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A Re-examination of the Nominal Shortjaw Cisco (*Coregonus zenithicus*) in Barrow Lake, Alberta and Taxonomic Evaluation of Neighboring Cisco Populations

By

Mark Steinhilber 

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Systematics and Evolution

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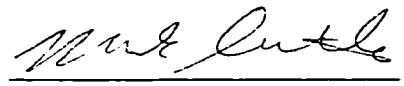

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Abstract

The morphology, ecology, and genetics of the putative *Coregonus zenithicus* (shortjaw cisco) in Barrow Lake, Alberta were examined to verify the distinctiveness and specific identity of this population. Ciscoes from five nearby lakes provided comparative specimens for assessment of local variation, and samples of known *C. zenithicus* from eight lakes across North America were used to assist in identification. Of the six Alberta lakes sampled, four contained sympatric cisco populations. Sympatric forms in Ryan Lake and Unnamed Lake were believed to be *C. artedi* (lake cisco) in different stages of divergence. One form of the sympatric pair in Bocquene Lake may represent *C. sardinella* (least cisco). The low gillraker cisco in Barrow Lake conformed morphologically to *C. zenithicus*. Despite minor differences, the Barrow Lake *C. zenithicus* overlapped completely in principal component plots with known *C. zenithicus* populations. Mitochondrial DNA d-loop sequence analysis was inconclusive but consistent with other studies examining genetic variation between *C. zenithicus* and *C. artedi*. The morphological and ecological data do not support an hypothesis of sympatric speciation. A scenario of secondary, post-Pleistocene contact between *C. zenithicus* and *C. artedi* in this lake is favoured.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A Re-examination of the Putative Shortjaw Cisco (*Coregonus zenithicus*) in Barrow Lake, Alberta and Taxonomic Evaluation of Neighboring Cisco Populations submitted by Mark Steinhilber in partial fulfillment of the requirements for the degree of Master of Science in Systematics and Evolution.

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Introduction

The Question

In 1969, Colin Paterson reported the occurrence of *Coregonus zenithicus* (Jordan and Evermann 1909), the shortjaw cisco, in sympatry with *C. artedi* Le Sueur 1818, the lake cisco, from Barrow Lake in northeastern Alberta. To date, this remains the only verifiable report of a cisco other than *C. artedi* in the province but ichthyologists consider the identification provisional (Nelson and Paetz 1992). As is often the case in cisco taxonomy, this population was identified almost exclusively on the basis of gillraker number. Reliance on a single character for identification is always tenuous and is particularly so in the highly plastic whitefishes. Paterson (1969) found few other characters useful in discriminating between the Barrow Lake forms. However, consideration should be given to his use of ratios to represent quantitative shape differences. Ratios have many undesirable statistical properties, including a propensity to mask differences between samples and increase the probability of Type II errors (Atchley 1978, Pimental 1979). The present study attempts to find characters, in addition to gillraker number, that are significantly different between forms of northeastern Alberta ciscoes and to suggest the optimal taxonomic placement of these forms based on comparisons with populations of known identity.

Recognizing character convergence or parallelism is a common and daunting challenge in systematics. Is phenotypic resemblance due to convergence, by genetic or non-genetic processes, among distinct taxa with unique origins and evolutionary histories or is it due to monophyly of the groups? Specifically, is the putative *C. zenithicus* in Barrow Lake derived from a *C. zenithicus* ancestor or is it a descendent of a *C. artedi* ancestor (or some other species) that has subsequently evolved, or undergone phenotypic divergence in response to environmental stimuli (i.e., "non-genetic" modification), to superficially

resemble *C. zenithicus*? Is the most compelling evidence for species delimitation and identification based on one or very few characters that appear diagnostic in a limited sample of specimens, or is it more plausible to expect equivalent "species" to share features representing a variety of character systems spread over the entire body? Reyment et al. (1984) listed numerous studies that demonstrated significant geographical or environmentally mediated character variation but found that the combination of characters effecting discrimination among species was relatively invariant. Mayr (1963:144) wrote "Of phenotypic variability observed in nature, it is never possible to tell, except by careful breeding experiments, what part should be ascribed to nongenetic modification and what part to genetic factors." In a phenotypically plastic group like the Coregoninae, a multivariate phenetic approach seems a reasonable means of hypothesizing species boundaries in the absence of experimental studies on reproductive isolation. I assume sufficient evolutionarily meaningful morphological trends will emerge from the ecophenotypic "noise" to permit an estimation of species limits congruent with the concept of a biological species.

Objective

The primary objective of this study is to provide evidence for the distinctiveness and specific identity of the putative *C. zenithicus* in Barrow Lake, Alberta using morphological, ecological, genetic, and biogeographic data. Examination of ciscoes from several nearby lakes will establish an important baseline against which to judge the uniqueness of the Barrow Lake form and will afford an opportunity to locate undiscovered populations of *C. zenithicus* or other cisco species. This biogeographic data may help explain the origin of the apparently disjunct *C. zenithicus* populations spread across northern inland Canada (McPhail and Lindsey 1970). An examination of the morphological variation observed in ciscoes from the same geographic area, and therefore subjected to similar large-scale environmental conditions, will help put the Barrow Lake populations

into a morphological and ecological context. This is a microtaxonomic study focussing on species delimitation and identification. Analyses are not based on a cladistic algorithm and so considerations fundamental to constructing phylogenies (e.g., synapomorphies versus plesiomorphies, character polarity, etc.) are not of primary concern.

