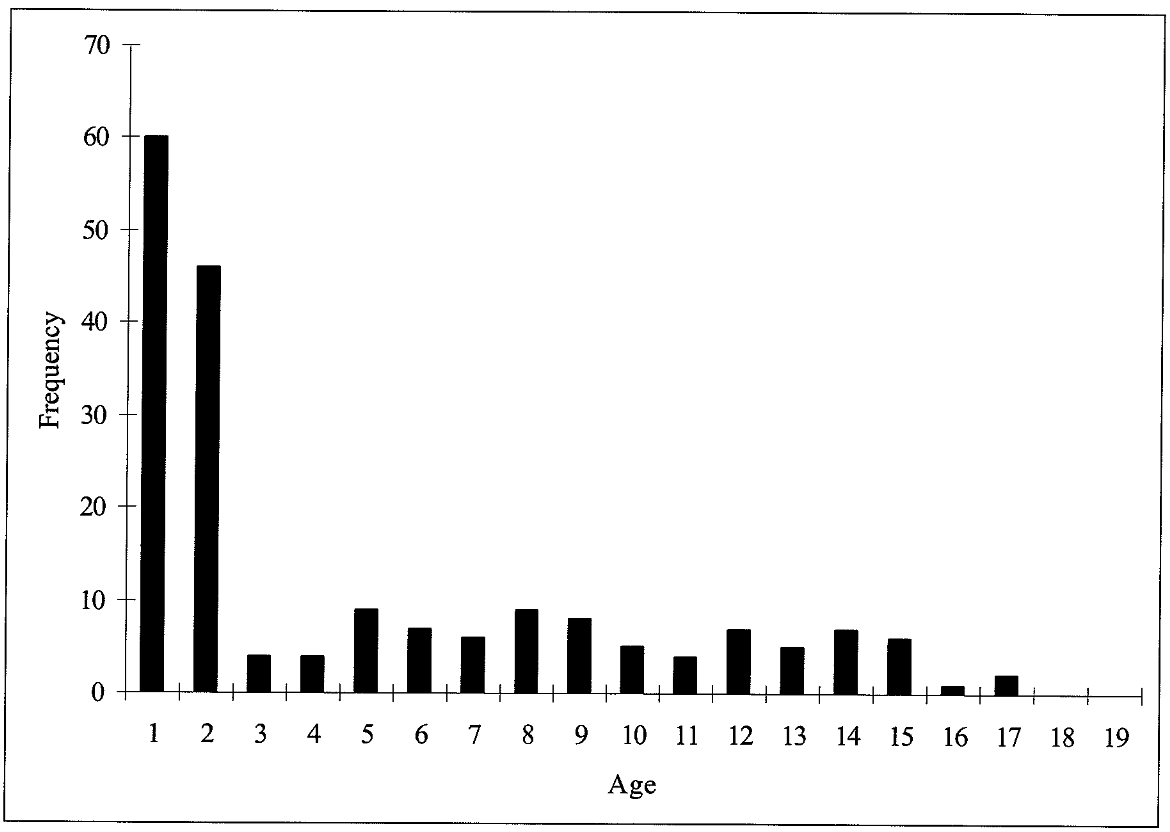
	N	Minimum	Maximum	Mean
Total gillraker count	11	32	37	33.7
Upper gillraker count	11	11	12	11.6
Lower gillraker count	11	20	25	22.1
Premaxillary angle	11	40	50	46.8
Dorsal ray count	11	10	12	11.1
Anal ray count	11	12	14	12.6
Pectoral ray count	11	16	17	16.4
Pelvic ray count	11	10	12	11.2
Age	11	4	14	8.4
Weight	11	27	93	54.7
Standard length	11	122.0	181.0	152.0
Fork length	10	135.0	200.0	167.6
Gillraker length	11	4.2	6.4	5.2
Lower arch length	11	12.5	19.3	15.8
Preorbital length	11	7.6	11.2	9.9
Orbital length	11	8.1	11.2	9.5
Post orbital length	11	14.8	21.6	18.7
Trunk length	11	29.1	51.5	38.6
Dorsal length	11	13.8	22.0	17.3
Lumbar length	11	18.4	29.1	24.3
Anal length	11	12.1	17.7	15.4
Caudal peduncle length	11	13.7	21.1	17.2
Head depth	11	13.4	20.8	17.1
Body depth	11	28.0	42.8	35.6
Caudal peduncle depth	11	8.9	13.1	10.7
Interorbital width	11	6.2	10.0	7.8
Maxillary length	11	11.0	16.3	13.0
Maxillary width	11	2.5	5.2	3.8
Pectoral length	11	21.0	30.1	25.7
Pelvic length	11	18.6	30.1	26.0
Adipose length	11	8.5	13.3	10.9



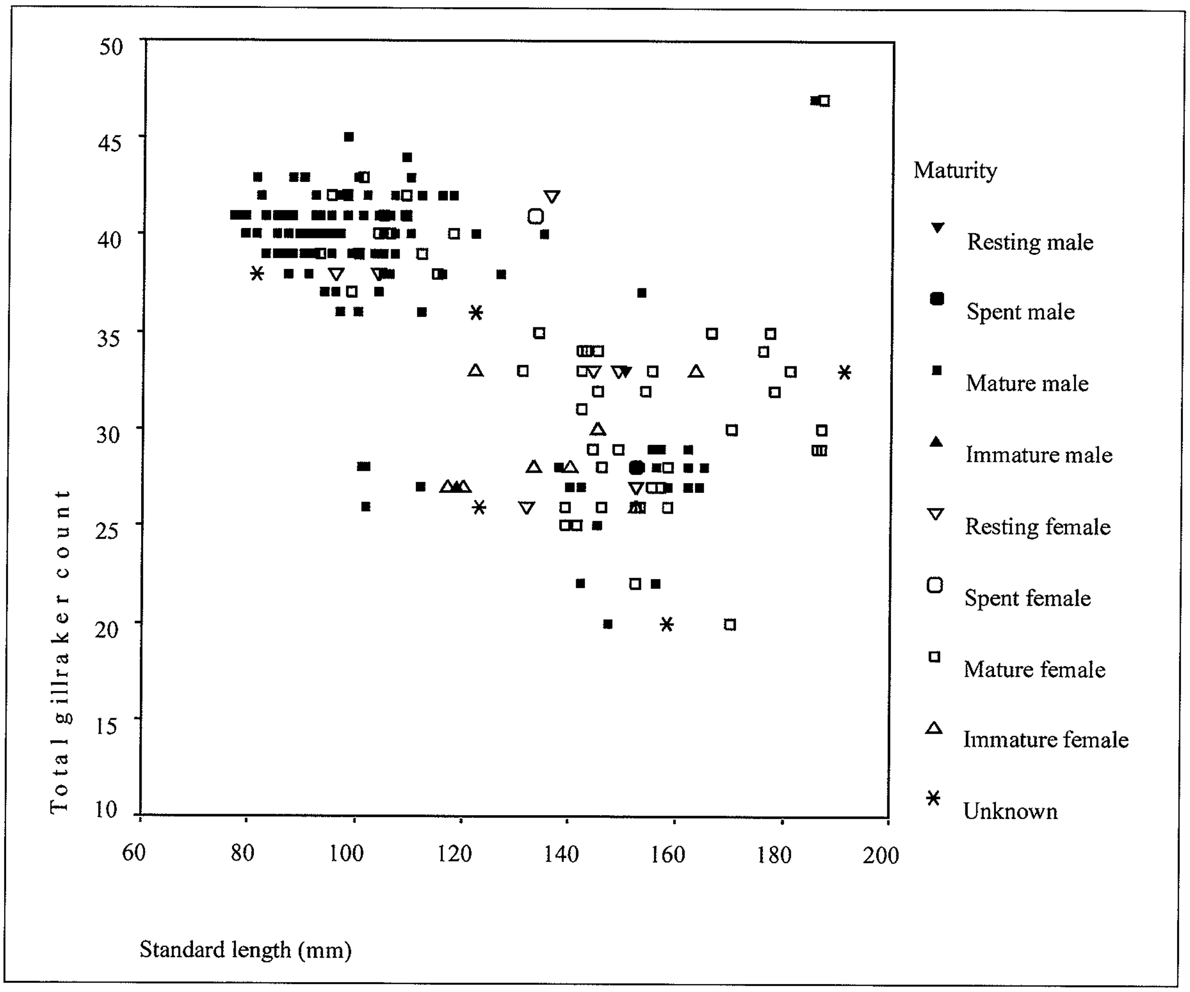
Appendix 3-2. Standard length frequency distribution for all ciscoes from both basins of Lake Athapapuskow.



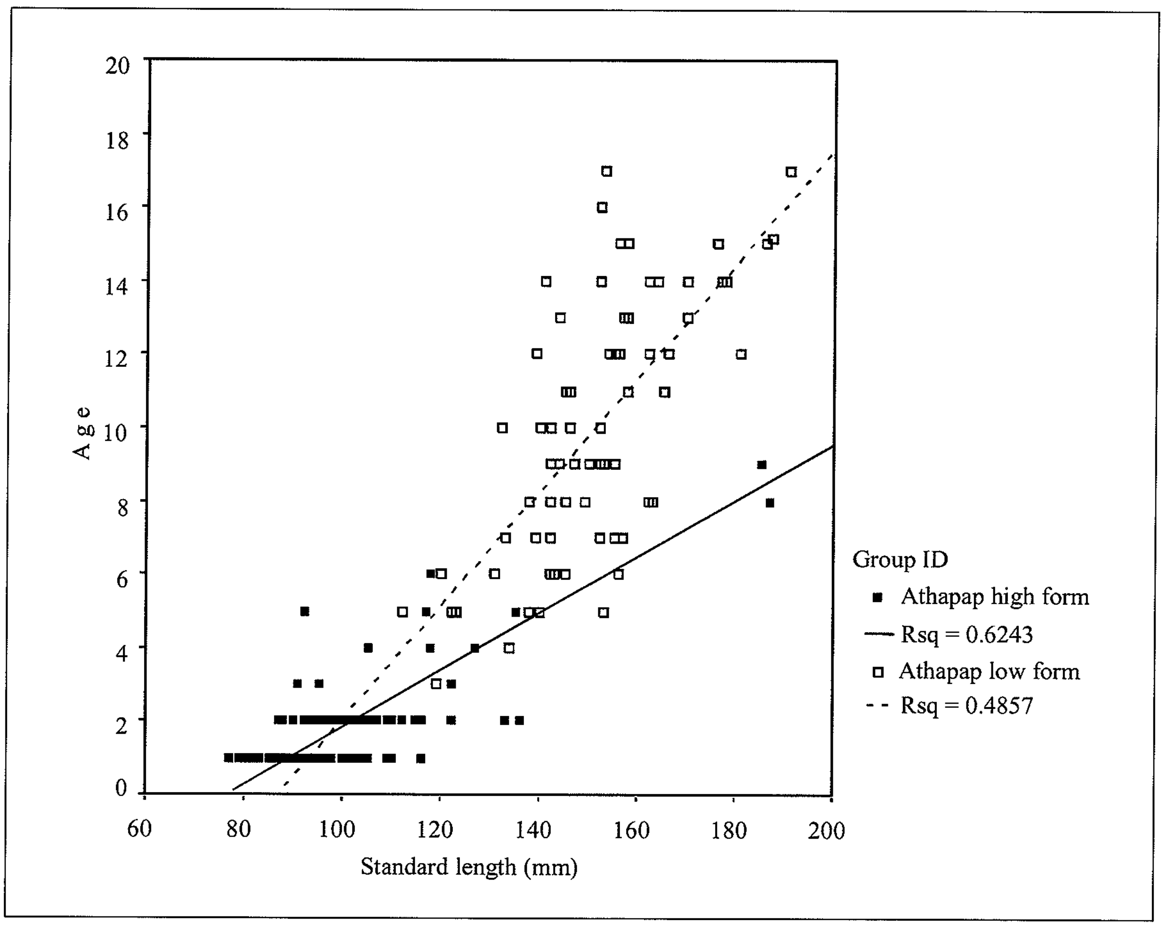
Appendix 3-3. Standard length versus weight for ciscoes from Lake Athapapuskow collection sites. Set number, date, depth, and number of number of fish captured and included in the legend.



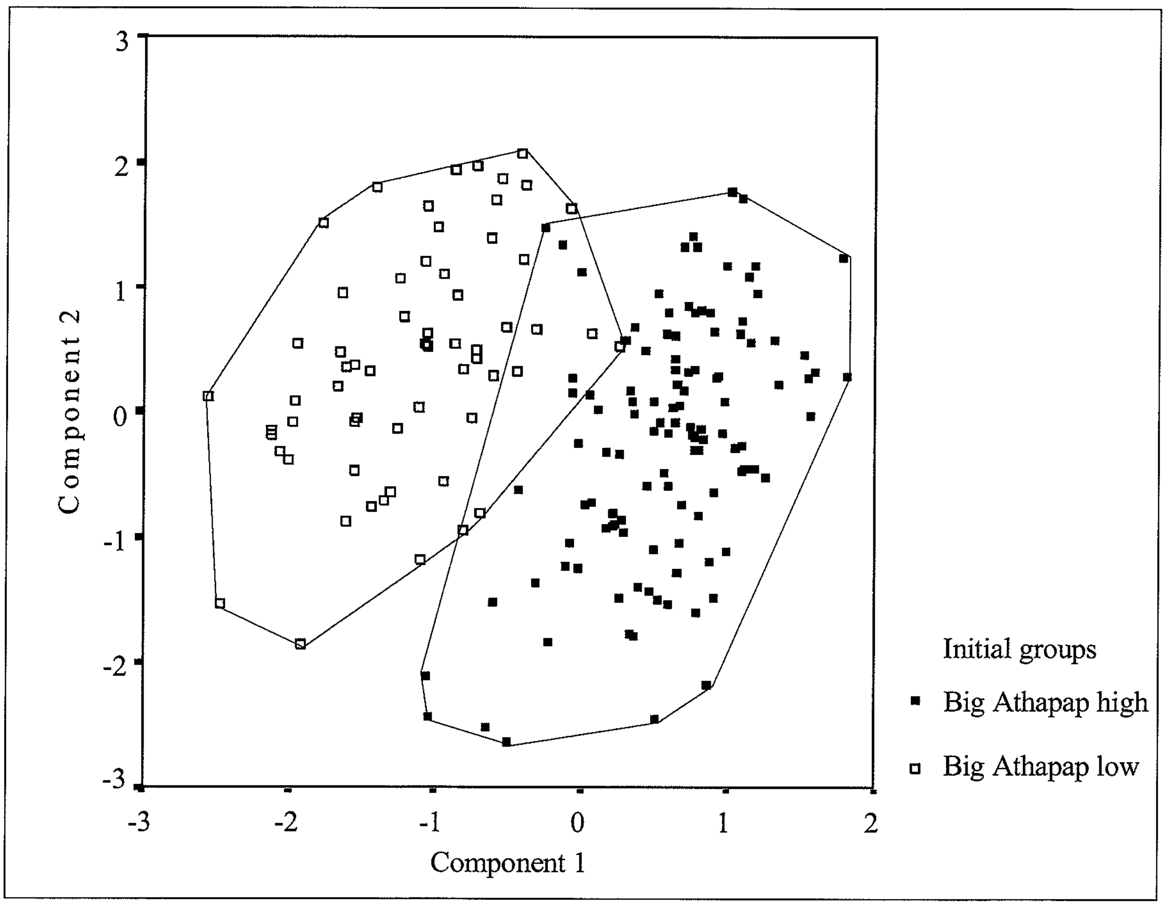
Appendix 3-4. Age frequency distribution for Lake Athapapuskow.



Appendix 3-5. Relationship between total gillraker count and standard length for all ciscoes collected from Lake Athapapuskow with individuals identified to maturity state.



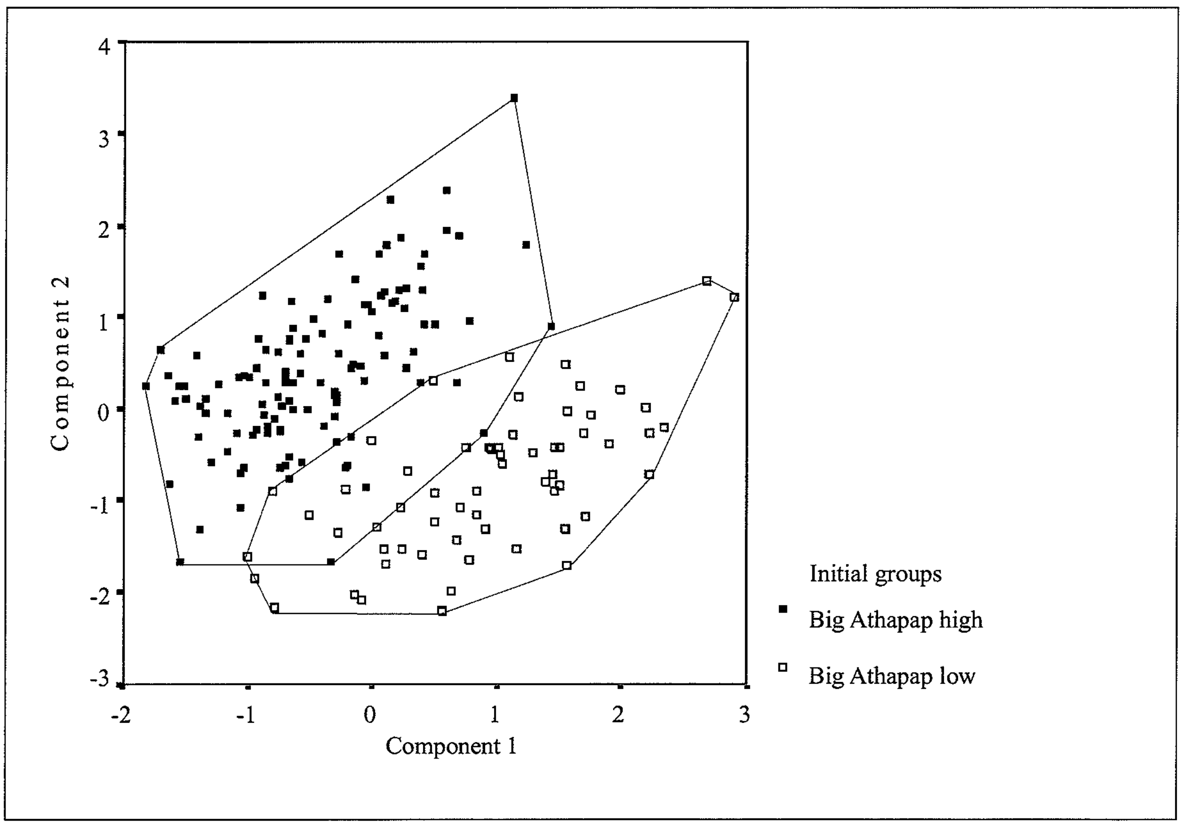
Appendix 3-6. Size-at-age for Lake Athapapuskow cisco forms.



Appendix 3-7. Plot of components 1 and 2 of PCA for ciscoes from Big Athapapuskow based upon meristic variables. Form was assigned *a posteriori* using key character criteria outlined in the text.

Appendix 3-8. Character loadings and variance explained by PCA of Big Athapapuskow ciscoes based upon meristic variables and premaxillary angle.

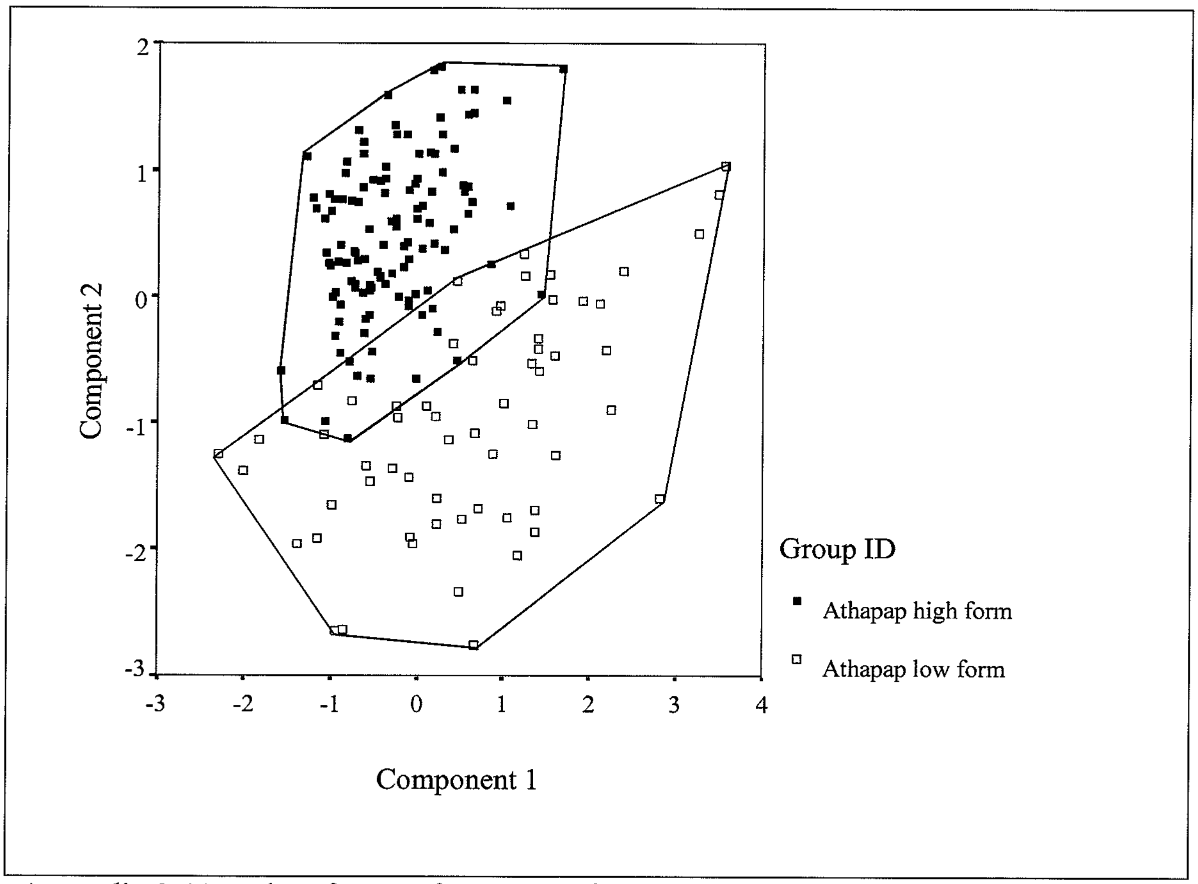
	Component	
	1	**2**
Premaxillary angle	-0.610	0.372
Dorsal ray count	0.149	0.764
Anal ray count	0.372	0.649
Pectoral ray count	0.180	0.684
Pelvic ray count	0.452	0.361
Upper gillraker count	0.896	-0.132
Lower gillraker count	0.800	-0.370
Eigenvalues	2.21	1.90
Percent of Variance	31.59	27.08
Cumulative Percent	31.59	58.67



Appendix 3-9. PCA plots for ciscoes from Big Athapapuskow based upon morphometric characters adjusted by ratios. Form was assigned *a posteriori* using key character criteria outlined in the text.

Appendix 3-10. Character loadings and variance explained for PCA of Big Athapapuskow morphometric characters adjusted by ratios.

	Component	
	1	2
Preorbital length	0.59	0.14
Orbital length	0.34	0.18
Postorbital length	0.73	0.12
Trunk length	0.19	-0.50
Dorsal length	-0.02	0.60
Lumbar length	0.08	-0.70
Anal length	-0.06	0.49
Caudal peduncle length	0.25	0.12
Head depth	0.46	0.38
Body depth	0.56	-0.56
Caudal peduncle depth	0.60	0.13
Interorbital width	0.32	0.55
Maxillary length	0.68	0.16
Maxillary width	0.05	0.42
Pectoral length	0.30	0.00
Pelvic length	0.27	-0.11
Adipose length	0.49	-0.09
Lower arch length	0.72	-0.08
Gillraker length	-0.35	0.55
Eigenvalues	3.60	2.73
Percent of Variance	18.95	14.39
Cumulative Percent	18.95	33.34



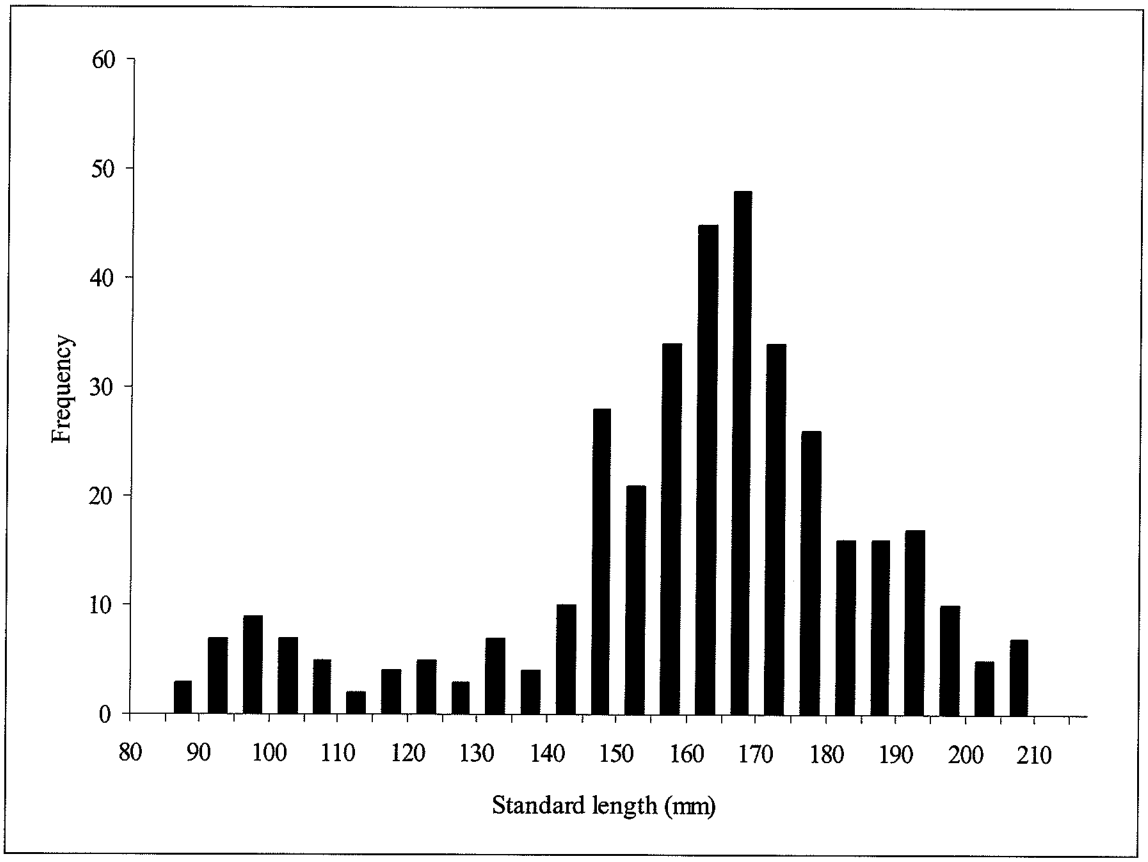
Appendix 3-11. Plot of scores from PCA of Big Athapapuskow cisco using morphometric characters adjusted by common within-groups residuals.

Appendix 3-12. Character loadings and variance explained by PCA of Big Athapapuskow ciscoes with morphometric characters adjusted by common within-group residuals.

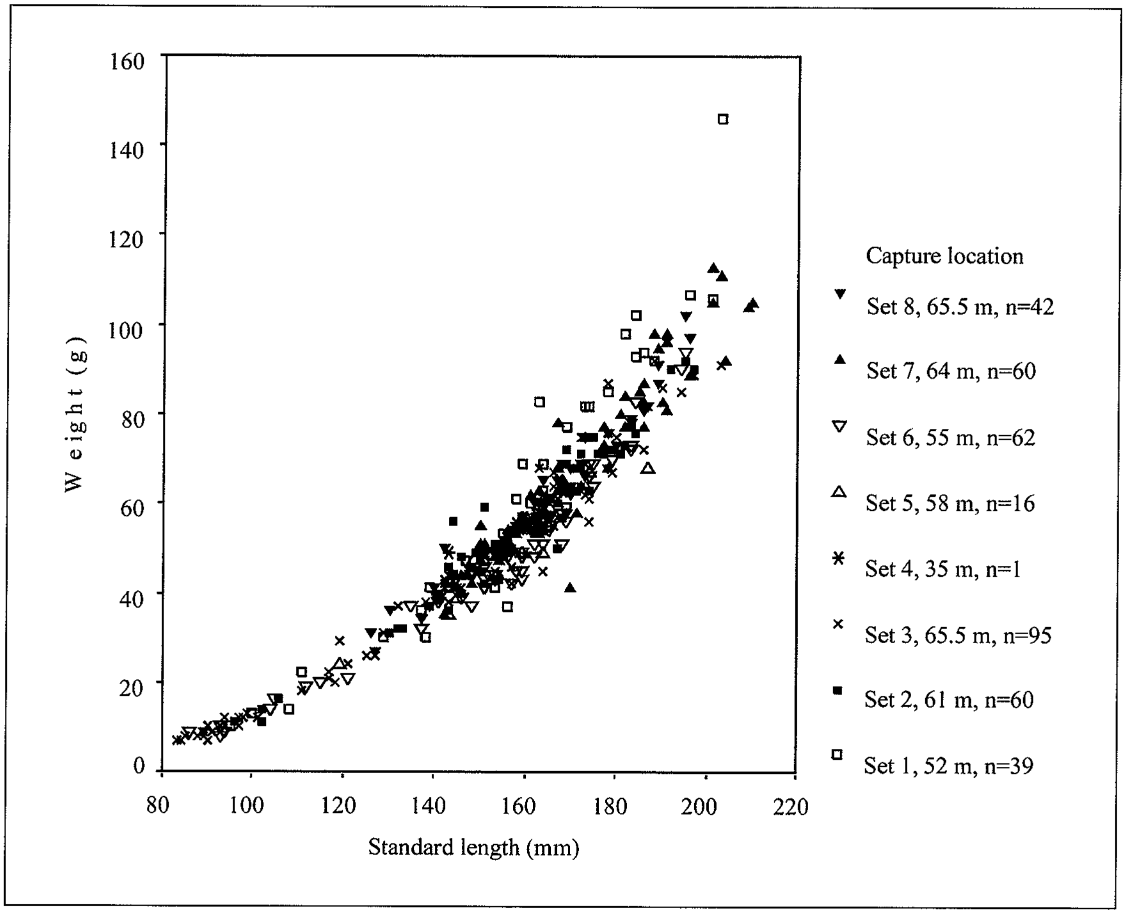
	Component	
	1	2
Preorbital length	0.69	0.09
Orbital length	0.60	-0.35
Postorbital length	0.79	0.10
Trunk length	-0.19	-0.06
Dorsal length	0.22	0.29
Lumbar length	-0.20	-0.52
Anal length	0.22	0.36
Caudal peduncle length	0.20	0.12
Head depth	0.52	0.42
Body depth	0.23	-0.47
Caudal peduncle depth	0.54	-0.26
Interorbital width	0.21	0.74
Maxillary length	0.74	-0.02
Maxillary width	0.14	0.29
Pectoral length	0.36	-0.44
Pelvic length	0.30	-0.55
Adipose length	0.45	0.02
Lower arch length	0.71	-0.01
Gillraker length	-0.08	0.52
Eigenvalues	3.83	2.51
Percent of Variance	20.16	13.24
Cumulative Percent	20.16	33.39

Appendix 4-1. Descriptive statistics for all ciscoes from Reindeer Lake. All variables are represented by raw, untransformed values.

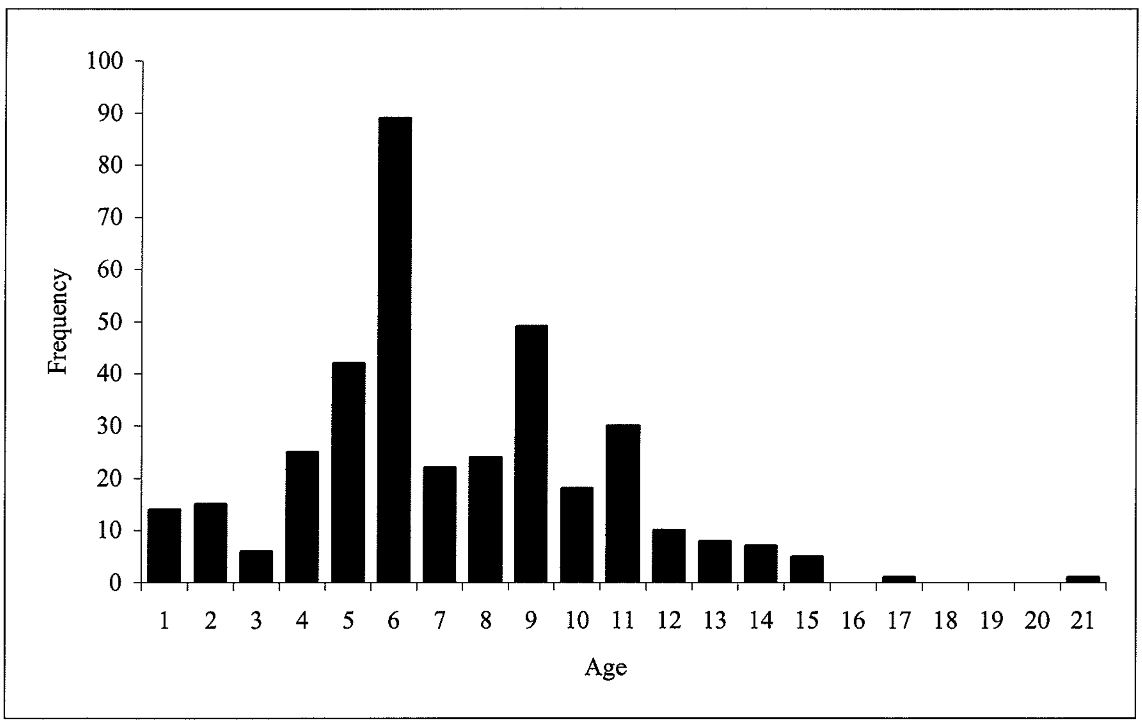
	N	Minimum	Maximum	Mean
Total gillraker count	375	23	48	32.3
Upper gillraker count	375	7	17	11.2
Lower gillraker count	375	14	32	21.1
Premaxillary angle	375	30	65	48.2
Dorsal ray count	375	9	13	10.6
Anal ray count	375	9	14	11.4
Pectoral ray count	373	12	18	16.0
Pelvic ray count	375	9	13	10.9
Age	366	1	21	7.2
Weight	375	7	146	54.2
Standard length	375	83.0	210.0	156.0
Fork length	340	91.0	291.0	171.6
Gillraker length	375	1.8	9.8	4.7
Lower arch length	375	8.5	28.5	18.9
Preorbital length	375	5.5	16.5	10.9
Orbital length	375	5.2	13.6	10.2
Post orbital length	375	8.4	28.6	19.2
Trunk length	375	14.9	55.5	37.4
Dorsal length	375	8.2	26.3	15.5
Lumbar length	375	11.8	39.5	26.3
Anal length	375	8.7	24.9	15.9
Caudal peduncle length	375	9.4	28.7	19.9
Head depth	375	8.8	25.4	16.8
Body depth	375	13.8	52.3	32.1
Caudal peduncle depth	375	4.9	17.0	10.2
Interorbital width	375	3.0	13.6	7.6
Maxillary length	375	6.5	20.9	14.1
Maxillary width	375	1.6	6.5	4.0
Pectoral length	375	12.5	38.5	25.0
Pelvic length	375	12.0	35.7	24.3
Adipose length	375	3.8	14.5	9.1



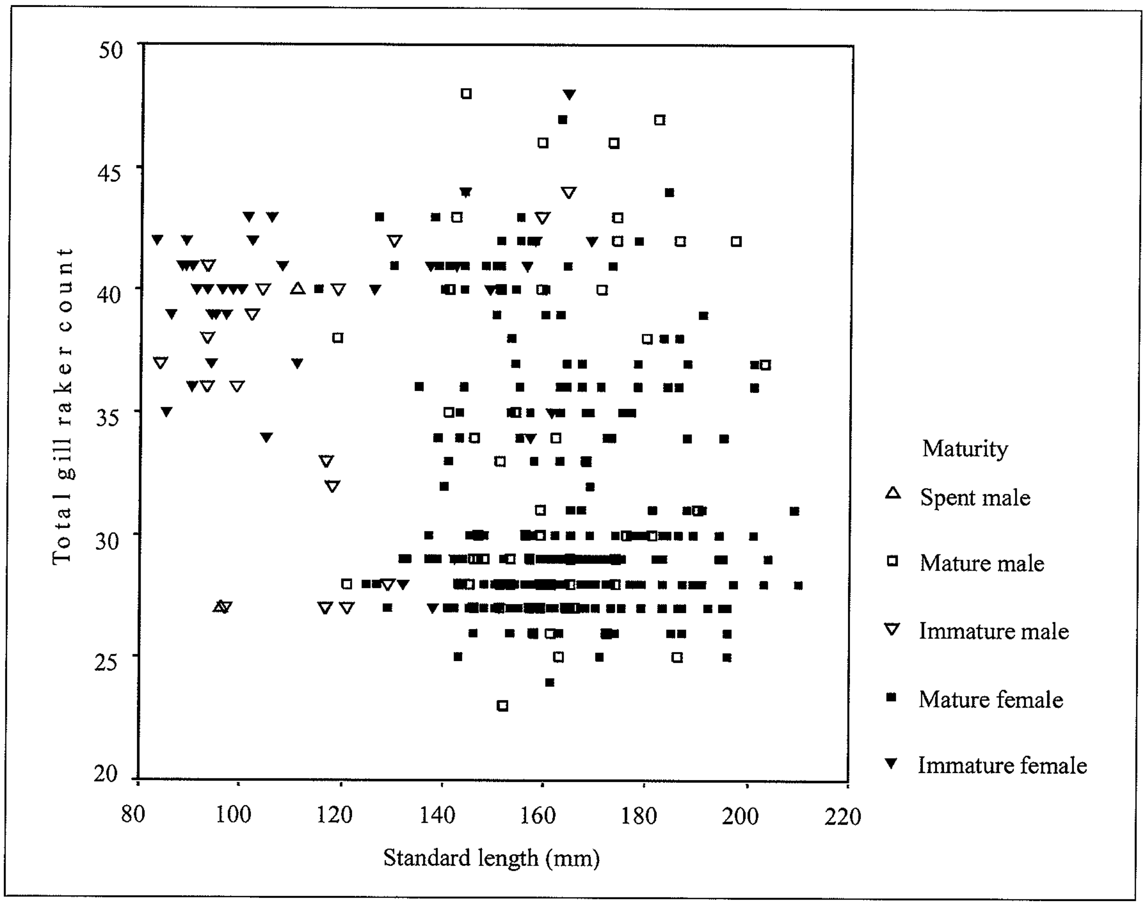
Appendix 4-2. Standard length frequency distribution for all ciscoes from Reindeer Lake.