The Coregoninae

Ciscoes, whitefishes, and inconnu comprise the subfamily Coregoninae. Nelson (1994) places this as the basal group in the family Salmonidae that also includes the graylings (Thymallinae) and the trout and salmon (Salmoninae). Coregonines are freshwater or anadromous fishes with typical trout-like bodies (terete shape, abdominal pelvic fins, adipose fin) but with larger scales than trout or salmon and with toothless maxillae. They are holarctic in distribution with many species endemic to North America or Eurasia. The taxonomic relationships among the three genera, approximately 32 currently recognized species (Nelson 1994) and an unknown number of subspecies and races in this subfamily, remain speculative.

The round whitefishes (*Prosopium*) are believed to be the basal genus in the Coregoninae. Members of this group possess a single nostril flap, a basibranchial plate on the floor of the branchial chamber, and young with parr marks. Morphological and genetic evidence suggests that they are relatively distantly related to *Coregonus* and *Stenodus*, the other two genera in the subfamily (Bernatchez et al. 1991, Ermolenko 1992, Smith and Todd 1992, Lockwood et al. 1993, Reist et al. 1998).

The lake whitefishes and ciscoes comprise the genus *Coregonus*. These fishes have a double nostril flap, no basibranchial plate, and young without parr marks. Generally, the whitefishes are distinguishable from ciscoes by the presence of a small, subterminal mouth and relatively few and short gillrakers. However, rare exceptions to this relationship

do exist. Nelson (1994) retains a separate subgeneric status for the whitefishes (subgenus *Coregonus*) and ciscoes (subgenus *Leucichthys*) although notes that these subgenera are probably not strictly monophyletic. Phylogenetic analyses of ciscoes suggest two distinct clades; one group represents the North American endemics plus *C. autumnalis* (Pallas 1776), the Arctic cisco, and *C. laurettae* Bean 1882, the Bering cisco; the other group is comprised of all the Eurasian forms plus *C. sardinella* Valenciennes 1848, the least cisco (Smith and Todd 1992, Reist et al. 1998). The relationships of these two groups to each other and to other coregonines varies depending on the data analysed. However, they are often found to be more closely related to other taxa than to each other (Reist et al. 1998).

Stenodus leucichthys (Guldenstadt 1772), the inconnu, can be distinguished from ciscoes and whitefishes (*Prosopium* and *Coregonus*) by its large mouth and many small teeth on the jaws, vomer, and palatine. However, the validity of separate generic status for the two subspecies of inconnu has been questioned by recent taxonomic evidence (Bernatchez et al. 1991, Smith and Todd 1992; Hamada et al. 1998, Reist et al. 1998). It seems probable that inconnu are nested phylogenetically within the *Coregonus* group and are likely aligned most closely with the Eurasian ciscoes (Smith and Todd 1992, Reist et al. 1998).

Attempts at phylogenetic reconstruction in the Coregoninae have proceeded despite many questions regarding the delimitation and validity of taxa in this group. Much of the difficulty in defining species boundaries stems from differing opinions as to what constitutes a species and from the difficulty in testing hypotheses of reproductive isolation. Operational species definitions based on theoretical species concepts are needed to address the delimitation question that seems fundamental to understanding the evolutionary history of Coregonines.

Species Concepts

Numerous concepts of what defines a species and how they arise have been proposed (Mayr 1963, Bush 1975, Paterson 1985, Templeton 1989, Nelson 1999) but most recognize speciation as an evolutionary genetic process. There is general agreement that the process of speciation requires that gene flow between diverging populations be minimal and that hybrids be at a selective disadvantage (Bush 1975). There is, however, debate over how barriers to reproduction arise - either as a result of direct selection for reproductive isolating mechanisms between populations or as a byproduct of selection for traits that promote reproductive cohesion or niche specialization within populations. In other words, does reproductive isolation lead to speciation or does the process of speciation lead to reproductive isolation? Templeton (1989) has suggested that this confusion over product versus process has been a stumbling block in understanding the process of divergence and multiplication of species.

The Typological (Morphological) Species Concept is an old concept based on the idea that all natural variation is derived from a limited number of types that are constant through time and sharply distinct from all other kinds. Variation merely represents morphological imperfection in the manifestation of a type (Mayr and Ashlock 1991). The degree of morphological similarity or difference is the only criterion used to delimit species under this concept. Biological attributes like reproductive cohesion (or isolation) are not explicit; however, they are often inferred. In theory, this concept has been abandoned by modern taxonomists. However, in practice, the necessary biological evidence to unequivocally support an alternative species concept based on reproductive isolation is often unavailable and may be unknowable. Because many isolating mechanisms, such as assortative mate selection (Foote 1988) and selection against hybrids (Hatfield 1995) are not discernible by common collecting or laboratory techniques, inferences about reproductive isolation based on these kinds of studies are speculative. It has been suggested

that, at the species level, it is impossible to conduct enough breeding experiments to prove that all members of a presumed interbreeding population breed with each other to the total exclusion of all others (Sokal and Crovello 1970, Reist 1983). The only way to construct interbreeding groups with certainty is to observe individuals breeding in nature. Even when this is possible, initial delimitation and recognition of spawning groups is still based on phenetic similarity (Sokal and Crovello 1970). Thus, despite theoretical difficulties, much current species-level taxonomy is, of necessity, based largely on morphological similarity and difference.