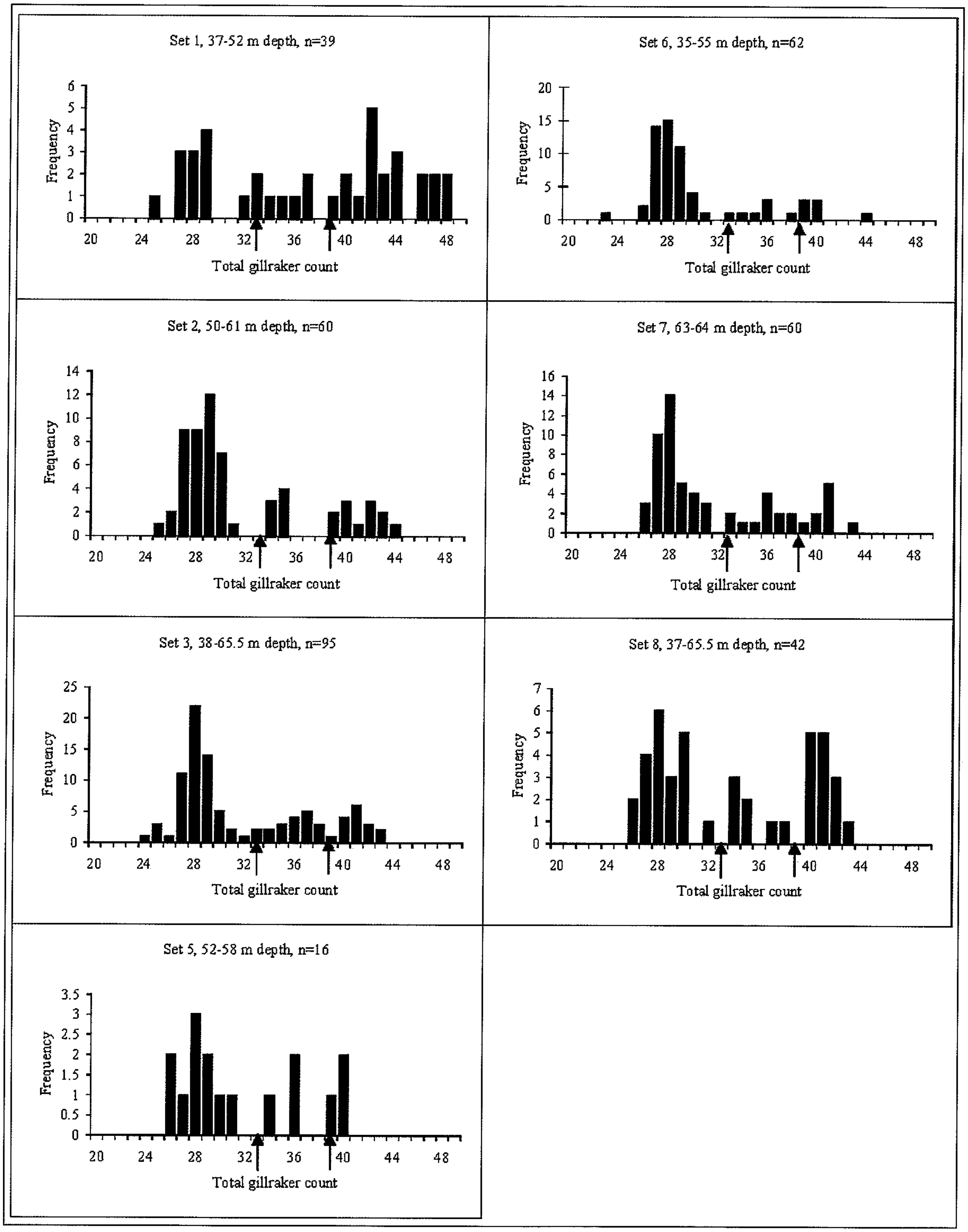
Appendix 4-3. Standard length versus weight for ciscoes from Reindeer Lake. Set number, date, depth, and number of number of fish captured and included in the legend.



Appendix 4-4. Age frequency distribution for ciscoes from Reindeer Lake.



Appendix 4-5. Relationship between total gillraker count and standard length for all ciscoes from Reindeer Lake with individuals identified to maturity state.



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.

Appendix 4-7. Descriptive statistics for the Reindeer Lake low gillraker form. All characters are represented by raw, untransformed values.

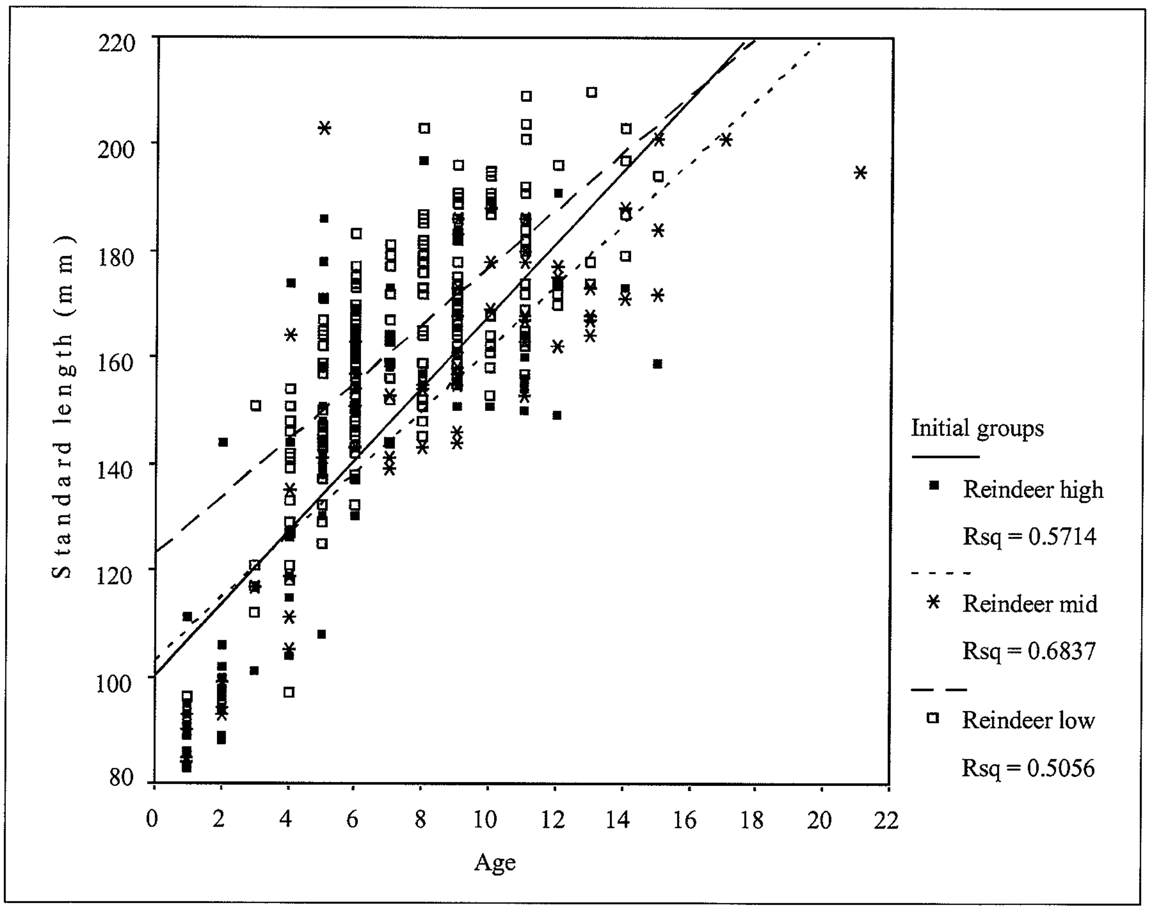
	N	Minimum	Maximum	Mean
Total gillraker count	231	23	32	28.2
Upper gillraker count	231	7	12	10.1
Lower gillraker count	231	14	21	18.0
Premaxillary angle	231	30	65	51.2
Dorsal ray count	231	9	12	10.5
Anal ray count	231	9	13	11.3
Pectoral ray count	230	13	18	16.0
Pelvic ray count	231	9	13	10.9
Age	225	1	15	7.4
Weight	231	11	111	57.8
Standard length	231	96.0	210.0	163.0
Fork length	216	103.0	291.0	177.2
Gillraker length	231	1.8	6.3	4.1
Lower arch length	231	11.0	26.0	19.5
Preorbital length	231	7.2	14.7	11.3
Orbital length	231	6.8	12.6	10.4
Post orbital length	231	10.7	26.2	20.1
Trunk length	231	21.0	55.5	39.3
Dorsal length	231	8.8	21.5	15.9
Lumbar length	231	13.6	39.5	28.0
Anal length	231	10.1	23.3	16.2
Caudal peduncle length	231	12.7	28.7	21.0
Head depth	231	10.7	24.8	17.1
Body depth	231	16.3	46.2	33.3
Caudal peduncle depth	231	5.5	13.6	10.4
Interorbital width	231	4.7	10.9	7.5
Maxillary length	231	9.1	18.7	14.5
Maxillary width	231	2.6	5.7	4.1
Pectoral length	231	14.7	32.0	25.2
Pelvic length	231	14.7	31.2	24.4
Adipose length	231	4.4	13.7	9.4

Appendix 4-8. Descriptive statistics for the Reindeer Lake mid gillraker form. All characters are represented by raw, untransformed values.

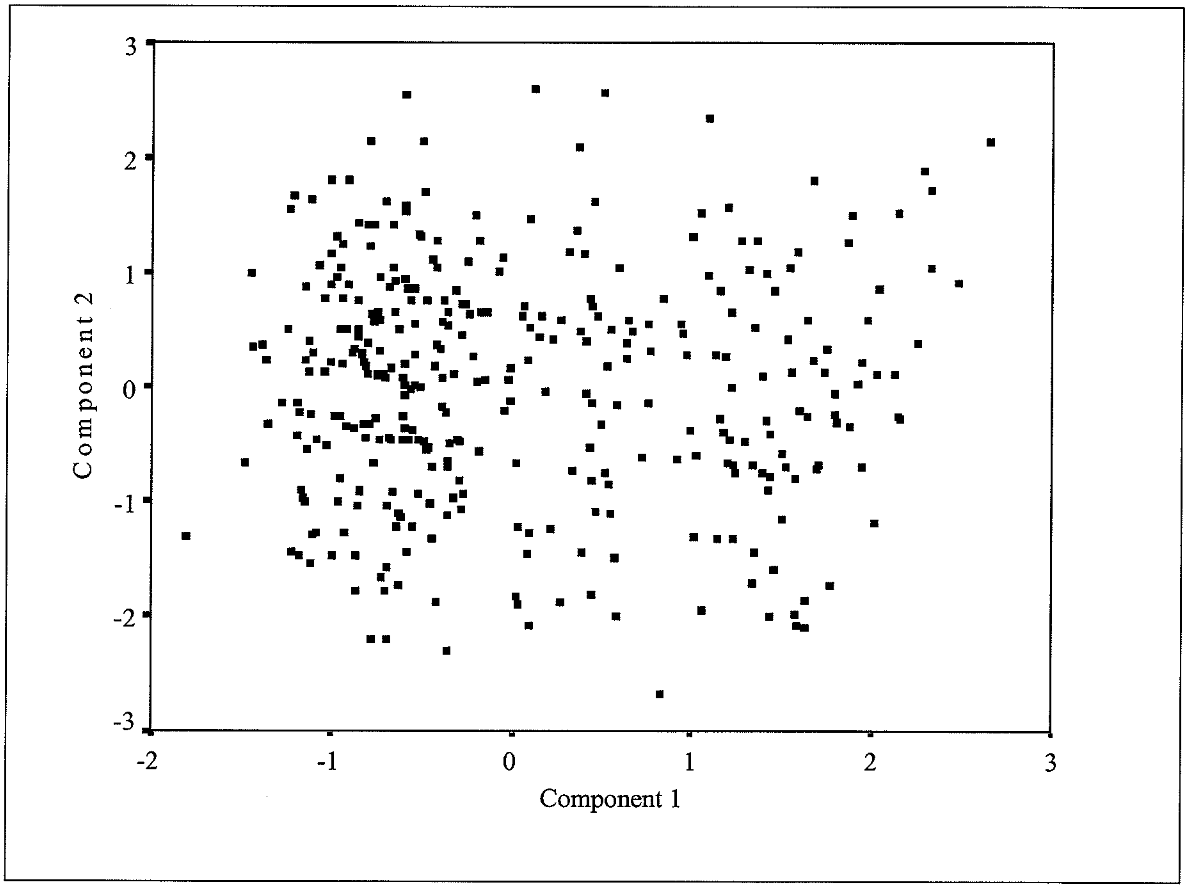
	N	Minimum	Maximum	Mean
Total gillraker count	63	33	38	35.5
Upper gillraker count	63	10	14	11.8
Lower gillraker count	63	21	26	23.7
Premaxillary angle	63	30	65	46.0
Dorsal ray count	63	10	12	10.9
Anal ray count	63	10	13	11.6
Pectoral ray count	63	12	18	16.0
Pelvic ray count	63	10	12	10.7
Age	63	1	21	8.6
Weight	63	7	146	55.5
Standard length	63	84.0	203.0	153.5
Fork length	53	94.0	223.0	171.4
Gillraker length	63	3.2	7.8	5.6
Lower arch length	63	9.2	28.5	19.7
Preorbital length	63	5.5	16.5	11.2
Orbital length	63	5.2	13.6	10.3
Post orbital length	63	8.7	28.6	19.2
Trunk length	63	14.9	52.5	36.1
Dorsal length	63	8.3	26.3	15.6
Lumbar length	63	11.8	37.0	25.2
Anal length	63	8.7	24.9	15.5
Caudal peduncle length	63	9.8	27.7	19.6
Head depth	63	9.6	25.4	17.8
Body depth	63	14.7	52.3	31.7
Caudal peduncle depth	63	4.9	17.0	10.2
Interorbital width	63	3.0	13.6	8.2
Maxillary length	63	6.5	20.9	15.0
Maxillary width	63	2.0	6.5	4.1
Pectoral length	63	12.7	38.5	24.9
Pelvic length	63	12.0	35.3	24.0
Adipose length	63	3.8	14.5	9.1

Appendix 4-9. Descriptive statistics for the Reindeer Lake high gillraker form. All characters are represented by raw, untransformed values.

	N	Minimum	Maximum	Mean
Total gillraker count	81	39	48	41.5
Upper gillraker count	81	12	17	13.7
Lower gillraker count	81	26	32	27.8
Premaxillary angle	81	30	60	41.1
Dorsal ray count	81	9	13	10.6
Anal ray count	81	10	14	11.7
Pectoral ray count	80	13	18	15.9
Pelvic ray count	81	9	12	10.9
Age	78	1	15	5.6
Weight	81	7	102	43.0
Standard length	81	83.0	197.0	138.1
Fork length	71	91.0	216.0	154.5
Gillraker length	81	3.2	9.8	5.6
Lower arch length	81	8.5	24.6	16.4
Preorbital length	81	5.5	13.6	9.5
Orbital length	81	5.2	13.3	9.4
Post orbital length	81	8.4	24.4	16.6
Trunk length	81	15.9	48.8	33.1
Dorsal length	81	8.2	23.8	14.3
Lumbar length	81	12.1	36.6	22.5
Anal length	81	9.4	22.8	15.4
Caudal peduncle length	81	9.4	26.4	16.9
Head depth	81	8.8	20.8	15.5
Body depth	81	13.8	47.8	28.8
Caudal peduncle depth	81	5.2	15.5	9.9
Interorbital width	81	3.3	10.7	7.0
Maxillary length	81	6.6	19.8	12.2
Maxillary width	81	1.6	5.8	3.8
Pectoral length	81	12.5	35.4	24.4
Pelvic length	81	12.4	35.7	24.1
Adipose length	81	4.0	14.4	8.4



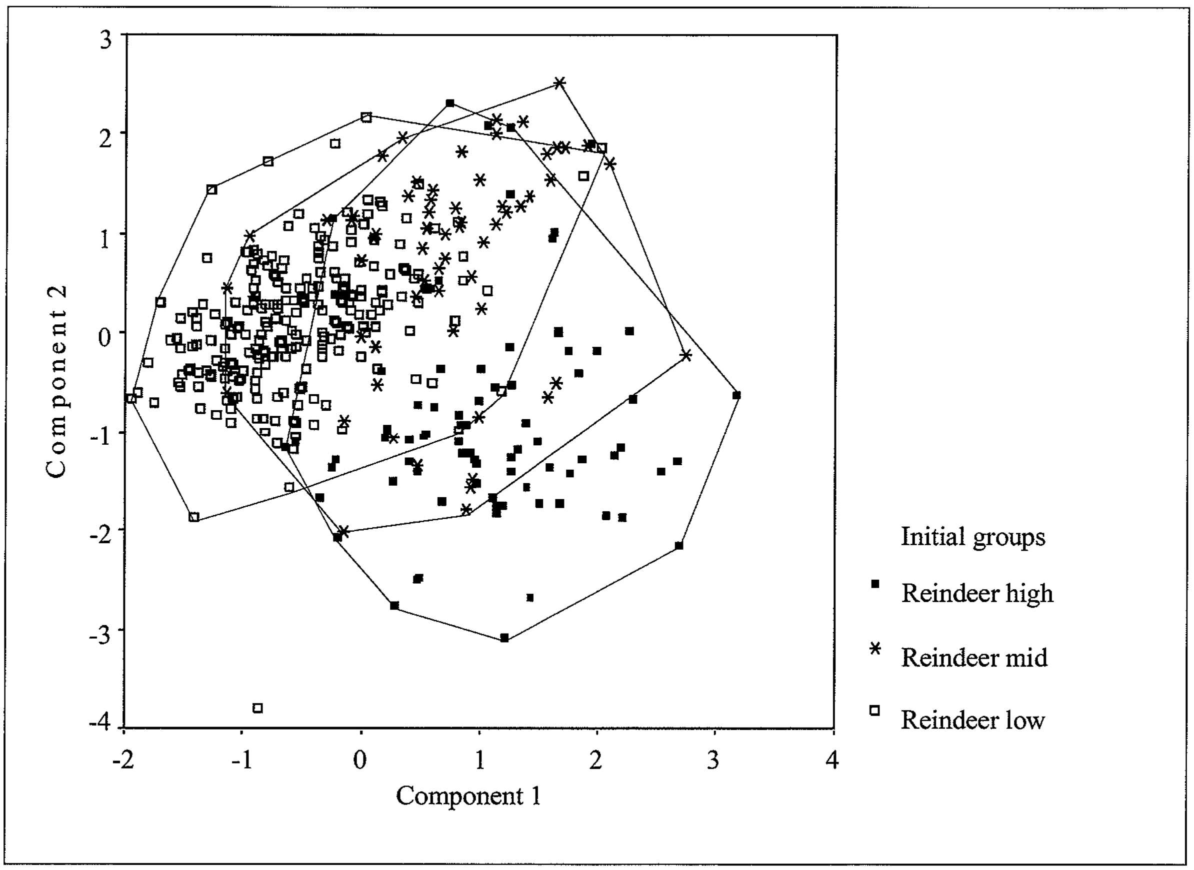
Appendix 4-10. Size-at-age plots for Reindeer Lake cisco groups.



Appendix 4-11. Plot of PCA scores on components 1 and 2 for Reindeer Lake ciscoes using meristic characters and premaxillary angle.

Appendix 4-12. Character loadings and variance explained from PCA of ciscoes from Reindeer Lake using meristic characters and premaxillary angle.

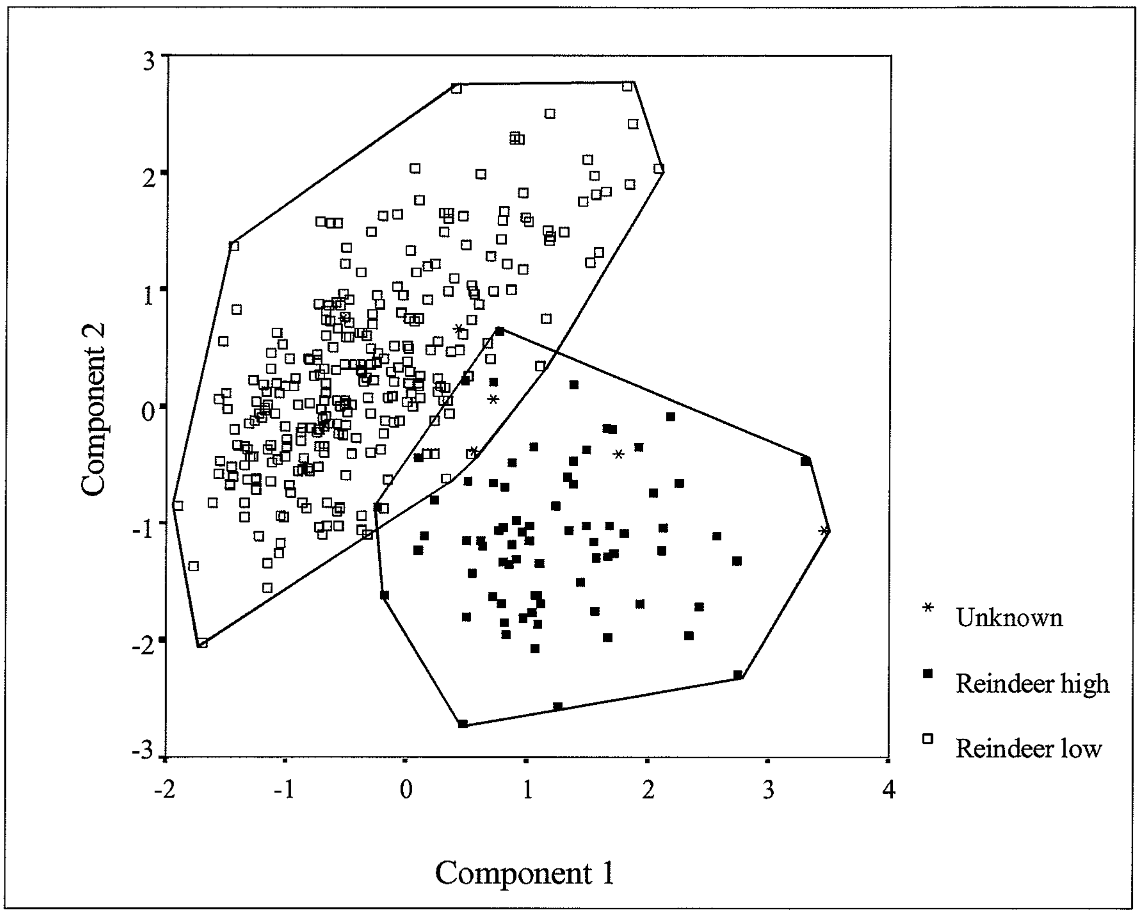
	Component 1	Component 2
Premaxillary angle	-0.719	0.207
Dorsal ray count	0.120	0.386
Anal ray count	0.397	0.555
Pectoral ray count	-0.066	0.617
Pelvic ray count	-0.028	0.612
Upper gillraker count	0.919	-0.045
Lower gillraker count	0.929	-0.020
Eigenvalues	2.40	1.26
Percent of Variance	34.31	17.97
Cumulative Percent	34.31	52.28



Appendix 4-13. Plot of PCA scores for ciscoes from Reindeer Lake using morphometric characters adjusted by ratios. Form was assigned *a posteriori* using criteria outlined in text.

Appendix 4-14. Character loadings and variance explained by PCA of Reindeer Lake ciscoes using morphometric characters adjusted by ratios.

	Component	
	1	2
Preorbital length	0.29	0.55
Orbital length	0.67	0.18
Postorbital length	0.11	0.53
Trunk length	-0.32	-0.26
Dorsal length	0.51	-0.14
Lumbar length	-0.43	0.11
Anal length	0.49	-0.47
Caudal peduncle length	-0.29	0.24
Head depth	0.63	0.31
Body depth	0.28	0.12
Caudal peduncle depth	0.57	-0.29
Interorbital width	0.61	0.18
Maxillary length	0.36	0.69
Maxillary width	0.24	-0.20
Pectoral length	0.71	-0.27
Pelvic length	0.72	-0.32
Adipose length	0.31	0.05
Lower arch length	0.25	0.65
Gillraker length	0.73	-0.19
Eigenvalues	4.49	2.38
Percent of Variance	23.64	12.53
Cumulative Percent	23.64	36.17



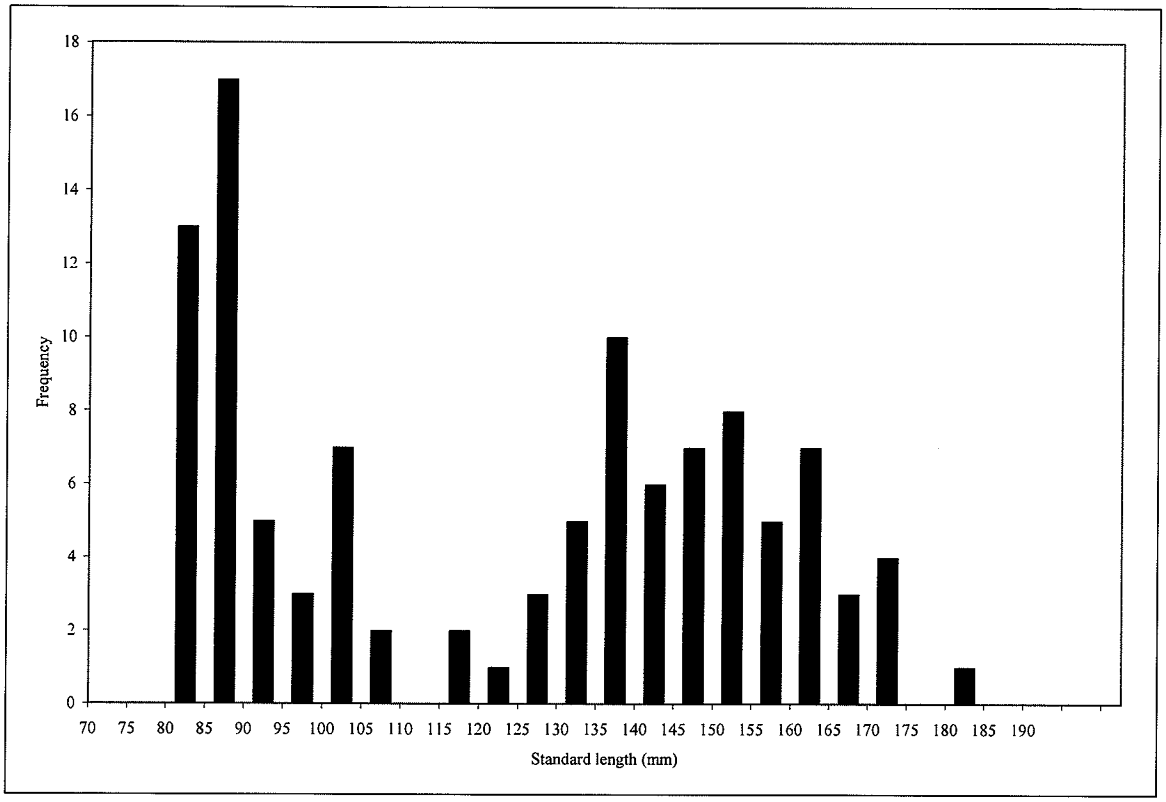
Appendix 4-15. PCA plot for Reindeer Lake ciscoes using morphometric characters adjusted to common within-group residual values. Groups were identified *a posteriori*.

Appendix 4-16. Character loadings and variance explained by PCA for Reindeer Lake ciscoes using morphometric characters adjusted by common within-group residuals.

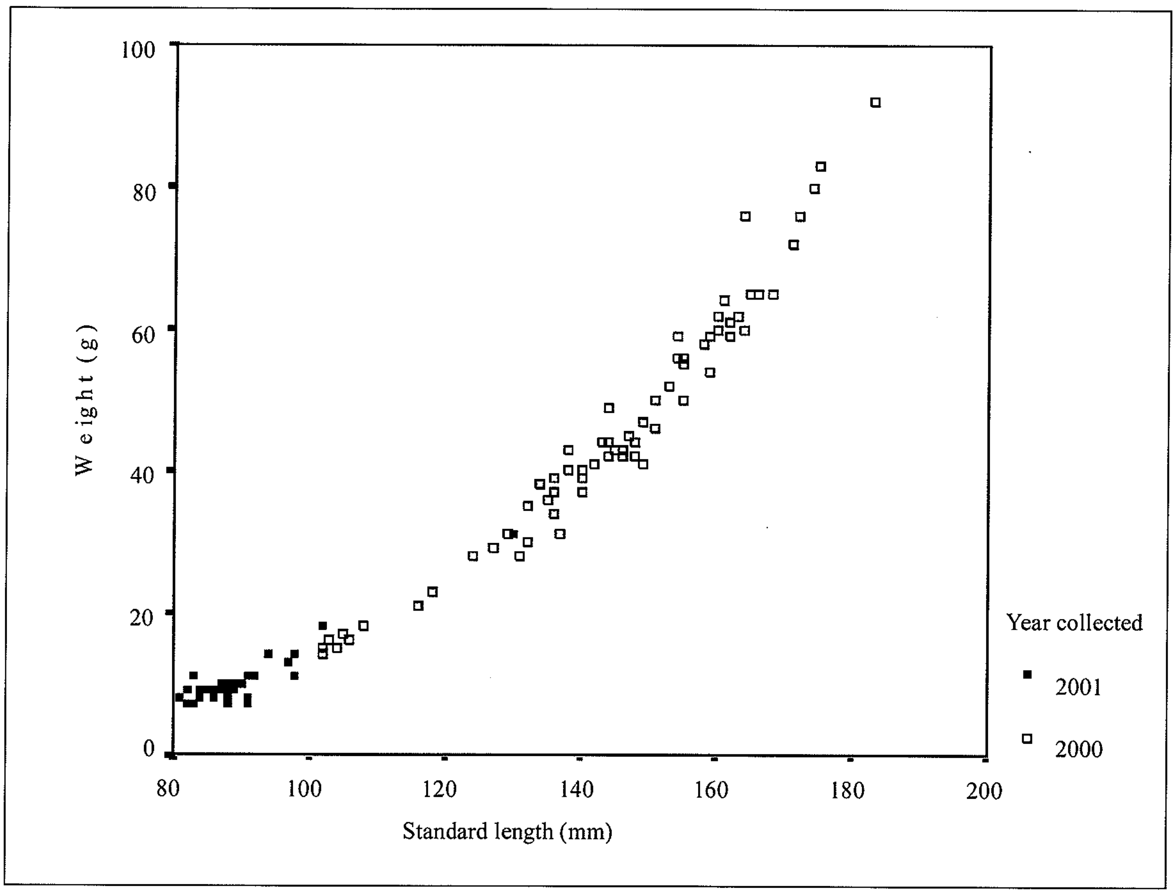
	Component	
	1	2
Preorbital length	0.19	0.63
Orbital length	0.61	0.23
Post orbital length	0.20	0.45
Trunk length	-0.17	-0.38
Dorsal length	0.52	-0.08
Lumbar length	-0.42	-0.03
Anal length	0.54	-0.32
Caudal peduncle length	-0.31	0.21
Head depth	0.56	0.43
Body depth	0.48	-0.14
Caudal peduncle depth	0.64	-0.37
Interorbital width	0.65	0.21
Maxillary length	0.25	0.74
Maxillary width	0.40	0.09
Pectoral length	0.72	-0.32
Pelvic length	0.73	-0.35
Adipose length	0.38	-0.06
Lower arch length	0.20	0.71
Gillraker length	0.75	-0.12
Eigenvalues	4.70	2.64
Percent of Variance	24.76	13.89
Cumulative Percent	24.76	38.65

Appendix 5-1. Descriptive statistics for the combined cisco catch from George Lake. All characters are represented by raw, untransformed data.

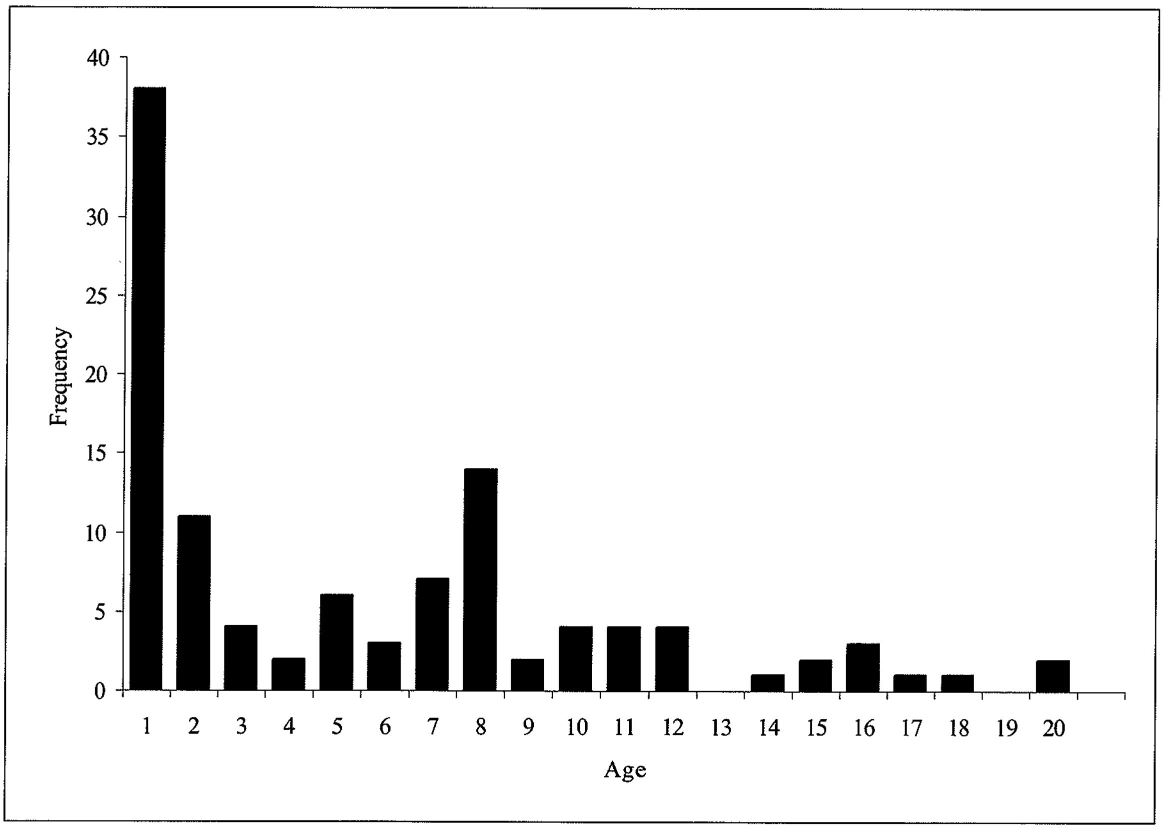
	N	Minimum	Maximum	Mean
Total gillraker count	109	30	45	36.8
Upper gillraker count	109	9	17	12.5
Lower gillraker count	109	20	30	24.3
Premaxillary angle	109	35	60	46.7
Dorsal ray count	109	9	12	10.8
Anal ray count	108	11	14	12.0
Pectoral ray count	109	14	17	15.4
Pelvic ray count	109	9	12	10.8
Age	109	1	20	5.6
Weight	109	7	92	32.4
Standard length	109	81.0	183.0	123.7
Fork length	104	88.0	203.0	138.7
Gillraker length	109	1.7	5.4	3.3
Lower arch length	109	8.0	21.2	13.9
Preorbital length	109	4.8	12.4	7.9
Orbital length	109	4.6	12.0	8.3
Post orbital length	109	8.6	23.6	15.2
Trunk length	109	18.4	47.3	30.2
Dorsal length	109	6.2	19.4	12.3
Lumbar length	109	11.4	34.4	20.9
Anal length	109	8.4	19.8	13.0
Caudal peduncle length	109	8.4	22.5	15.1
Head depth	109	8.8	21.7	14.2
Body depth	109	12.5	45.2	27.2
Caudal peduncle depth	109	5.1	13.1	8.8
Interorbital width	109	3.9	9.6	6.7
Maxillary length	109	5.3	17.4	10.9
Maxillary width	109	1.7	5.8	3.3
Pectoral length	109	11.5	32.6	21.1
Pelvic length	109	10.9	33.5	20.9
Adipose length	109	2.2	14.7	7.8



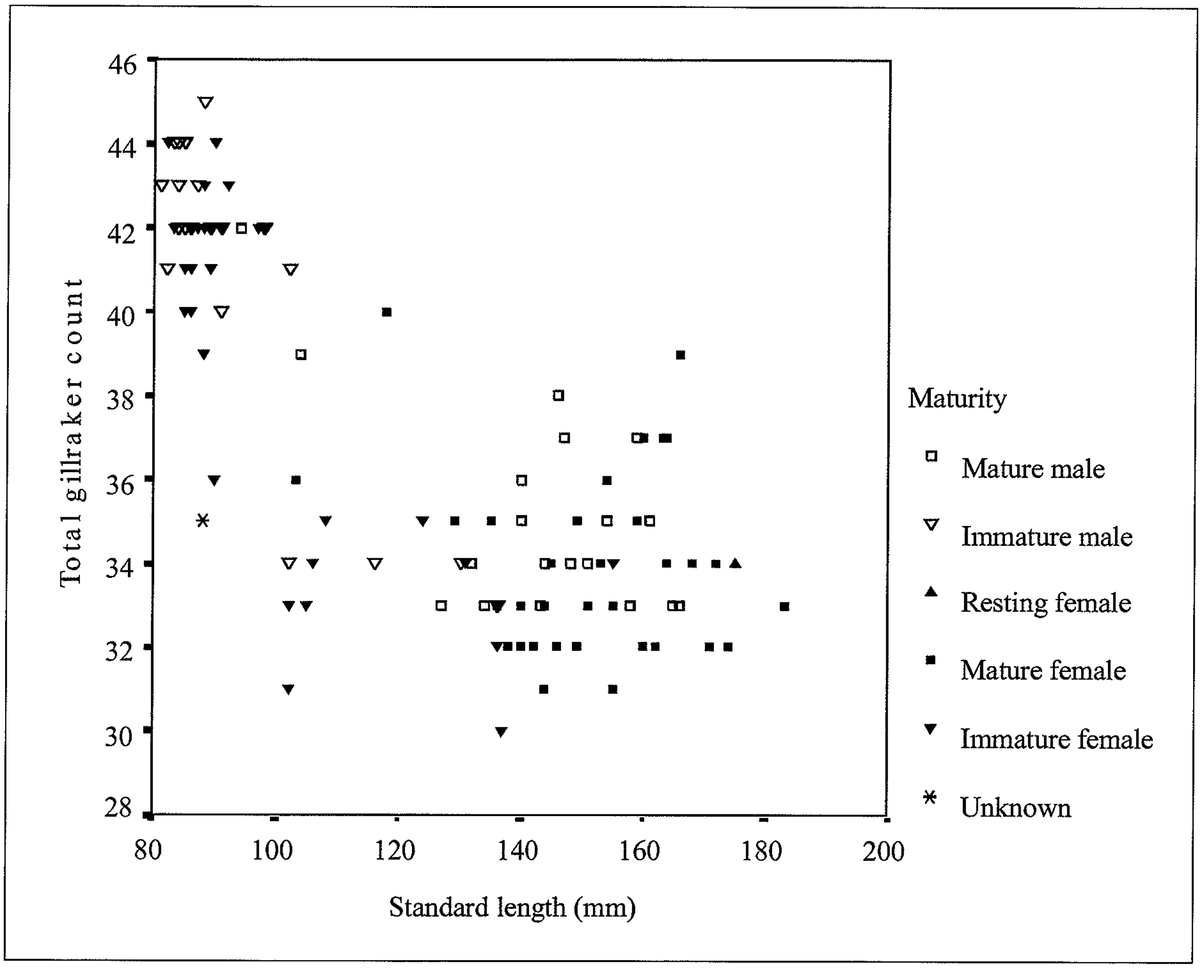
Appendix 5-2. Standard length frequency distribution for all ciscoes collected from George Lake.