The Biological Species Concept (Mayr 1940, 1963, 1969, Dobzhansky 1937, 1970) proposes that species are groups of interbreeding, or potentially interbreeding, populations that are reproductively isolated from other such groups. This concept is defined in terms of reproductive isolating mechanisms that delimit the reproductive community and preserve the genetic integrity of the species in sympatric situations. These isolating mechanisms can be either pre- or post-zygotic. Pre-zygotic mechanisms include spatial, temporal, or behavioural isolation; post-zygotic mechanisms include physical (mechanical) or gametic incompatibility and hybrid sterility or inviability. Under the biological species concept, isolating mechanisms typically evolve in physically separated populations as incidental byproducts of adaptive divergence (speciation is the process, isolation the product). If these differentiated forms come into contact, accrued differences function to reduce or eliminate inter-specific reproduction. If gene flow continues between these sympatric incipient species (i.e., the differences are not so great as to completely prevent interbreeding), and if hybrids are inferior to the parental phenotypes, selection against hybrids may favour those individuals that do not mate to produce incompatible or less fit gene combinations. In this situation, reinforcement of pre-mating isolating mechanisms becomes part of the speciation process leading to increased isolation and further divergence (reproductive isolation is the process, speciation the product). In this way, a

biological species is protected from unsettling gene flow from other gene pools by isolating mechanisms (Mayr and Ashlock 1991).

Potential confusion over the function of isolating mechanisms and speciation products versus processes prompted Paterson (1985) to examine "isolation" from a different perspective. Under his Recognition Species Concept the isolating mechanisms of the Biological Species Concept are defined not in terms of preventing hybridization but rather in terms of promoting intra-specific fertilization. Selection acts to maximize reproduction among individuals best adapted to a specific environment. The reproductive isolation function arises only incidentally as a byproduct of evolutionary forces operating to promote reproduction. Tinbergen (1953) pointed out that supposed behavioural isolating mechanisms function primarily to synchronize mating activities, persuade potential mates to continue courtship, suppress escape or aggressive behavior in courted individuals - in general to promote fertilization. These functions are under strong selective pressure and the isolation function may be inconsequential in the speciation process (Paterson 1985). Under this concept, species are defined as the most inclusive population of individual biparental organisms which share a common fertilization system (Templeton 1989). The product is the same as the under the biological species concept - a closed interbreeding population - but the evolutionary process leading to the observed species pattern is different.

Systematists have long been plagued by the problem of explaining patterns and processes in the speciation of asexual organisms with closed reproductive systems and in those species with very open systems in which natural hybridization is widespread and frequent. Neither the biological species concept nor the recognition species concept can cope adequately with these groups. Under the Evolutionary Species Concept (Simpson 1961) a species is considered a member of a lineage evolving separately from others and

with its own evolutionary fate and tendencies. This definition can be applied to living, extinct, asexual, and sexual populations (including those with exceptionally open breeding systems) because it assumes that species are defined by developmental, ecological, and genetic constraints in addition to reduced gene flow between related populations. While theoretically attractive, it offers no mechanistic explanations for the evolutionary cohesion observed (Mayr and Ashlock 1991). Therefore, it does not permit the testing of speciation hypotheses based on population genetics (Templeton 1989). The subjectivity of judging the commonality of evolutionary fate among species is another difficulty with this concept. Is it possible to know if morphotypes are following different evolutionary pathways, and how similar must evolutionary fates be to be judged the same?

In response to these conceptual shortcomings, Templeton (1989) proposed the Cohesion Species Concept under which a species is defined as the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. This concept can be applied to the entire spectrum of breeding systems, as in the evolutionary species concept, but focuses on the mechanisms that promote the observed cohesion. These mechanisms are considered in light of their most likely evolutionary function, not simply their direct effect on reproductive cohesion (or isolation). They are seen to promote genetic relatedness through ease of exchange of gene products intra-specifically (unrestricted gene flow) and difficulty of inter-specific gene exchange (reduced gene flow). The importance of intra-specific gene flow in promoting cohesion is common to all modern species concepts, but the cohesion concept emphasizes as well the role of genetic drift and natural selection as speciation processes that are not necessarily based on genetic exchange. Genetic drift promotes cohesion through identity-by-descent. The limits of genetic variation, introduced by random drift, that can be tolerated by a population, is a major cohesive factor (Templeton 1989). Individual ecological tolerance is acted upon by natural selection, within the limits of ecological constraints,

to further increase species cohesiveness. Natural selection may also favor genetic relatedness by driving allelic variants (neutral or advantageous mutations) to fixation. Other linked genes and pleiotropic effects can "hitchhike" with this trend and further increase genetic relatedness. Thus, Templeton (1989) contends that gene flow should not be the only microevolutionary mechanism used to define an evolutionary lineage as is the case with the Biological and Recognition Species Concepts.

Under the Biological Species Concept, morphological differences among populations are a by-product of the genetic discontinuity resulting from reproductive isolation. This implies that differentiation is a consequence of reproductive isolation. Under the Cohesion and Recognition Species Concepts, reproductive isolation is a potential by-product of genetic differentiation (via adaptation or drift) resulting from geographical or ecological barriers to gene flow. Reproductive isolation is, therefore, a potential consequence of the differentiation process (Cracraft 1989, Templeton 1989). In sympatry, reinforcement of characters that happen to reduce inter-specific reproduction may occur under appropriate conditions (e.g., post-mating isolation is well established - the intermediate phenotype of hybrids is distinctly inferior, some pre-mating isolation is established, and there is sufficient genetic variation in mate preference and recognition abilities). This may serve to enhance the distinctiveness of each population by further limiting gene flow; however, there is a surprising paucity of experimental proof of reinforcement and few convincing examples of this process in nature (Butlin 1989). Most speciation probably occurs in the presence of some extrinsic (geographic or ecological) barrier to gene flow where isolating mechanisms *per se* are irrelevant.

Species Definitions

Speciation theory requires that species are discrete, natural entities with unique evolutionary histories (Cracraft 1989). However, the recognition of environmentally induced phenotypic modification without concomitant genetic change has caused much debate over whether morphologically distinct forms represent valid species and whether phenotypically similar forms are genetically related (Bernatchez and Dodson 1990a). Transplantation experiments (Svardson 1965, Loch 1974, Lindsey 1981) have demonstrated that few characters are stable phenotypically under varying environmental conditions. This plasticity hinders the recognition of equivalent, homologous character states among allopatric populations. However, where forms occur sympatrically, with little or no apparent introgression, it can be argued that some mechanism must be maintaining the integrity of forms in the absence of a geographical barrier. Svardson (1949) felt that sympatric whitefish populations that are believed to have persisted for some time must be considered different species. In discussing the systematic importance of proportional measurements in coregonines, Svardson (1970:40) concluded "As a character to identify whitefish species that live together in one lake, where they mostly have different growth rates, these body proportions are excellent. In an allopatric situation, however, where real species criteria are concerned, they seem to be of very limited value." On the other hand, Dymond (1943) felt that each species exhibits a characteristic combination of characters and, while recognizing that species will show some inter-locality character variation, believed this variation is usually insufficient to obscure the similarity demonstrated by a combination of characters. It is often these character combinations that we use intuitively to recognize objects despite the ever-present variation in organic systems.

The observed morphological variability within and among cisco species is probably best described as environmental modification superimposed on a distinctive genetic background. The relative contributions of the genotype and the environment to the phenotype can be

estimated by transplantation or hybridization experiments, but this is rarely done on a large scale in which all species and forms in a taxonomic study are examined (with the possible exception of Svardson's work). How then do we sort out the plastic responses of no evolutionary significance from the heritable differences defining natural, or "good" species?

Discrete, environmentally stable characters that provide 100% diagnosis of all populations of a species have eluded cisco taxonomists. Gillraker number has been accepted as one of the most stable and taxonomically useful individual characters in coregonine taxonomy. However, recent empirical evidence suggests that this trait is also phenotypically plastic, albeit to a lesser extent than many other characters (Lindsey 1981, Todd 1998). Masking of evolutionarily meaningful change by non-genetic effects can potentially confound estimates of species limits based on a consideration of individual characters. If, however, we assume that some genetic signal is still evident in a combination of morphological characters, an objective, multi-character analysis may reveal enough of the underlying heritable component to permit the best possible estimate of species boundaries.

Estimates of similarity or morphological likeness are often subjective, and this subjectivity has led to the failure of many hypotheses of conspecificity. Recognizing species based on continuously varying quantitative differences requires some means of delimiting taxa that is not arbitrary (Cracraft 1989). Objective multivariate analytical procedures such as Principal Components Analysis or the more statistically powerful but restrictive Discriminant Function Analysis reduce this subjective bias in much the same way the cladistic algorithm minimizes subjectivity in analyses of ancestor-descendent relationships. The use of multivariate analyses is based on the recognition that no one external, morphometric or meristic character can be absolutely relied upon to consistently define highly plastic species (Dymond 1943, Reist et al. 1992). Todd et al. (1981)

observed that distinct though closely related species usually cluster without overlap on principal-components projections. One, or a few characters like gillraker number, may be useful initially to hypothesize membership in a species but these hypotheses should be tested by congruence with a combined "score" of several objectively weighted informative characters.

This is the approach adopted in this study. Univariate comparisons and multiple pairwise comparisons are included to illustrate character variation. However, decisions regarding identification and species boundaries have relied heavily on interpretation of multivariate ordination patterns to reveal morphological similarities and traces of equivalency among populations. In the absence of direct experimental evidence for reproductive isolation or cohesion, multivariate analyses that identify character combinations contributing most to the variation among phenotypes may provide reasonable estimates of species limits and identities.

This phenetic approach to species delimitation is here considered distinct from the problem of phylogenetic estimation, an endeavor not addressed in this study. I am in full agreement with the cladistic method for elucidation of historical relationships. It seems, however, that traditional phylogenetic analysis of many coregonine taxa is hindered by the lack of resolution of species limits. Generally, I agree with Cracraft (1989) that the resolution of phylogenetic pattern is strongly influenced by decisions about species limits: "...an interpretation of patterns of variation is predicated upon a correct description of the pattern itself, and sometimes the latter is influenced by the choice of species boundaries" (Cracraft 1989:47). If several species are inadvertently combined into a single terminal taxon, or if several terminal taxa actually represent a single species, confusion and misinterpretation of cladograms is inevitable. It is for this reason that I have chosen to focus on the problem of species delimitation as a necessary basis for subsequent phylogenetic analysis.

Morphological Markers of *Coregonus artedi* and *C. zenithicus* Populations

Equating allopatric populations at the species level for the purpose of determining a collective identity has been a formidable problem in coregonine taxonomy. This is due to the scarcity of consistent diagnostic characters (markers) that reliably infer common genetic ancestry in geographically separated populations (Lindsey et al. 1970). Morphologically, gillraker number has proven useful due to its proven heritable component. However, a review of the literature reveals other characters noted consistently in descriptions of *C. artedi* and *C. zenithicus* (and synonymous taxa) from a wide range of localities over almost two centuries of study. Although the validity of these characters is still unresolved, when considered in combination, they may provide a reasonable morphological baseline for the estimation of specific identities of unknown populations suspected of belonging to either *C. artedi* or *C. zenithicus*.

The following descriptions are taken from selected literature dealing with the identification of these species. Incorporated into the descriptions are character states for currently accepted synonyms. Character states relevant to the present study are summarized in Table 1.

Coregonus zenithicus

Jordan and Evermann (1909). *Argyrosomus zenithicus* (new species). Type locality: deep water off Isle Royale, Lake Superior. September 1908. Type description: gillrakers 17 + 25 = 42 (recounted by Koelz [1929] = 45), very slender, the longest 6 in head; eye small, 5 1/3 in head; maxillary long, 2 3/5 in head. Mouth larger than in related species, mandible usually included in upper jaw, snout pointed. Lateral line scales 72. Reported to live in much deeper water than sympatric *C. artedi* in Lake Superior.