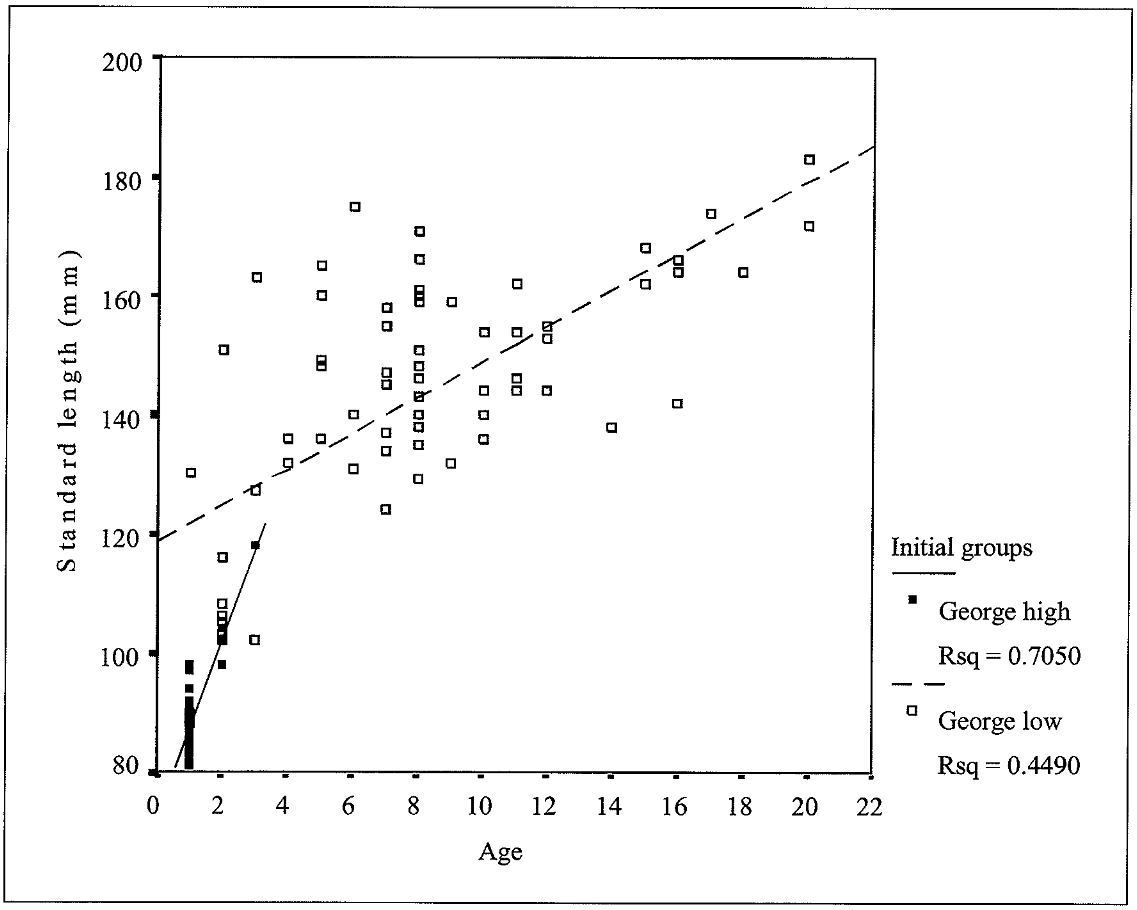
Appendix 5-3. Standard length versus weight for ciscoes collected from George Lake in 2000 and 2001.



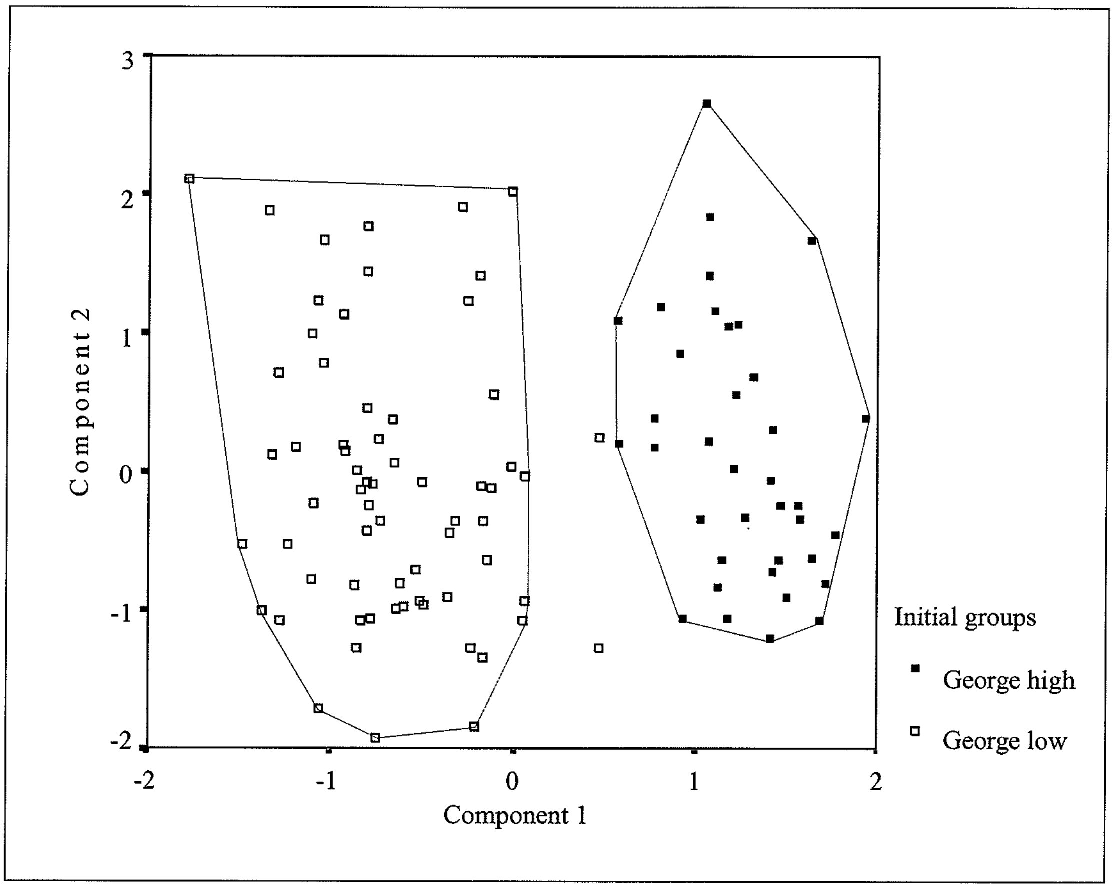
Appendix 5-4. Age frequency distribution for George Lake ciscoes.



Appendix 5-5. Relationship between total gillraker count and standard length for all ciscoes form George Lake with maturity identified.



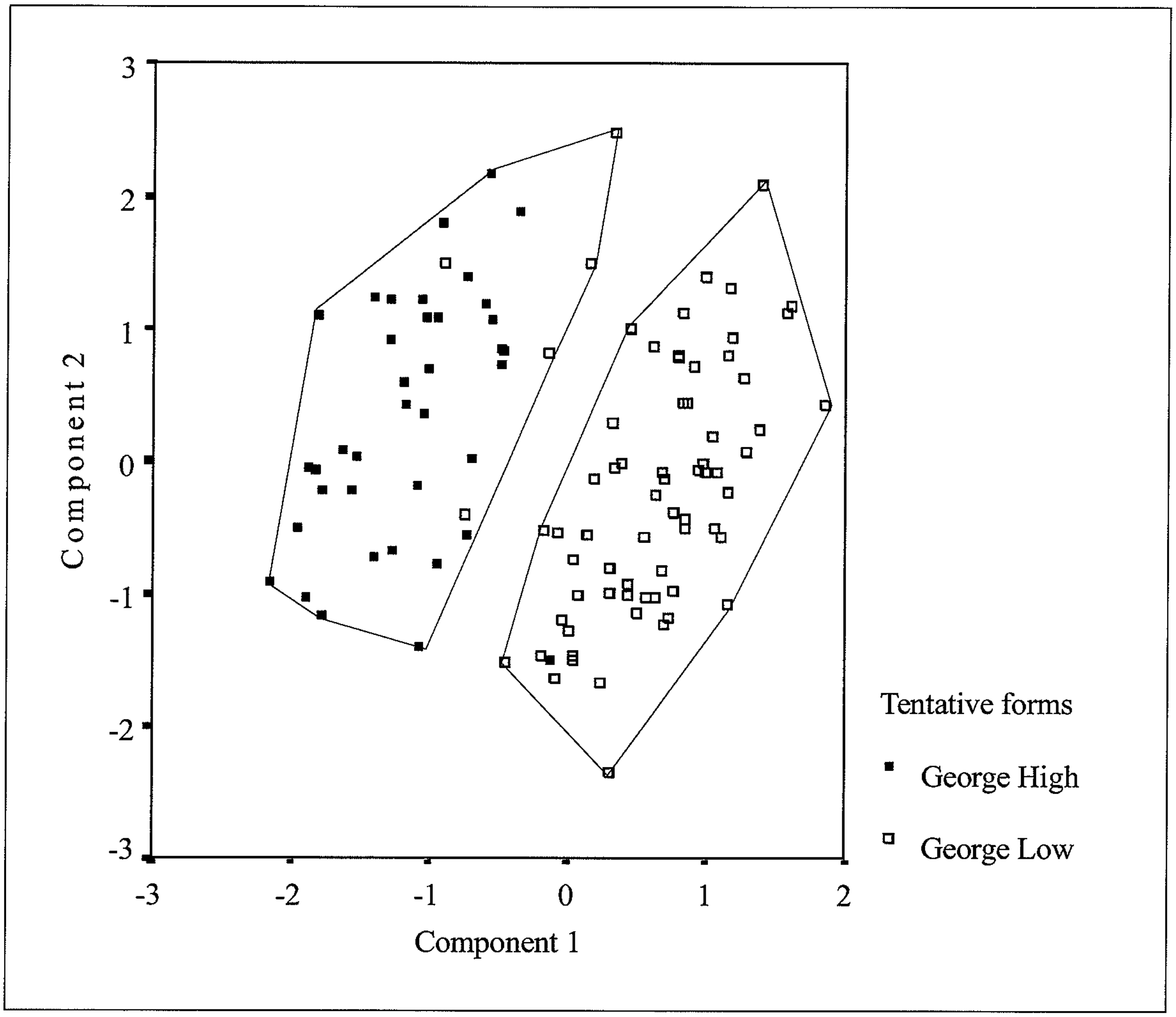
Appendix 5-6. Size-at-age plots for George Lake cisco forms.



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 *a posteriori* as outlined in text.

Appendix 5-8. Character loadings and variance explained from PCA of George Lake ciscoes using meristic characters and premaxillary angle.

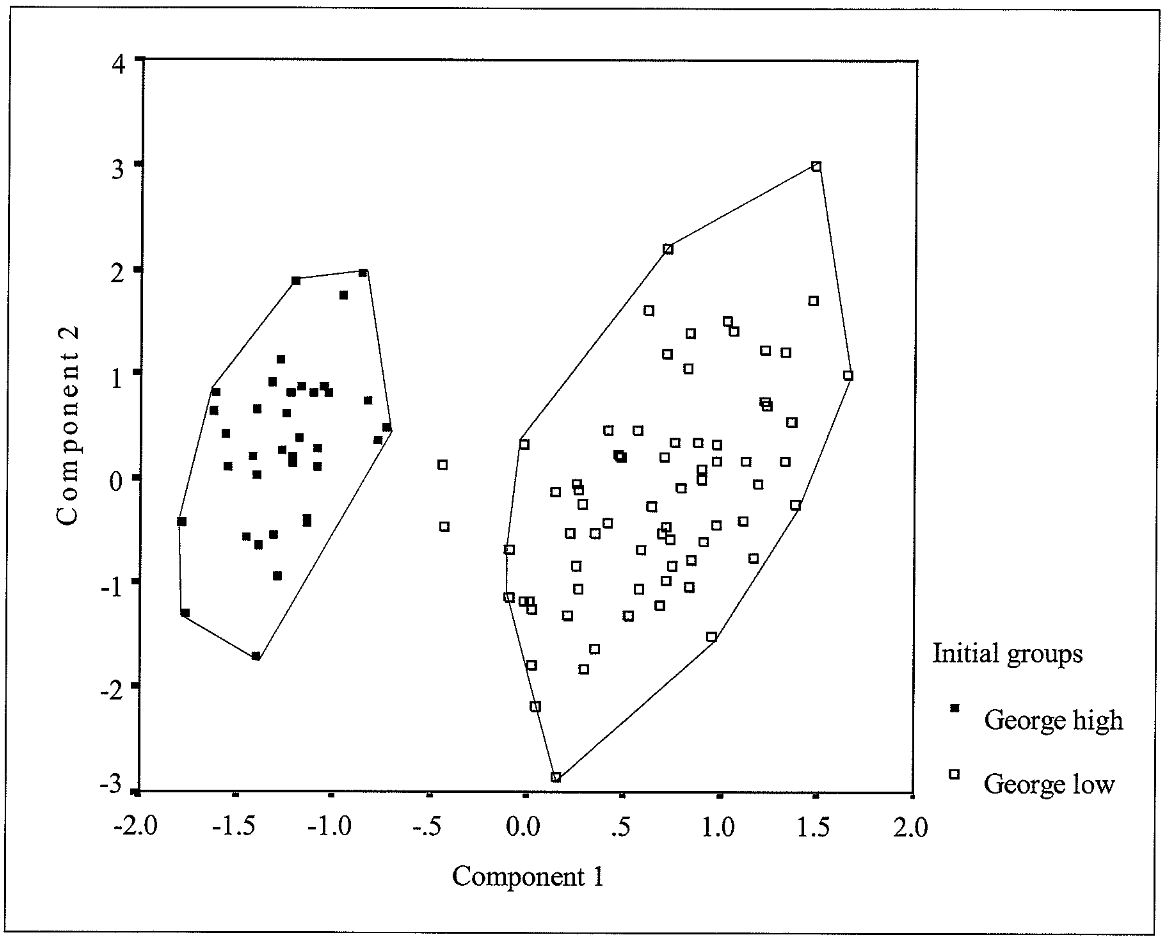
	Component 1	Component 2
Premaxillary angle	-0.756	-0.012
Upper gillraker count	0.870	0.218
Lower gillraker count	0.878	0.224
Dorsal ray count	-0.383	0.560
Anal ray count	-0.407	0.591
Pectoral ray count	0.143	0.752
Pelvic ray count	-0.226	0.209
Eigenvalues	2.48	1.37
Percent of Variance	35.47	19.58
Cumulative Percent	35.47	55.05



Appendix 5-9. PCA plot for ciscoes collected from George Lake using morphometric characters adjusted by ratios. Groups were identified *a posteriori* following PCA using meristic characters. Boundaries indicate groups suggested by this PCA.

Appendix 5-10. Character loadings and variance explained by PCA of George Lake ciscoes using morphometric characters adjusted by ratios.