Jordan and Evermann (1911). *Leucichthys zenithicus* and *L. cyanopterus* (new species). Body elongate, somewhat compressed. Head rather large, about 4 in SL. Snout proportionally long, about 3.5 in head. Maxillaries long, 2.8 in head, extending almost to below centre of pupil. Lower jaw equal to or longer than upper, distance from snout to occiput long, eye variable, smaller in *L. cyanopterus*. Gillrakers 37-44. Lateral line scales 76-87.

Harper and Nichols (1919). *Leucichthys entomophagus, L. athabascae*, and *L. macrognathus* (all new species). All three species synonymized with *C. zenithicus* by Dymond (1943). McPhail and Lindsey (1970) felt *C. athabascae* and *C. macrognathus* belong to *C. artedi* complex and *C. entomophagus* may represent *C. zenithicus*. Clarke (1973) felt all three most closely resembled *C. artedi*.

L. entomophagus (Tazin River, N.W.T.): Gillrakers 33 and long (1.6 in eye). Lateral line scales about 65. Small mouth, short maxillary (reaching to front of eye). Profile of head low and nearly straight. Lower jaw included in upper jaw; no vertical protuberance at tip of mandible, or notch at tip of upper jaw. Dorsal fin base 2.06 in head. The type specimen, 165 mm total length, was the largest of 27 specimens examined.

L. athabascae (Lake Athabasca): Gillrakers 35 [gill arch has been cut short and the number is undoubtedly higher (J. S. Nelson pers. comm.)], long and slender. Lateral line scales about 66. Head narrow and pointed with a straight, low profile. Large mouth with projecting lower jaw. Maxillary reaches to pupil. A vertical protuberance at tip of lower jaw and slight notch in tip of upper jaw. Dorsal fin base 2.44 in head. One specimen encountered.

L. macrognathus (Great Slave Lake): Gillrakers 41. Lateral line scales about 68. Head narrow and pointed with a low, straight profile. Maxillary reaching to front of pupil; mandible distinctly projecting beyond upper jaw. A vertical protuberance on tip of mandible and a slight notch in tip of upper jaw. Dorsal fin base 2.18 in head. A single specimen encountered.

Koelz (1929). *Leucichthys zenithicus, L. reighardi dymondi* (new subspecies), *L. nigripinnis cyanopterus* (Jordan and Evermann 1909). Includes descriptions of forms of *L. zenithicus* from Lakes Superior ("typical" race), Nipigon, Michigan, and Huron. Gillraker number 31-48. Lateral line scales 66-96. Elongate, subterete fishes of moderate size with short, usually included mandible (in 3/4 of specimens observed). Snout relatively long, about 3.1-4 in head length. Eye moderate but variable. Maxillary long, about 2.1-2.7 in head length; extends past anterior margin of pupil. Premaxillaries nearly vertical (55-75° from horizontal axis of head). Head relatively long and shallow, depth 3.6-4.4 in total length. *L. reighardi dymondi* (Lakes Superior and Nipigon) has a longer snout, head, and maxillary than typical *L. reighardi* (Lakes Michigan and Ontario). *L. nigripinnis cyanopterus* (Lake Superior) has fewer gillrakers, a longer head. and longer snout than typical *L. nigripinnis*. All forms inhabit moderate depths and spawn in the fall. Rarely found more than a few miles from 30 or 40 fathom shoals that drop abruptly to 80 fathoms or more. "*Zenithicus* may be distinguished readily from *artedi* by the fewer rakers on the first branchial arch, longer snout, maxillary, head, and paired fins, and the more truncated head as seen from the side." (Koelz 1929:381)

Dymond and Pritchard (1930). *Leucichthys zenithicus*. Reported from Lake Athabasca, Alberta. Fewer than 43 gillrakers (usually 38-40), eye very large, maxillary long, lateral line scales 58-69. Of the four species examined from western Canada (*L. nigripinnis, L. nipigon, L. tullibee* [all=*L. artedi*], and *L. zenithicus*), *L. zenithicus* was on average the smallest, with longest maxillary, narrowest interorbital, and shortest dorsal fin base.

Bajkov, A. (1932). *Leucichthys zenithicus*. Reported from Lake Winnipeg, Manitoba. Gillrakers usually 31-44 (mode=37), large eye. Bottom feeder.

Dymond (1943). *Leucichthys zenithicus*. Gillrakers 33-40 (one aberrant individual had

29 on one side and 35 on the other), low lateral line scale count (64-76), and long maxillary. Body depth and fin length highly variable. Synonymized three species (*C. entomophagus*, *C. macrognathus*, and *C. athabascae*) described by Harper and Nichols (1919) with *C. zenithicus* on the basis of a combination of characters including gillraker number, maxillary length, and number of lateral line scales.

Hubbs and Lagler (1964). *Coregonus zenithicus*. Jaws usually equal. In Great Lakes, found at depths of 11 to 100 fathoms, usually less than 30 fathoms.

Paterson (1969). *Coregonus zenithicus*. Gillrakers 37-41. Lateral line scales 69-77. Head length 4.04-4.54 in fork length. Maxillaries 2.04-2.81in head length. Predorsal and snout lengths were significantly longer than sympatric *C. artedi*.

Scott and Crossman (1973). *Coregonus zenithicus*. Gillrakers 32-46. Head elongate but not deep, eye moderate (20-25% of head length), snout usually longer than eye. Maxillary long, extending to middle of eye or beyond. Lower jaw protruding beyond, or included in upper. Lateral line scales 58-90.

Clarke (1973). *Coregonus prognathus*. ["low group" includes *C. cyanopterus, C. reighardi*, and *C. hoyi* from George Lake, Manitoba and Sandy Lake, Ontario]. When *C. prognathus* and *C. artedi* occur in sympatry, *C. prognathus* always has fewer gillrakers (50% of *C. prognathus* have 35 or fewer gillrakers; 77% of *C. artedi* have 44 or more), longer upper jaws, and a longer snout. Most populations also have a longer head, shorter gillrakers, premaxillary at a larger angle to the snout, and a lower jaw included in the upper jaw. [Clarke felt that of the names applicable to his low gillraker group, *C. prognathus* (Smith 1894) had priority over *C. zenithicus* (Jordan and Evermann 1909). Todd (1981) has since re-examined all existing specimens of *C. prognathus* and found

them to represent "... nearly every species of cisco described in the Great Lakes." This combined with the poor condition and uncertain identity of the holotype led Todd to suggest *C. prognathus* should be considered a *nomen dubium*.]

Todd and Smith (1980). *Coregonus zenithicus*. Long snout, short fins, few and short gillrakers, premaxillaries nearly vertical, and lower jaw usually included in upper. Considered the most readily identifiable species of cisco in Lake Superior.

Smith and Todd (1992). *Coregonus zenithicus*. Considered a change in chromosomal fundamental number from 104-108 to 98-102 to be an autapomorphy defining *C. zenithicus* (based on data from Rab and Jankun 1992). However, Phillips et al. (1996) found no karyotypical differences between *C. artedi*, *C. hoyi*, *C. nigripinnis*, and *C. zenithicus*. All had a fundamental number of 98.

Coregonus artedi

Le Sueur (1818). *Coregonus artedi* (new species) and *C. albus* (new species). Type locality (*artedi*): Lake Erie, and at Lewiston, upper Canada. [Koelz (1929) discusses how specimens from these 2 localities, above and below Niagara Falls, probably represented 2 distinct races]. Body sub-fusiform, a little elevated at the back, head small and narrow, snout short and pointed, maxillaries wide, mandibles carinate, very small conical teeth at extremity of jaws in small individual but not visible in larger specimen. Lateral line straight and near the middle. Length 10-12 inches. Fin rays: dorsal 12, pectoral 16, pelvic 12, anal 13. *C. albus* deeper bodied than *C. artedi*, back elevated from nape to dorsal fin. Proportions stronger in body, fins, and scales.

Richardson (1836). *Salmo (Coregonus) tullibee, S. (C.) lucidus,* and *S. (C.) harengus* (all new species). Form much compressed, belly rounded. Eyes large, more than their own

diameter from the snout. Mouth small. Lower jaw a little longer than the upper jaw: its knobbed tip fits into a depression between the intermaxillaries. Small plate of minute teeth on centre of tongue. The longest gillrakers measure half an inch. *S. (C.) lucidus.* (Great Bear Lake) described as having a larger mouth than any other coregonine. Maxillaries large and widely oblong, extending to middle of orbit. 88 lateral line scales. *S. (C.) harengus.* (Lake Huron) is similar to *S.(C.) lucidus* but with a larger head and smaller scales. Richardson did not think *S. (C.) tullibee* and *S. (C.) artedi* were the same based on a more pointed snout and rounder scales in the latter. Did not find *S. (C.) artedi* but quotes the description by Le Sueur (1818).

Evermann and Smith (1896). *Argyrosomus artedi, A. osmeriformis* (Smith 1894), *A. lucidus,* and *A. tullibee.* Gillrakers 43-58, long and slender, usually 1-1.5 in eye. Body slender, mouth large, lower jaw projecting or subequal, maxillary extending to front edge of pupil, snout to occiput 2.5 in occiput to dorsal fin origin. Lateral line scales 62-87 (usually 74-83). *A. osmeriformis* (Seneca and Skaneateles lakes, New York) has a large head (snout to occiput 2.25 in occiput to dorsal fin origin), large eye, and premaxillaries not at angle to dorsal margin of head. *A. lucidus* has a small head (snout to occiput 2 3/5 to 3 in occiput to dorsal fin origin), a snout almost vertically truncate, a lower jaw included in upper, and a maxillary extending to midway between front and midpoint of pupil. *A. tullibee* has a small head (snout to occiput 2 in occiput to dorsal fin origin), a projecting lower jaw, and maxillaries extending to anterior edge of pupil.

Jordan and Evermann (1911). *Leucichthys artedi, L. harengus, L. osmeriformis, L. sisco* (Jordan 1875), *L. ontariensis* (new species), *L. lucidus, L. eriensis* (Jordan and Evermann 1909), *L. manitoulinus* (new species), *L. supernas* (new species), *L. nigripinnis* (Gill 1872), and *L. tullibee.* Most differences based on geography, size and robustness of body, size of adipose fin, and coloration. Gillrakers 37-55. Lateral line scales 67-87.