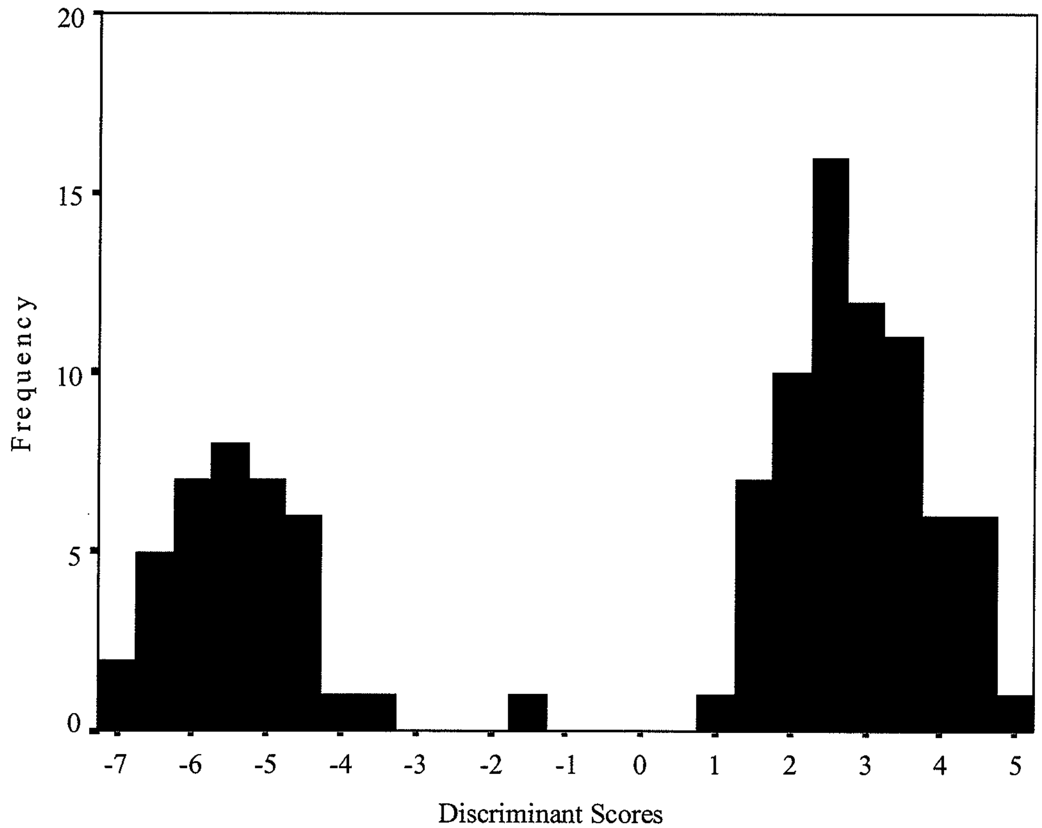
	Component	
	1	2
Preorbital length	0.34	0.65
Orbital length	0.68	0.28
Postorbital length	0.66	0.03
Trunk length	0.04	-0.61
Dorsal length	0.39	0.23
Lumbar length	0.31	-0.17
Anal length	-0.65	0.38
Caudal peduncle length	-0.39	0.41
Head depth	0.51	0.27
Body depth	0.80	-0.38
Caudal peduncle depth	0.62	0.26
Interorbital width	0.09	0.13
Maxillary length	0.81	0.05
Maxillary width	0.36	0.02
Pectoral length	0.71	0.05
Pelvic length	0.78	0.00
Adipose length	0.26	-0.01
Lower arch length	0.24	0.65
Gillraker length	-0.78	0.33
Eigenvalues	5.77	2.11
Percent of Variance	30.35	11.12
Cumulative Percent	30.35	41.47



Appendix 5-11. Plot of PCA scores for George Lake ciscoes using morphometric characters adjusted by common-within-group residuals. Forms were assigned *a posteriori* as outlined in the text. Boundaries show forms suggested by this PCA.

Appendix 5-12. Character loadings and variance explained for PCA of George Lake ciscoes using morphometric characters adjusted with common-within-group residuals.

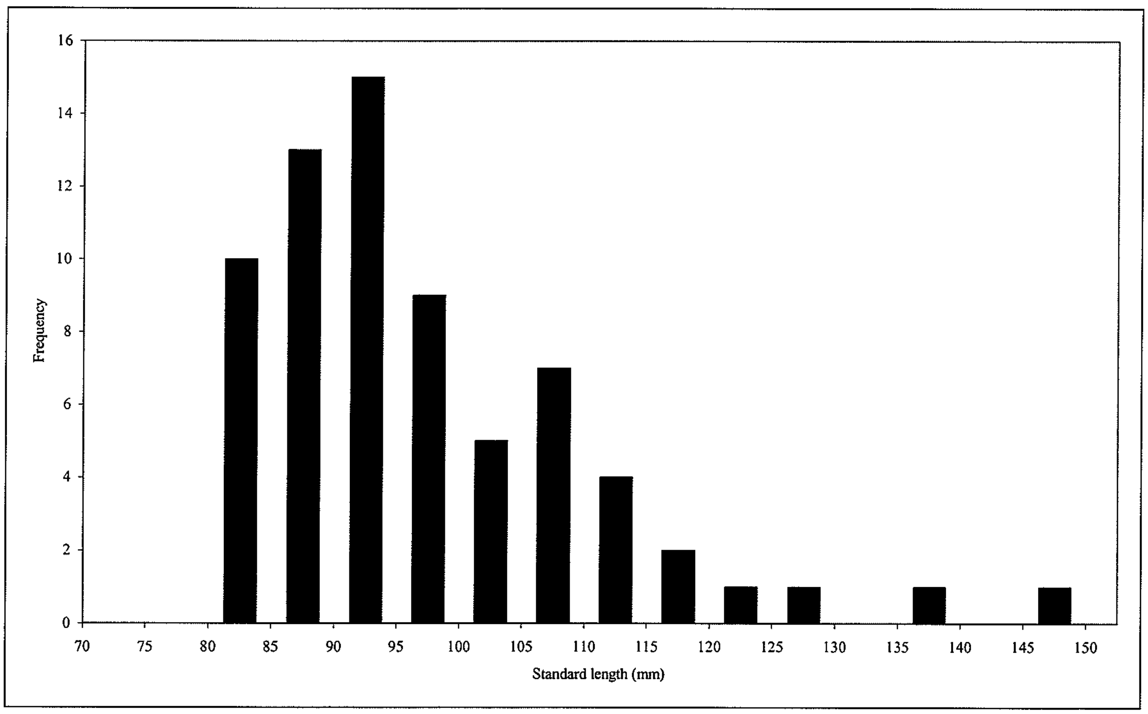
	Component	
	1	2
Preorbital length	0.80	0.14
Orbital length	0.89	-0.04
Postorbital length	0.77	0.07
Trunk length	-0.26	-0.07
Dorsal length	0.61	-0.05
Lumbar length	0.10	0.34
Anal length	0.41	-0.36
Caudal peduncle length	-0.49	0.01
Head depth	0.81	0.16
Body depth	-0.03	0.67
Caudal peduncle depth	0.05	0.75
Interorbital width	-0.38	0.33
Maxillary length	0.80	0.13
Maxillary width	-0.14	0.45
Pectoral length	0.78	0.18
Pelvic length	0.59	0.35
Adipose length	-0.02	0.12
Lower arch length	0.78	0.06
Gillraker length	-0.82	0.27
Eigenvalues	7.29	2.12
Percent of Variance	30.36	8.83
Cumulative Percent	30.36	39.18



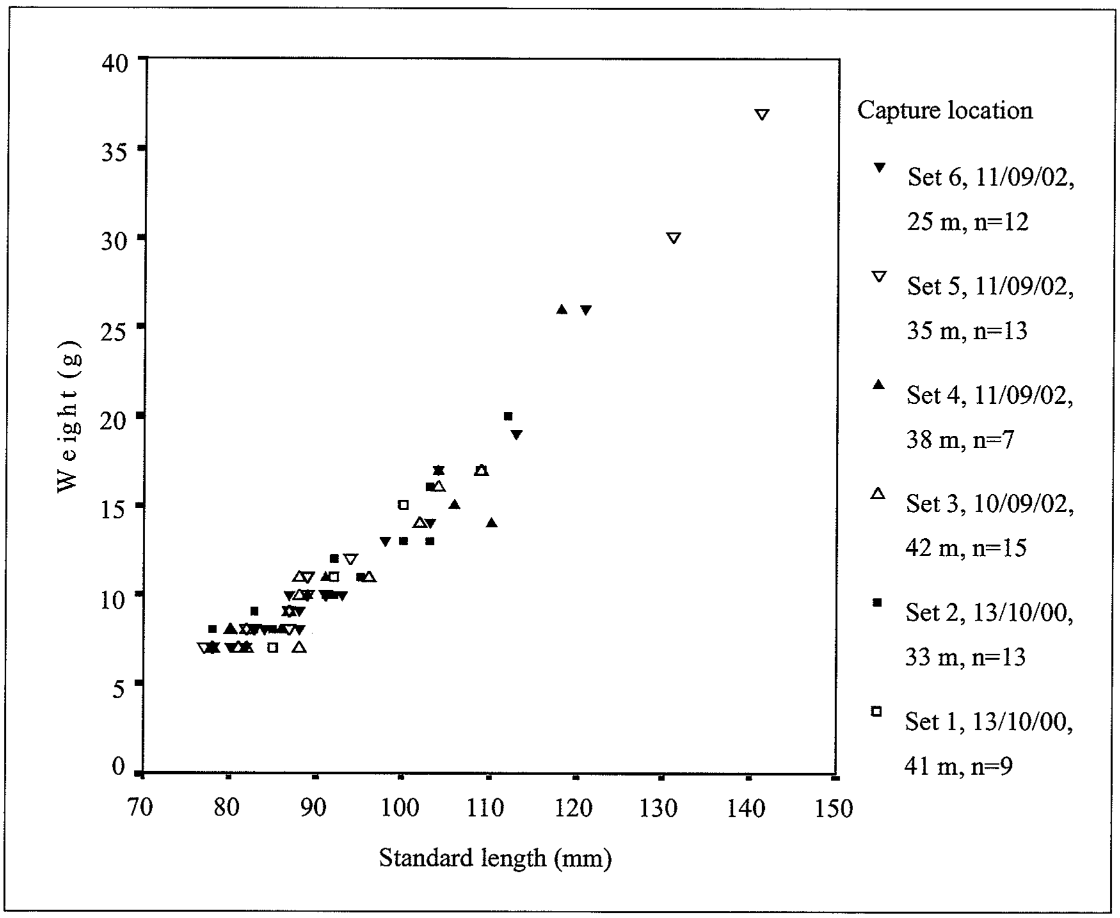
Appendix 5-13. Frequency distribution of discriminant scores from DA of George Lake cisco forms.

Appendix 6-1. Descriptive statistics for the combined cisco catch from Clearwater Lake. All variables are represented by raw, untransformed values.

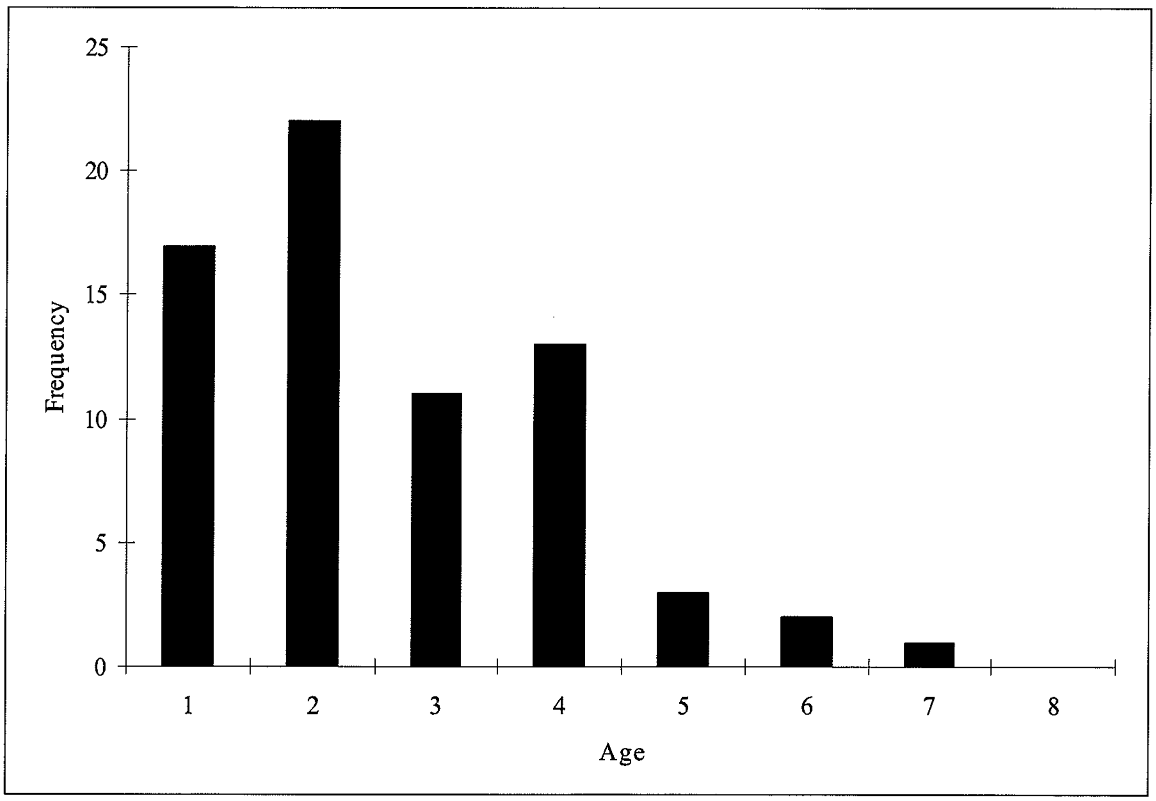
	N	Minimum	Maximum	Mean
Total gillraker count	69	31	49	39.5
Upper gillraker count	69	10	19	13.6
Lower gillraker count	69	21	31	25.8
Premaxillary angle	69	35	70	49.3
Dorsal ray count	69	10	12	10.8
Anal ray count	69	11	14	12.7
Pectoral ray count	69	14	18	16.1
Pelvic ray count	69	9	12	10.9
Age	69	1	7	2.6
Weight	69	7	37	11.7
Standard length	69	77.0	141.0	92.7
Fork length	48	84.0	152.0	102.2
Gillraker length	69	2.5	14.5	4.5
Lower arch length	69	2.7	14.2	9.8
Preorbital length	69	3.0	7.1	4.8
Orbital length	69	5.4	10.3	7.7
Post orbital length	69	9.3	16.3	11.2
Trunk length	69	15.8	36.4	22.1
Dorsal length	69	6.0	15.1	9.3
Lumbar length	69	11.3	27.4	15.1
Anal length	69	3.6	12.4	7.6
Caudal peduncle length	69	7.9	19.3	10.6
Head depth	69	8.6	14.4	11.0
Body depth	69	11.8	26.4	18.0
Caudal peduncle depth	69	4.6	10.0	6.0
Interorbital width	69	3.6	8.0	5.0
Maxillary length	69	5.1	9.9	7.5
Maxillary width	69	1.7	3.5	2.5
Pectoral length	69	9.6	19.9	14.3
Pelvic length	69	9.5	21.8	14.6
Adipose length	69	2.9	7.7	5.1



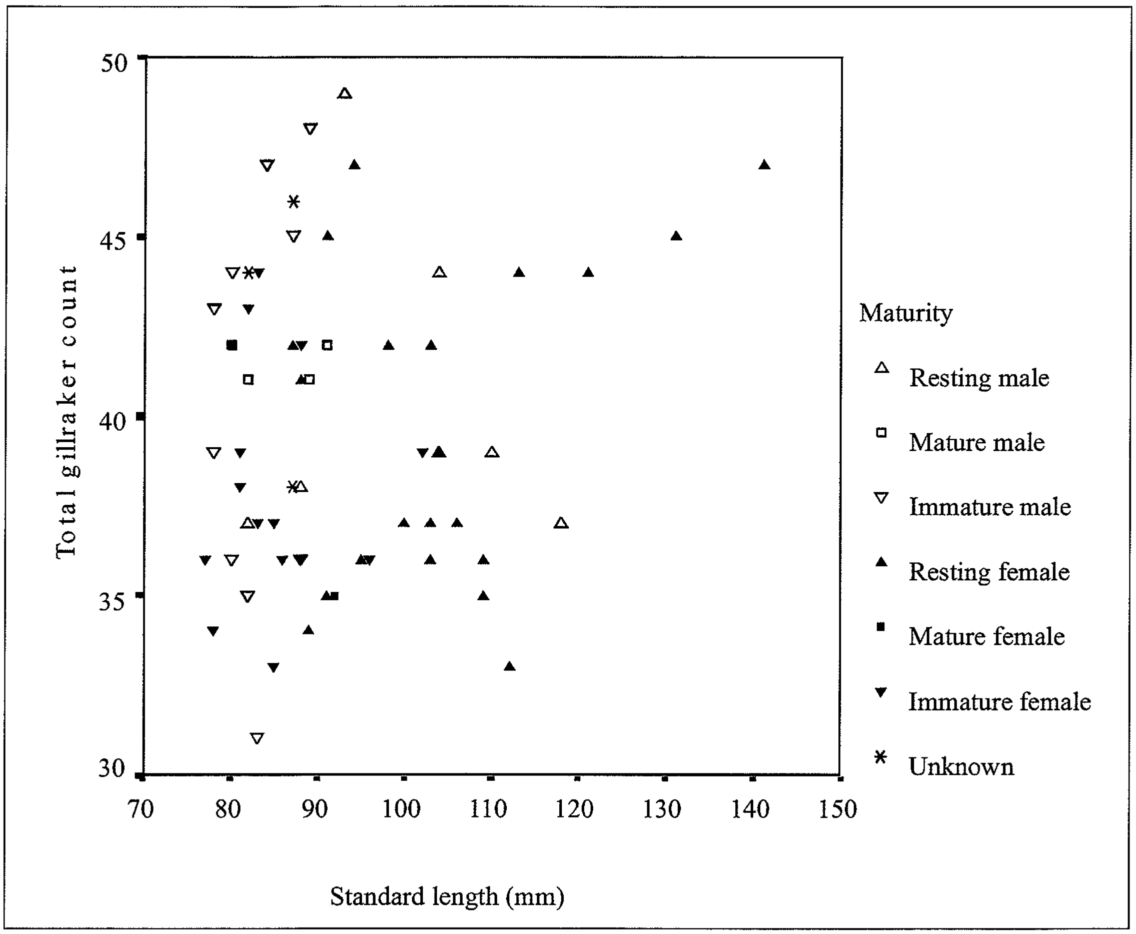
Appendix 6-2. Standard length frequency distribution for all ciscoes from Clearwater Lake.



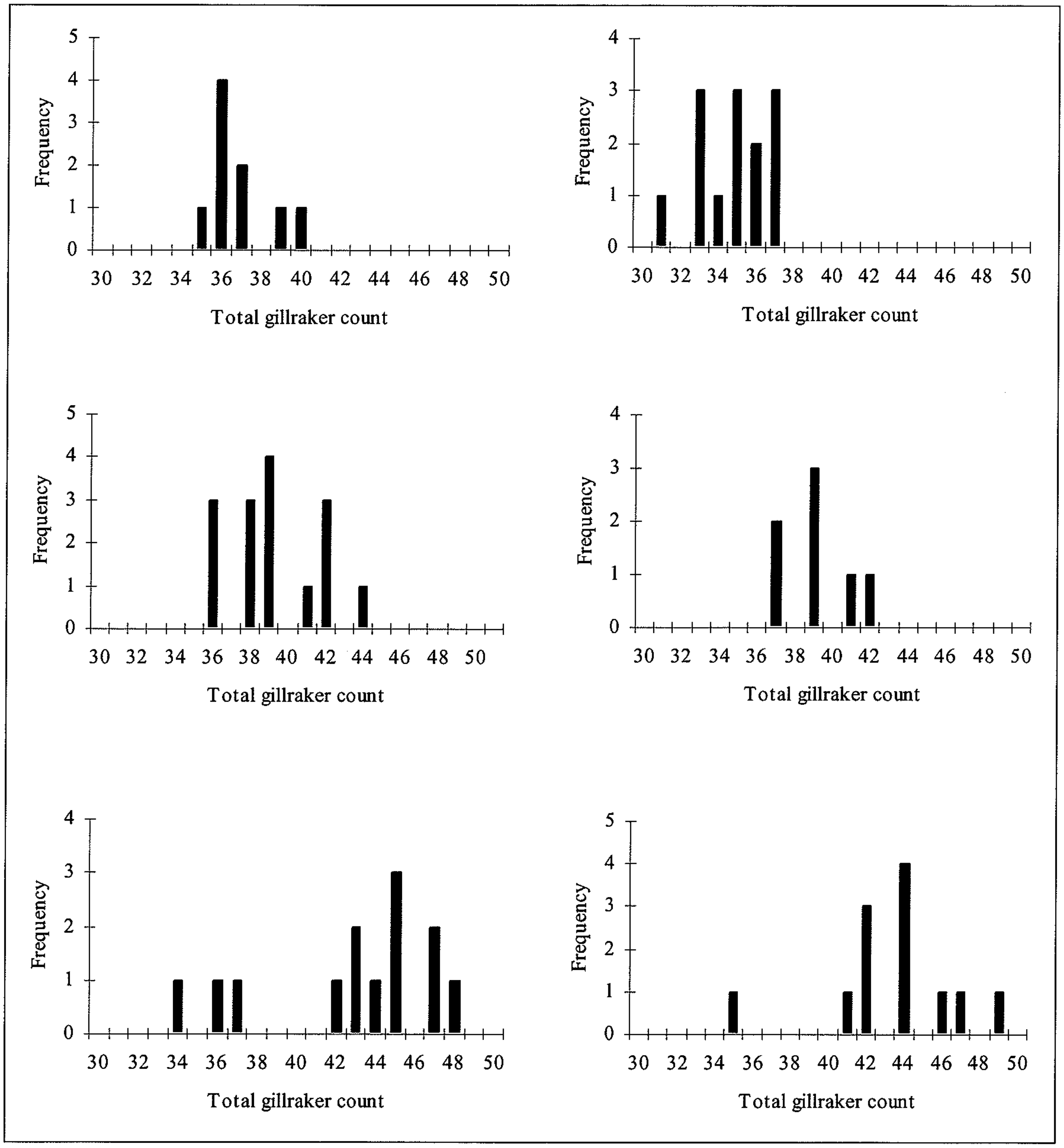
Appendix 6-3. Standard length versus weight for ciscoes from Clearwater Lake. Capture information is indicated in the legend including set number, date, depth of set, and number of ciscoes collected.



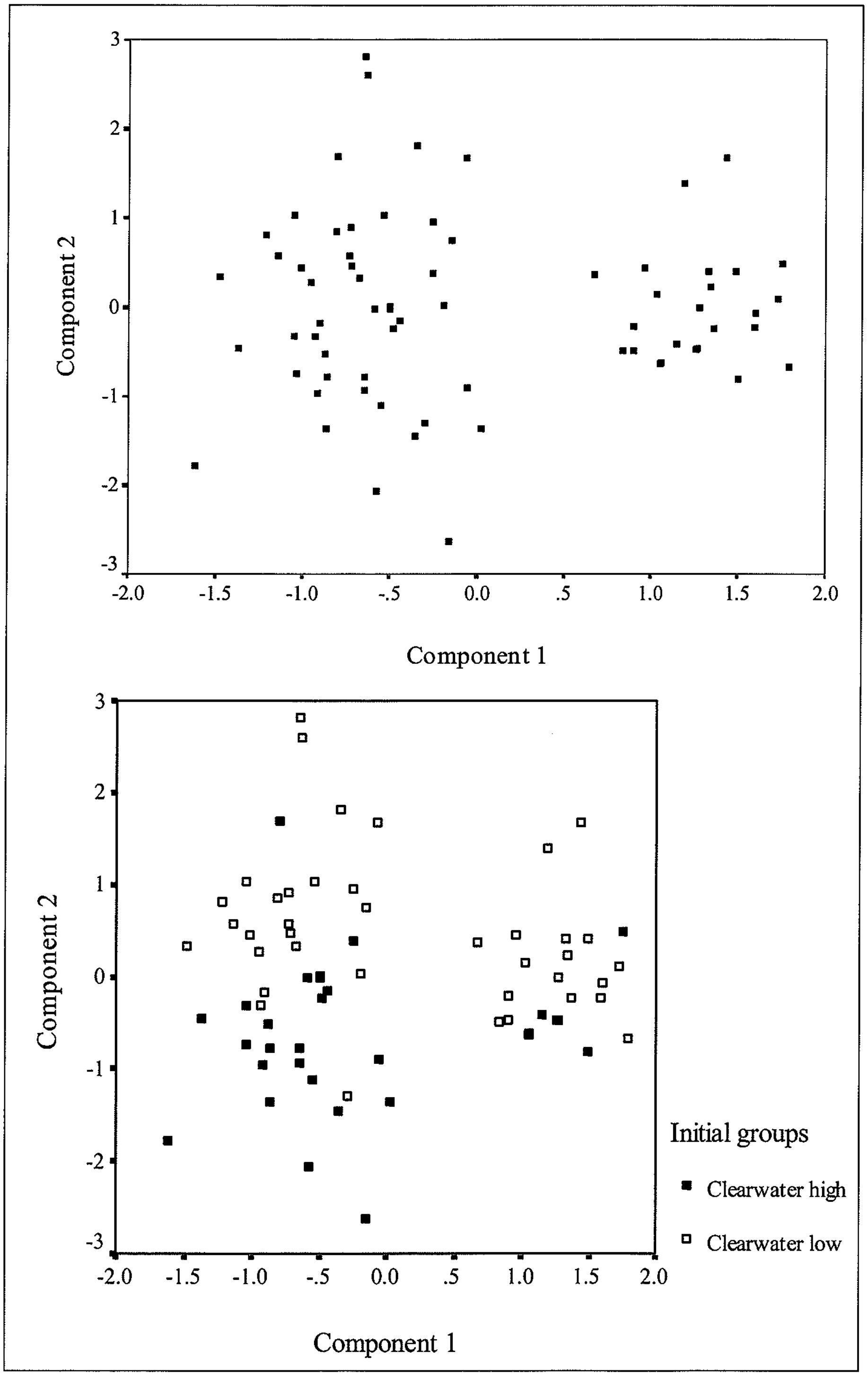
Appendix 6-4. Age frequency distribution for Clearwater Lake ciscoes.



Appendix 6-5. Relationship between total gillraker count and standard length for all ciscoes from Clearwater Lake with individuals identified by maturity state.



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.



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*.

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

	Component	
	1	2
Preorbital length	0.83	-0.20
Orbital length	-0.47	0.76
Postorbital length	-0.27	0.68
Trunk length	-0.34	-0.06
Dorsal length	0.81	0.19
Lumbar length	-0.06	-0.15
Anal length	0.67	-0.04
Caudal peduncle length	-0.22	-0.17
Head depth	0.17	0.78
Body depth	0.65	0.33
Caudal peduncle depth	0.66	-0.11
Interorbital width	-0.64	0.43
Maxillary length	0.73	0.31
Maxillary width	0.38	0.32
Pectoral length	0.70	0.13
Pelvic length	0.64	0.31
Adipose length	0.57	0.03
Lower arch length	-0.28	0.56
Gillraker length	-0.05	-0.33
Eigenvalues	5.54	2.83
Percent of Variance	29.14	14.89
Cumulative Percent	29.14	44.03

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 ($P<0.05$).

	Levene Statistic	Sig.	F	Sig.
Premaxillary angle	1.59	0.12	40.15	0.00
Dorsal ray count	1.50	0.15	5.54	0.00
Anal ray count	5.23	0.00	3.96	0.00
Pectoral ray count	2.16	0.03	1.60	0.12
Pelvic ray count	2.90	0.00	3.56	0.00
Upper gillraker count	7.79	0.00	196.73	0.00
Lower gillraker count	15.43	0.00	342.13	0.00
Preorbital length	8.22	0.00	111.49	0.00
Orbital length	12.33	0.00	87.97	0.00
Post orbital length	7.05	0.00	21.18	0.00
Trunk length	5.32	0.00	17.29	0.00
Dorsal length	3.92	0.00	49.42	0.00
Lumbar length	3.16	0.00	4.76	0.00
Anal length	5.02	0.00	41.98	0.00
Caudal peduncle length	5.75	0.00	58.83	0.00
Head depth	10.04	0.00	31.91	0.00
Body depth	6.95	0.00	52.96	0.00
Caudal peduncle depth	10.37	0.00	49.33	0.00
Interorbital width	3.21	0.00	85.22	0.00
Maxillary length	5.22	0.00	109.67	0.00
Maxillary width	3.04	0.00	13.29	0.00
Pectoral length	4.50	0.00	67.52	0.00
Pelvic length	6.80	0.00	69.16	0.00
Adipose length	7.56	0.00	16.37	0.00
Lower arch length	22.84	0.00	163.49	0.00
Gillraker length	91.72	0.00	206.74	0.00

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.

		PREMAX	DRC	ARC	PRC	VRC	UGR	LGR	POL	OOL	PSL	TTL	DOL
Athapap low form	Athapap high form	**-0.91**	-0.34	0.22	-0.14	**0.47**	**1.63**	**1.64**	**-0.47**	**-1.10**	**-0.80**	0.04	0.23
	Clearwater low form	-0.06	0.03	0.18	0.21	0.40	**0.44**	0.28	-1.15	1.42	-0.55	-0.05	-0.04
	Clearwater high form	**-1.31**	-0.57	0.07	-0.54	0.11	**1.86**	**2.12**	**-2.29**	**1.03**	**-1.15**	0.02	**-2.01**
	George low form	-0.12	0.05	0.26	-0.13	0.36	**0.39**	**0.35**	-0.20	0.37	0.38	-0.27	**-0.64**
	George high form	**-1.36**	**-0.67**	-0.09	-0.02	0.13	**2.13**	**2.23**	**-1.07**	**-1.45**	**-0.77**	-0.20	**-1.90**
	Reindeer low form	-0.15	-0.32	-0.06	-0.04	0.36	**0.38**	**0.32**	**0.58**	0.12	0.04	**-0.81**	**-0.86**
	Reindeer mid form	**-0.80**	0.23	0.24	-0.10	-0.11	**1.44**	**1.63**	**0.85**	0.29	0.17	**-1.06**	**-0.62**
	Reindeer high form	**-1.61**	-0.32	**0.60**	-0.24	0.44	**2.54**	**2.58**	0.23	0.26	-0.40	-0.40	-0.45
Athapap high form	Athapap low form	**0.91**	0.34	-0.22	0.14	**-0.47**	**-1.63**	**-1.64**	**0.47**	**1.10**	**0.80**	-0.04	-0.23
	Clearwater low form	**0.85**	0.37	-0.04	0.35	-0.07	**-1.19**	**-1.36**	**-0.68**	**2.52**	0.25	-0.09	-0.27
	Clearwater high form	-0.40	-0.23	-0.15	-0.40	-0.36	0.23	**0.48**	**-1.82**	**2.13**	-0.35	-0.02	**-2.24**
	George low form	**0.79**	0.39	0.04	0.01	-0.11	**-1.24**	**-1.29**	0.27	1.46	1.18	-0.31	**-0.87**
	George high form	-0.45	-0.33	-0.31	0.12	-0.34	**0.50**	**0.59**	**-0.61**	-0.35	0.03	-0.24	**-2.13**
	Reindeer low form	**0.76**	0.03	-0.28	0.10	-0.11	**-1.25**	**-1.32**	**1.04**	**1.22**	**0.84**	**-0.85**	**-1.09**
	Reindeer mid form	0.11	**0.58**	0.02	0.04	**-0.59**	-0.19	-0.01	1.32	1.39	0.97	**-1.10**	**-0.85**
	Reindeer high form	**-0.70**	0.02	0.38	-0.10	-0.03	**0.91**	**0.95**	**0.70**	**1.36**	0.40	-0.44	**-0.68**
Clearwater low form	Athapap low form	0.06	-0.03	-0.18	-0.21	-0.40	**-0.44**	-0.28	1.15	-1.42	0.55	0.05	0.04
	Athapap high form	**-0.85**	-0.37	0.04	-0.35	0.07	**1.19**	**1.36**	**0.68**	**-2.52**	-0.25	0.09	0.27
	Clearwater high form	**-1.25**	-0.60	-0.11	**-0.75**	-0.29	**1.42**	**1.84**	**-1.14**	-0.39	-0.60	0.06	**-1.97**
	George low form	-0.06	0.02	0.08	-0.34	-0.04	-0.04	0.07	0.95	-1.05	0.93	-0.22	**-0.60**
	George high form	**-1.30**	**-0.70**	-0.27	-0.23	-0.27	**1.69**	**1.95**	0.07	-2.87	-0.22	-0.15	**-1.86**
	Reindeer low form	-0.09	-0.35	-0.24	-0.25	-0.04	-0.05	0.04	1.72	-1.30	0.59	**-0.76**	**-0.82**
	Reindeer mid form	**-0.74**	0.21	0.06	-0.31	-0.52	**1.00**	**1.35**	**2.00**	**-1.13**	**0.73**	**-1.01**	**-0.58**
	Reindeer high form	**-1.55**	-0.35	0.42	-0.45	0.04	**2.10**	**2.31**	**1.38**	**-1.16**	0.15	-0.35	-0.41

Appendix 2. con't.

		PREMAX	DRC	ARC	PRC	VRC	UGR	LGR	POL	OOL	PSL	TTL	DOL
Clearwater high form	Athapap low form	**1.31**	0.57	-0.07	0.54	-0.11	**-1.86**	**-2.12**	**2.29**	**-1.03**	**1.15**	-0.02	**2.01**
	Athapap high form	0.40	0.23	0.15	0.40	0.36	-0.23	**-0.48**	**1.82**	**-2.13**	0.35	0.02	**2.24**
	Clearwater low form	**1.25**	0.60	0.11	**0.75**	0.29	**-1.42**	**-1.84**	**1.14**	0.39	0.60	-0.06	**1.97**
	George low form	**1.19**	**0.62**	0.19	0.41	0.25	**-1.47**	**-1.77**	**2.09**	**-0.66**	**1.53**	-0.29	**1.37**
	George high form	-0.05	-0.10	-0.16	0.51	0.02	0.27	0.11	1.21	-2.48	0.38	-0.22	0.11
	Reindeer low form	**1.16**	0.25	-0.12	0.50	0.25	**-1.48**	**-1.79**	**2.86**	**-0.91**	**1.19**	**-0.83**	**1.15**
	Reindeer mid form	0.51	**0.80**	0.17	0.43	-0.23	-0.42	**-0.48**	**3.14**	**-0.74**	**1.33**	**-1.08**	**1.39**
	Reindeer high form	-0.30	0.25	0.53	0.30	0.33	**0.68**	**0.47**	**2.52**	**-0.77**	**0.75**	-0.41	**1.56**
George low form	Athapap low form	0.12	-0.05	-0.26	0.13	-0.36	**-0.39**	**-0.35**	0.20	-0.37	-0.38	0.27	**0.64**
	Athapap high form	**-0.79**	-0.39	-0.04	-0.01	0.11	**1.24**	**1.29**	-0.27	-1.46	-1.18	0.31	**0.87**
	Clearwater low form	0.06	-0.02	-0.08	0.34	0.04	0.04	-0.07	-0.95	1.05	-0.93	0.22	**0.60**
	Clearwater high form	**-1.19**	**-0.62**	-0.19	-0.41	-0.25	**1.47**	**1.77**	**-2.09**	**0.66**	**-1.53**	0.29	**-1.37**
	George high form	**-1.24**	**-0.72**	-0.35	0.11	-0.23	**1.74**	**1.88**	**-0.87**	**-1.82**	**-1.15**	0.07	**-1.26**
	Reindeer low form	-0.03	-0.36	-0.31	0.09	0.00	-0.01	-0.03	0.78	-0.25	-0.34	**-0.54**	-0.23
	Reindeer mid form	**-0.68**	0.19	-0.02	0.03	**-0.48**	**1.04**	**1.28**	**1.05**	-0.07	-0.21	**-0.79**	0.01
	Reindeer high form	**-1.49**	-0.37	0.34	-0.11	0.08	**2.15**	**2.23**	**0.43**	-0.11	-0.78	-0.13	0.19
George high form	Athapap low form	**1.36**	**0.67**	0.09	0.02	-0.13	**-2.13**	**-2.23**	**1.07**	**1.45**	**0.77**	0.20	**1.90**
	Athapap high form	0.45	0.33	0.31	-0.12	0.34	**-0.50**	**-0.59**	**0.61**	0.35	-0.03	0.24	**2.13**
	Clearwater low form	**1.30**	**0.70**	0.27	0.23	0.27	**-1.69**	**-1.95**	-0.07	2.87	0.22	0.15	**1.86**
	Clearwater high form	0.05	0.10	0.16	-0.51	-0.02	-0.27	-0.11	-1.21	2.48	-0.38	0.22	-0.11
	George low form	**1.24**	**0.72**	0.35	-0.11	0.23	**-1.74**	**-1.88**	**0.87**	**1.82**	**1.15**	-0.07	**1.26**
	Reindeer low form	**1.21**	0.35	0.03	-0.02	0.23	**-1.75**	**-1.91**	**1.65**	**1.57**	**0.81**	**-0.61**	**1.04**
	Reindeer mid form	**0.56**	**0.90**	0.33	-0.08	-0.25	**-0.69**	**-0.60**	**1.93**	**1.74**	**0.95**	**-0.86**	**1.28**
	Reindeer high form	-0.25	0.35	**0.69**	-0.22	0.31	**0.41**	**0.36**	**1.31**	**1.71**	0.37	-0.20	**1.45**

Appendix 2. con't.