L. artedi with premaxillaries variably oblique and maxillaries extending to or slightly beyond front margin of pupil. *L. harengus* (Lakes Huron and Michigan) with mandible projecting beyond upper jaw, maxillary not quite extending to front of pupil, and short dorsal fin base (shorter than the eye). *L. osmeriformis* with long maxillary extending to anterior margin of pupil, lower jaw projecting beyond upper, large eye, and long head. *L. sisco* (lakes of northern Indiana and southern Wisconsin) is very similar to *L. harengus*. *L. ontariensis* (Lake Ontario and Cayuga Lake, New York) with mandible slightly projecting beyond upper jaw and maxillary extending to below anterior edge of pupil. *L. lucidus* (Mackenzie River basin particularly Great Bear Lake) with short head, small eye, mandible included in upper jaw, maxilla extending to midway between front and middle of pupil, and vertically truncate snout. *L. eriensis* (Lake Erie, northward) with blunt snout, mandible included in upper jaw, and maxillary extending to front of pupil. *L. manitoulinus* (north channel of Lake Huron and probably lakes of Minnesota) with lower jaw not included in upper jaw and maxillary extending to anterior one-third of eye. *L. supernas* (Lake Superior) is similar to *L. artedi* and *L. harengus* but with short maxillary and deeper body. *L. nigripinnis* is of large size with black on all fins. *L. tullibee* (Winnipeg basin, perhaps Lake Superior) with very deep body, lower jaw included in upper, maxillaries not extending to anterior edge of pupil, and premaxillaries projecting very obliqely forward.

Koelz (1929). *Leucichthys artedi, L. nigripinnis* (except *L. nigripinnis cyanopterus*), and *L. nipigon* (Koelz 1925). Gillrakers 41-66. Lateral Line scales 64-89. Maxillaries short (2.5-3.3 in head), snout short (3.3-4.5 in head), premaxillaries usually at an angle of 45-60° with horizontal axis of head, and head broadly triangular in side view. Recognized three subspecies of *L. artedi* - *L. a. artedi* (widespread), *L. a. albus* (Lakes Erie, Superior, and Ontario), and *L. a. manitoulinus* (north channel of Lake Huron). Subspecies differ slightly in body depth, eye size, head length, gillraker number and

lateral line scales but are described as being similar among Great Lakes. Recognized three subspecies of *L. nigripinnis* - *L. n. nigripinnis* (Lakes Michigan and Huron), *L. n. regalis* (Lake Nipigon), and *L. n. prognathus* (Lake Ontario). All described as large in size with deep body, a maxillary seldom extending beyond anterior margin of pupil, and a large eye. *L. nipigon* is considered the largest species of *Leucichthys* with a very deep body and many gillrakers (54-66).

Dymond and Pritchard (1930). *Leucichthys tullibee, L. nigripinnis,* and *L. nipigon.* 41–62 gillrakers. Short head, small eye, short snout and maxillary in *C. tullibee.* Larger head, eye, snout, and maxillary in *L. nigripinnis* and *L. nipigon.* Believed western Canadian *L. tullibee* were distinct from Great Lakes *L. artedi*, the former being larger,. deeper bodied, and faster growing.

Bajkov, A. (1932). *Leucichthys artedi tullibee, L. a. artedi, L. lucidus, L. nigripinnis,* and *L. nipigon.* Gillrakers 37-66. Found *L. tullibee* to vary in body shape from deep bodied to slim and elongate with no distinct difference from typical *artedi* of the Great Lakes. Therefore, considered *L. tullibee* a subspecies of *L. artedi. L. nipigon* has more gillrakers, a larger maxillary and snout and smaller eye than *L. artedi. L. nigripinnis* has a larger head than *L. artedi.*

Dymond (1943). *Leucichthys artedi, L. lucidus, L. tullibee,* and *L. nigripinnis.* Gillrakers 40-52. Premaxillaries at wide angle to vertical. Synonymized *L. lucidus* with *L. artedi.* Had earlier redescribed *L. tullibee* in Dymond (1928) but was unable to determine if *L. tullibee* was closer to *L. nigripinnis* or *L. artedi.*

Hubbs and Lagler (1964). *Coregonus artedi* (22 subspecies recognized). Gillrakers usually 43-52 and long. Jaws equal, fins medium length.

Paterson (1969). *Coregonus artedii*. Gillrakers 42 or more. Lateral line scales 64-74. Relatively long predorsal and snout length (compared to sympatric *C. zenithicus*).

McPhail and Lindsey (1970). *Coregonus artedii* complex. Gillrakers 41-51. Lateral line scales 67-89. Upper jaw extending to about middle of pupil, snout about equal to horizontal eye diameter, premaxillaries in line with forehead, tip of lower jaw projects beyond upper jaw.

Clarke (1973). *Coregonus artedii* ["high group" includes *C. nigripinnis*, *C. nipigon*, and *C. hoyi*]. Gillrakers long, mean number 39.3-62.9. Short head and short upper jaw.

Scott and Crossman (1973). *Coregonus artedii* and *C. nigripinnis*. Gillrakers 36-64. Head length 20-24% of total length with *C. nigripinnis* at upper end of size range. Eye moderate, 21-26% of head length. Snout usually longer than eye, lower jaw often projecting beyond upper. Maxillary extending to below anterior half of eye. Lateral line scales 63-94.

Table 1. Selected references and characters used in descriptions of *C. zenithicus* and *C artedi* (and synonyms).

Reference	**Gillraker number**		**Head length**		**Lateral line scale number**		**Angle of premaxilla**	
	C. zenithicus	*C. artedi*	*C. zenithicus*	*C. artedi*	*C. zenithicus*	*C. artedi*	*C. zenithicus*	*C. artedi*
Jordan and Evermann (1909 and 1911)[a]	37-42	37-55	long 3.8-4 in SL	Short (4.3-5.3 in SL)	72-87	67-87	more or less vertical	variable
Koelz (1929)[b]	31-48 (usually 36-40)	41-66	relatively long	moderate	66-96	64-89	relatively vertical (55-75° with horiz. axis of head)	less vertical (45-60° with horiz. axis of head)
Dymond and Pritchard (1930)[c]	< 43 (usually 38-40)	41-62	moderate	short (longer in *nipigon* & *nigripinnis*	58-69	60-70		
Bajkov (1932)[d]	31-44	37-66		short in *artedi*; longer in *nigripinnis*				
Dymond (1943)[e]	33-40	40-52		longer in *nigripinnis*	64-76	67-89		at wide angle to vertical
Paterson (1969)	37-41	44-51	long (4.04-4.54 in FL)	short (4.25-4.67 in FL)	69-77	64-74		
Clarke (1973)[f]	29.4-40.2 (population means)	39.3-62.9	longer than sympatric "high" group	shorter than sympatric "low" group			larger than sympatric "high" group	smaller than sympatric "low" group
Scott and Crossman (1973)[g]	32-46	36-64	22.8-27 % of total length	20-26.4% of total length (*nigripinnis* a bit longer)	58-90	63-94		