		PREMAX	DRC	ARC	PRC	VRC	UGR	LGR	POL	OOL	PSL	TTL	DOL
	Athapap low form	0.15	0.32	0.06	0.04	-0.36	**-0.38**	**-0.32**	**-0.58**	-0.12	-0.04	**0.81**	**0.86**
	Athapap high form	**-0.76**	-0.03	0.28	-0.10	0.11	**1.25**	**1.32**	**-1.04**	**-1.22**	**-0.84**	**0.85**	**1.09**
	Clearwater low form	0.09	0.35	0.24	0.25	0.04	0.05	-0.04	-1.72	1.30	-0.59	**0.76**	**0.82**
	Clearwater high form	**-1.16**	-0.25	0.12	-0.50	-0.25	**1.48**	**1.79**	**-2.86**	**0.91**	**-1.19**	**0.83**	**-1.15**
	George low form	0.03	0.36	0.31	-0.09	0.00	0.01	0.03	-0.78	0.25	0.34	**0.54**	0.23
	George high form	**-1.21**	-0.35	-0.03	0.02	-0.23	**1.75**	**1.91**	**-1.65**	**-1.57**	**-0.81**	**0.61**	**-1.04**
	Reindeer mid form	**-0.65**	**0.55**	0.30	-0.06	**-0.48**	**1.05**	**1.31**	0.28	0.17	0.14	-0.25	0.24
	Reindeer high form	**-1.46**	-0.01	**0.66**	-0.20	0.08	**2.16**	**2.26**	**-0.34**	0.14	-0.44	0.42	**0.42**
Reindeer mid form	Athapap low form	**0.80**	-0.23	-0.24	0.10	0.11	**-1.44**	**-1.63**	**-0.85**	-0.29	-0.17	**1.06**	**0.62**
	Athapap high form	-0.11	**-0.58**	-0.02	-0.04	**0.59**	0.19	0.01	-1.32	-1.39	-0.97	**1.10**	**0.85**
	Clearwater low form	**0.74**	-0.21	-0.06	0.31	0.52	**-1.00**	**-1.35**	**-2.00**	**1.13**	**-0.73**	**1.01**	**0.58**
	Clearwater high form	-0.51	**-0.80**	-0.17	-0.43	0.23	0.42	**0.48**	**-3.14**	**0.74**	**-1.33**	**1.08**	**-1.39**
	George low form	**0.68**	-0.19	0.02	-0.03	**0.48**	**-1.04**	**-1.28**	**-1.05**	0.07	0.21	**0.79**	-0.01
	George high form	**-0.56**	**-0.90**	-0.33	0.08	0.25	**0.69**	**0.60**	**-1.93**	**-1.74**	**-0.95**	**0.86**	**-1.28**
	Reindeer low form	**0.65**	**-0.55**	-0.30	0.06	**0.48**	**-1.05**	**-1.31**	-0.28	-0.17	-0.14	0.25	-0.24
	Reindeer high form	**-0.81**	**-0.56**	0.36	-0.14	**0.56**	**1.10**	**0.95**	**-0.62**	-0.03	-0.58	**0.67**	0.18
Reindeer high form	Athapap low form	**1.61**	0.32	**-0.60**	0.24	-0.44	**-2.54**	**-2.58**	-0.23	-0.26	0.40	0.40	0.45
	Athapap high form	**0.70**	-0.02	-0.38	0.10	0.03	**-0.91**	**-0.95**	**-0.70**	**-1.36**	-0.40	0.44	**0.68**
	Clearwater low form	**1.55**	0.35	-0.42	0.45	-0.04	**-2.10**	**-2.31**	**-1.38**	**1.16**	-0.15	0.35	0.41
	Clearwater high form	0.30	-0.25	-0.53	-0.30	-0.33	**-0.68**	**-0.47**	**-2.52**	**0.77**	**-0.75**	0.41	**-1.56**
	George low form	**1.49**	0.37	-0.34	0.11	-0.08	**-2.15**	**-2.23**	**-0.43**	0.11	0.78	0.13	-0.19
	George high form	0.25	-0.35	**-0.69**	0.22	-0.31	**-0.41**	**-0.36**	**-1.31**	**-1.71**	-0.37	0.20	**-1.45**
	Reindeer low form	**1.46**	0.01	**-0.66**	0.20	-0.08	**-2.16**	**-2.26**	**0.34**	-0.14	0.44	-0.42	**-0.42**
	Reindeer mid form	**0.81**	**0.56**	-0.36	0.14	**-0.56**	**-1.10**	**-0.95**	**0.62**	0.03	0.58	**-0.67**	-0.18

Appendix 2. con't.

		LUL	ANL	CPL	HDD	BDD	CPD	IOW	MXL	MXW	PCL	PVL	ADL	LAL	GRL
Athapap low form	Athapap high form	-0.25	0.25	0.02	-0.13	**-0.83**	**-0.66**	**0.97**	**-0.71**	0.11	**-0.75**	**-0.88**	-0.31	**-0.61**	**0.76**
	Clearwater low form	-0.24	**-0.57**	**-1.21**	-0.44	**-0.68**	**-0.67**	-0.27	**-0.62**	**-0.60**	-0.37	**-0.50**	**-0.75**	**0.52**	-0.28
	Clearwater high form	0.42	**-1.50**	**1.07**	**-1.41**	**-2.25**	**-1.19**	0.38	**-1.75**	-0.24	**-1.22**	**-1.79**	**-1.46**	**-2.45**	**3.07**
	George low form	0.14	**0.45**	**0.52**	0.12	-0.07	0.04	**0.52**	**0.61**	0.25	**0.90**	**0.53**	0.41	0.29	**-0.89**
	George high form	0.06	0.48	**1.13**	**-1.03**	0.39	**0.58**	**1.71**	**-0.95**	**1.35**	**-0.68**	0.26	0.45	**-1.01**	**0.92**
	Reindeer low form	0.04	0.22	**1.11**	**-0.97**	**-1.30**	**-1.26**	**-0.69**	**0.53**	0.05	-0.13	**-0.80**	-0.25	**0.73**	**-0.49**
	Reindeer mid form	-0.39	**0.48**	**1.05**	0.30	**-1.27**	**-1.04**	0.29	**1.29**	0.26	0.11	**-0.63**	-0.21	**1.14**	**0.39**
	Reindeer high form	-0.45	**1.45**	**0.58**	-0.49	**-1.05**	0.03	0.05	0.04	0.40	**1.28**	**0.81**	0.14	**0.48**	**0.74**
Athapap high form	Athapap low form	0.25	-0.25	-0.02	0.13	**0.83**	**0.66**	**-0.97**	**0.71**	-0.11	**0.75**	**0.88**	0.31	**0.61**	**-0.76**
	Clearwater low form	0.01	**-0.83**	**-1.23**	-0.30	0.16	-0.01	**-1.23**	0.09	**-0.71**	**0.38**	**0.38**	-0.44	**1.14**	**-1.03**
	Clearwater high form	**0.68**	**-1.76**	**1.05**	**-1.27**	**-1.42**	**-0.53**	**-0.59**	**-1.04**	-0.35	-0.47	**-0.91**	**-1.16**	**-1.84**	**2.31**
	George low form	0.39	0.19	**0.49**	0.25	**0.76**	**0.70**	**-0.45**	**1.32**	0.14	**1.65**	**1.41**	**0.72**	**0.90**	**-1.64**
	George high form	0.31	0.23	**1.11**	**-0.90**	**1.22**	**1.25**	**0.74**	-0.23	**1.24**	0.07	**1.14**	**0.75**	**-0.40**	**0.17**
	Reindeer low form	0.29	-0.03	**1.08**	**-0.84**	**-0.47**	**-0.59**	**-1.66**	**1.24**	-0.06	**0.62**	0.08	0.05	**1.35**	**-1.25**
	Reindeer mid form	-0.14	0.22	**1.03**	0.43	**-0.44**	-0.38	**-0.67**	**2.01**	0.15	**0.85**	0.25	0.09	**1.75**	**-0.37**
	Reindeer high form	-0.20	**1.20**	**0.56**	**-0.36**	-0.21	**0.69**	**-0.91**	**0.75**	0.29	**2.03**	**1.69**	**0.45**	**1.09**	-0.01
Clearwater low form	Athapap low form	0.24	**0.57**	**1.21**	0.44	**0.68**	**0.67**	0.27	**0.62**	**0.60**	0.37	**0.50**	**0.75**	**-0.52**	0.28
	Athapap high form	-0.01	**0.83**	**1.23**	0.30	-0.16	0.01	**1.23**	-0.09	**0.71**	**-0.38**	**-0.38**	0.44	**-1.14**	**1.03**
	Clearwater high form	**0.67**	**-0.93**	**2.28**	**-0.97**	**-1.58**	**-0.53**	**0.64**	**-1.13**	0.36	**-0.85**	**-1.29**	**-0.72**	**-2.98**	**3.34**
	George low form	0.38	**1.02**	**1.72**	**0.55**	**0.60**	**0.70**	**0.78**	**1.23**	**0.85**	**1.27**	**1.03**	**1.16**	-0.23	**-0.61**
	George high form	0.30	**1.05**	**2.34**	**-0.59**	**1.06**	**1.25**	**1.97**	-0.32	**1.95**	-0.31	**0.76**	**1.19**	**-1.53**	**1.20**
	Reindeer low form	0.28	**0.80**	**2.31**	**-0.54**	**-0.63**	**-0.59**	**-0.42**	**1.15**	**0.65**	0.24	-0.30	0.49	0.21	-0.22
	Reindeer mid form	-0.15	**1.05**	**2.25**	**0.74**	**-0.60**	-0.37	**0.56**	**1.91**	**0.86**	**0.47**	-0.13	0.53	**0.61**	**0.66**
	Reindeer high form	-0.20	**2.02**	**1.79**	-0.06	-0.37	**0.70**	0.32	**0.66**	**1.00**	**1.65**	**1.31**	**0.89**	-0.05	**1.02**

Appendix 2. con't.

		LUL	ANL	CPL	HDD	BDD	CPD	IOW	MXL	MXW	PCL	PVL	ADL	LAL	GRL
Clearwater high form	Athapap low form	-0.42	**1.50**	**-1.07**	**1.41**	**2.25**	**1.19**	-0.38	**1.75**	0.24	**1.22**	**1.79**	**1.46**	**2.45**	**-3.07**
	Athapap high form	**-0.68**	**1.76**	**-1.05**	**1.27**	**1.42**	**0.53**	**0.59**	**1.04**	0.35	0.47	**0.91**	**1.16**	**1.84**	**-2.31**
	Clearwater low form	**-0.67**	**0.93**	**-2.28**	**0.97**	**1.58**	**0.53**	**-0.64**	**1.13**	-0.36	**0.85**	**1.29**	**0.72**	**2.98**	**-3.34**
	George low form	-0.28	**1.95**	**-0.55**	**1.52**	**2.18**	**1.23**	0.14	**2.36**	**0.50**	**2.12**	**2.32**	**1.88**	**2.74**	**-3.95**
	George high form	-0.37	**1.99**	0.06	0.38	**2.64**	**1.78**	**1.33**	**0.81**	**1.59**	**0.54**	**2.05**	**1.91**	**1.44**	**-2.14**
	Reindeer low form	-0.39	**1.73**	0.03	**0.43**	**0.95**	-0.06	**-1.07**	**2.28**	0.29	**1.09**	**0.99**	**1.21**	**3.19**	**-3.56**
	Reindeer mid form	**-0.82**	**1.98**	-0.02	**1.71**	**0.98**	0.15	-0.08	**3.05**	**0.50**	**1.33**	**1.17**	**1.25**	**3.59**	**-2.68**
	Reindeer high form	**-0.87**	**2.95**	**-0.49**	**0.91**	**1.20**	**1.23**	-0.32	**1.79**	**0.65**	**2.50**	**2.60**	**1.61**	**2.93**	**-2.32**
George low form	Athapap low form	-0.14	**-0.45**	**-0.52**	-0.12	0.07	-0.04	**-0.52**	**-0.61**	-0.25	**-0.90**	**-0.53**	-0.41	-0.29	**0.89**
	Athapap high form	-0.39	-0.19	**-0.49**	-0.25	**-0.76**	**-0.70**	**0.45**	**-1.32**	-0.14	**-1.65**	**-1.41**	**-0.72**	**-0.90**	**1.64**
	Clearwater low form	-0.38	**-1.02**	**-1.72**	**-0.55**	**-0.60**	**-0.70**	**-0.78**	**-1.23**	**-0.85**	**-1.27**	**-1.03**	**-1.16**	0.23	**0.61**
	Clearwater high form	0.28	**-1.95**	**0.55**	**-1.52**	**-2.18**	**-1.23**	-0.14	**-2.36**	**-0.50**	**-2.12**	**-2.32**	**-1.88**	**-2.74**	**3.95**
	George high form	-0.08	0.03	**0.62**	**-1.15**	**0.46**	**0.55**	**1.19**	**-1.56**	**1.09**	**-1.58**	-0.27	0.03	**-1.30**	**1.81**
	Reindeer low form	-0.10	-0.22	**0.59**	**-1.09**	**-1.23**	**-1.29**	**-1.21**	-0.08	-0.21	**-1.03**	**-1.33**	**-0.67**	**0.44**	**0.39**
	Reindeer mid form	-0.53	0.03	**0.53**	0.18	**-1.20**	**-1.08**	-0.22	**0.68**	0.01	**-0.80**	**-1.15**	**-0.63**	**0.85**	**1.27**
	Reindeer high form	**-0.59**	**1.00**	0.06	**-0.61**	**-0.97**	0.00	**-0.46**	**-0.57**	0.15	0.38	0.28	-0.27	0.19	**1.63**
George high form	Athapap low form	-0.06	-0.48	**-1.13**	**1.03**	-0.39	**-0.58**	**-1.71**	**0.95**	**-1.35**	**0.68**	-0.26	-0.45	**1.01**	**-0.92**
	Athapap high form	-0.31	-0.23	**-1.11**	**0.90**	**-1.22**	**-1.25**	**-0.74**	0.23	**-1.24**	-0.07	**-1.14**	**-0.75**	**0.40**	-0.17
	Clearwater low form	-0.30	**-1.05**	**-2.34**	**0.59**	**-1.06**	**-1.25**	**-1.97**	0.32	**-1.95**	0.31	**-0.76**	**-1.19**	**1.53**	**-1.20**
	Clearwater high form	0.37	**-1.99**	-0.06	-0.38	**-2.64**	**-1.78**	**-1.33**	**-0.81**	**-1.59**	**-0.54**	**-2.05**	**-1.91**	**-1.44**	**2.14**
	George low form	0.08	-0.03	**-0.62**	**1.15**	**-0.46**	**-0.55**	**-1.19**	**1.56**	**-1.09**	**1.58**	0.27	-0.03	**1.30**	**-1.81**
	Reindeer low form	-0.02	-0.26	-0.03	0.05	**-1.69**	**-1.84**	**-2.40**	**1.47**	**-1.30**	**0.55**	**-1.06**	**-0.70**	**1.74**	**-1.42**
	Reindeer mid form	-0.45	0.00	-0.08	**1.33**	**-1.66**	**-1.62**	**-1.41**	**2.24**	**-1.09**	**0.79**	**-0.88**	**-0.66**	**2.15**	**-0.54**
	Reindeer high form	-0.50	**0.97**	**-0.55**	**0.53**	**-1.43**	**-0.55**	**-1.65**	**0.99**	**-0.94**	**1.96**	**0.55**	-0.30	**1.49**	-0.18

Appendix 2. con't.

		LUL	ANL	CPL	HDD	BDD	CPD	IOW	MXL	MXW	PCL	PVL	ADL	LAL	GRL
Reindeer low form	Athapap low form	-0.04	-0.22	**-1.11**	**0.97**	**1.30**	**1.26**	**0.69**	**-0.53**	-0.05	0.13	**0.80**	0.25	**-0.73**	**0.49**
	Athapap high form	-0.29	0.03	**-1.08**	**0.84**	**0.47**	**0.59**	**1.66**	**-1.24**	0.06	**-0.62**	-0.08	-0.05	**-1.35**	**1.25**
	Clearwater low form	-0.28	**-0.80**	**-2.31**	**0.54**	**0.63**	**0.59**	**0.42**	**-1.15**	**-0.65**	-0.24	0.30	-0.49	-0.21	0.22
	Clearwater high form	0.39	**-1.73**	-0.03	**-0.43**	**-0.95**	0.06	**1.07**	**-2.28**	-0.29	**-1.09**	**-0.99**	**-1.21**	**-3.19**	**3.56**
	George low form	0.10	0.22	**-0.59**	**1.09**	**1.23**	**1.29**	**1.21**	0.08	0.21	**1.03**	**1.33**	**0.67**	**-0.44**	**-0.39**
	George high form	0.02	0.26	0.03	-0.05	**1.69**	**1.84**	**2.40**	**-1.47**	**1.30**	**-0.55**	**1.06**	**0.70**	**-1.74**	**1.42**
	Reindeer mid form	**-0.43**	0.25	-0.06	**1.27**	0.03	0.22	**0.98**	**0.77**	0.21	0.24	0.17	0.04	**0.40**	**0.88**
	Reindeer high form	**-0.49**	**1.23**	**-0.53**	**0.48**	0.26	**1.29**	**0.74**	**-0.49**	0.36	**1.41**	**1.61**	**0.40**	**-0.26**	**1.24**
Reindeer mid form	Athapap low form	0.39	**-0.48**	**-1.05**	-0.30	**1.27**	**1.04**	-0.29	**-1.29**	-0.26	-0.11	**0.63**	0.21	**-1.14**	**-0.39**
	Athapap high form	0.14	-0.22	**-1.03**	-0.43	**0.44**	0.38	**0.67**	**-2.01**	-0.15	**-0.85**	-0.25	-0.09	**-1.75**	**0.37**
	Clearwater low form	0.15	**-1.05**	**-2.25**	**-0.74**	**0.60**	0.37	**-0.56**	**-1.91**	**-0.86**	**-0.47**	0.13	-0.53	**-0.61**	**-0.66**
	Clearwater high form	**0.82**	**-1.98**	0.02	**-1.71**	**-0.98**	-0.15	0.08	**-3.05**	**-0.50**	**-1.33**	**-1.17**	**-1.25**	**-3.59**	**2.68**
	George low form	0.53	-0.03	**-0.53**	-0.18	**1.20**	**1.08**	0.22	**-0.68**	-0.01	**0.80**	**1.15**	**0.63**	**-0.85**	**-1.27**
	George high form	0.45	0.00	0.08	**-1.33**	**1.66**	**1.62**	**1.41**	**-2.24**	**1.09**	**-0.79**	**0.88**	**0.66**	**-2.15**	**0.54**
	Reindeer low form	**0.43**	-0.25	0.06	**-1.27**	-0.03	-0.22	**-0.98**	**-0.77**	-0.21	-0.24	-0.17	-0.04	**-0.40**	**-0.88**
	Reindeer high form	-0.06	**0.97**	**-0.47**	**-0.79**	0.23	**1.07**	-0.24	**-1.25**	0.14	**1.18**	**1.44**	0.36	**-0.66**	**0.36**
Reindeer high form	Athapap low form	0.45	**-1.45**	**-0.58**	0.49	**1.05**	-0.03	-0.05	-0.04	-0.40	**-1.28**	**-0.81**	-0.14	**-0.48**	**-0.74**
	Athapap high form	0.20	**-1.20**	**-0.56**	**0.36**	0.21	**-0.69**	**0.91**	**-0.75**	-0.29	**-2.03**	**-1.69**	**-0.45**	**-1.09**	0.01
	Clearwater low form	0.20	**-2.02**	**-1.79**	0.06	0.37	**-0.70**	-0.32	**-0.66**	**-1.00**	**-1.65**	**-1.31**	**-0.89**	0.05	**-1.02**
	Clearwater high form	**0.87**	**-2.95**	**0.49**	**-0.91**	**-1.20**	**-1.23**	0.32	**-1.79**	**-0.65**	**-2.50**	**-2.60**	**-1.61**	**-2.93**	**2.32**
	George low form	**0.59**	**-1.00**	-0.06	**0.61**	**0.97**	0.00	**0.46**	**0.57**	-0.15	-0.38	-0.28	0.27	-0.19	**-1.63**
	George high form	0.50	**-0.97**	**0.55**	**-0.53**	**1.43**	**0.55**	**1.65**	**-0.99**	**0.94**	**-1.96**	**-0.55**	0.30	**-1.49**	0.18
	Reindeer low form	**0.49**	**-1.23**	**0.53**	**-0.48**	-0.26	**-1.29**	**-0.74**	**0.49**	-0.36	**-1.41**	**-1.61**	**-0.40**	**0.26**	**-1.24**
	Reindeer mid form	0.06	**-0.97**	**0.47**	**0.79**	-0.23	**-1.07**	0.24	**1.25**	-0.14	**-1.18**	**-1.44**	-0.36	**0.66**	**-0.36**