Reference	Length of maxilla		Snout length		Size of eye		Depth of head	
	C. zenithicus	*C. artedi*	*C. zenithicus*	*C. artedi*	*C. zenithicus*	*C. artedi*	*C. zenithicus*	*C. artedi*
Jordan and Evermann (1909 - type description; 1911)[a]	long, 2.6-2.8 in head, extends to centre of pupil	short, 2.6-4 in head, extends to around front of pupil	long, 3.5 in head	short, 3.75-5 in head	variable, 4.6-5.3 in head	variable, 3.6-5 in head	slender, 4-4.75 in head length	variable, 3-5 in head length
Koelz (1929)[b]	long, 2.1-2.7 in head, extends past front of pupil	short, 2.5-3.3 in head	long, 3.1-4 in head	short, 3.3-4.5 in head	moderate, but variable	variable	shallow, about 3.6 in total length	broadly triangular in side view
Dymond and Pritchard (1930)[c]	long	short, longer in *nipigon* & *nigripinnis*	moderate	short, longer in *nipigon*	very large	small to moderate	relatively shallow	quite deep in *nipigon*
Bajkov (1932)[d]		relatively long in *nipigon*		relatively long in *nipigon*	large	small		
Dymond (1943)[e]	long							
Paterson (1969)	long, 2.04-2.81 in head	short, 2.59-2.99 in head	long, 3.24-3.8 in head	short, 3.75-4.2 in head				
Clarke (1973)[f]	longer than sympatric "high" group	shorter than sympatric "low" group	longer than sympatric "high" group	shorter than sympatric "low" group				
Scott and Crossman (1973)[g]	long, extends to middle of eye or beyond	short, extends to anterior 1/2 of eye	longer than eye	usually longer than eye	moderate, 19.7-25.6% of head length	moderate, 21-26% of head length	not deep	broadly triangular in *nigripinnis*

[a] *Leucichthys cyanopterus* synonym of *L. zenithicus*; *L. harengus, L. osmeriformis, L. sisco, L. ontariensis, L. lucidus, L. eriensis, L. manitoulinus, L. supernas, L. nigripinnis*, and *L. tullibee* synonym of *L. artedi.*

[b] *L. reighardi dymondi* and *L. nigripinnis cyanopterus* synonyms of *L. zenithicus*; *L. nigripinnis* (except *cyanopterus*) and *L. nipigon* synonmys of *L. artedi.*

[c] *L. nipigon, L. tullibee*, and *L. nigripinnis* synonyms of *L. artedi.*

[d] *L. nipigon, L. nigripinnis*, and *L. lucidus* synonyms of *L. artedi.*

[e] *L. lucidus, L. tullibee,* and *L. nigripinnis* synonyms of *L. artedi.*

[f] *Coregonus cyanopterus, C. reighardi,* and *C. hoyi* from George and Sandy lakes in low gillraker (*prognathus=zenithicus*) group; *C. nigripinnis, C. nipigon,* and *C. hoyi* in high gillraker (*artedi*) group.

Methods

Study Area

The lakes sampled in this study are located in the Canadian Shield region of northeastern Alberta (Fig. 1). The geology of the area is characterized by exposed Precambrian gneisses, granitoids, and metasedimentary rocks that form rolling hills rising in the order of 100 m above the surrounding muskeg lowlands. Soil development is minimal due to limited weathering of these highly resistant rocks (Hastings and Ellis 1990). Numerous rock basin lakes, aligned in a general north-south orientation, parallel major fault lines and the direction of Pleistocene ice movement (R. Mussieux pers. comm.). Drainage is to the Slave River via small, slow-moving rivers and creeks. The area is classified as the High Boreal Mixedwood Ecoregion. This is the coolest and wettest portion of the extensive Boreal Mixedwood in Alberta (Strong and Leggat 1992). *Salix* spp. (willow) and *Picea mariana* (Black Spruce) dominate in poorly drained areas, *Populus tremuloides* (Aspen), *Populus balsamifera* (Balsam Poplar), and *Picea glauca* (White Spruce) in moderately well drained areas, and *Pinus banksiana* (Jack Pine) on rocky uplands, along north-facing slopes, and on areas of glacial outwash (Hastings and Ellis 1990, Strong and Leggat 1992). Details of plant communities and soil types characteristic of this area can be found in Hastings and Ellis (1990).

Barrow Lake (59° 15' N, 111° 14'W) has a surface area of 3.81 km^2, a maximum length of 5.0 km, and mean width of 0.75 km (Turner 1967a). Turner (1967a) recorded a maximum depth of 21.9 m (72 ft) and calculated a mean depth of 11 m (36 ft). Fifteen percent of the surface area of the lake is shallower than 3.1 m (10 ft), 27% is shallower than 6.1 m (20 ft) , and 58% is deeper than 9.1 m (30 ft). One site sampled in the present study was 23 m in depth (sonar reading), but in general the bathymetric map presented in Turner (1967a) appears accurate. Ryan Creek, the only permanent stream feeding or

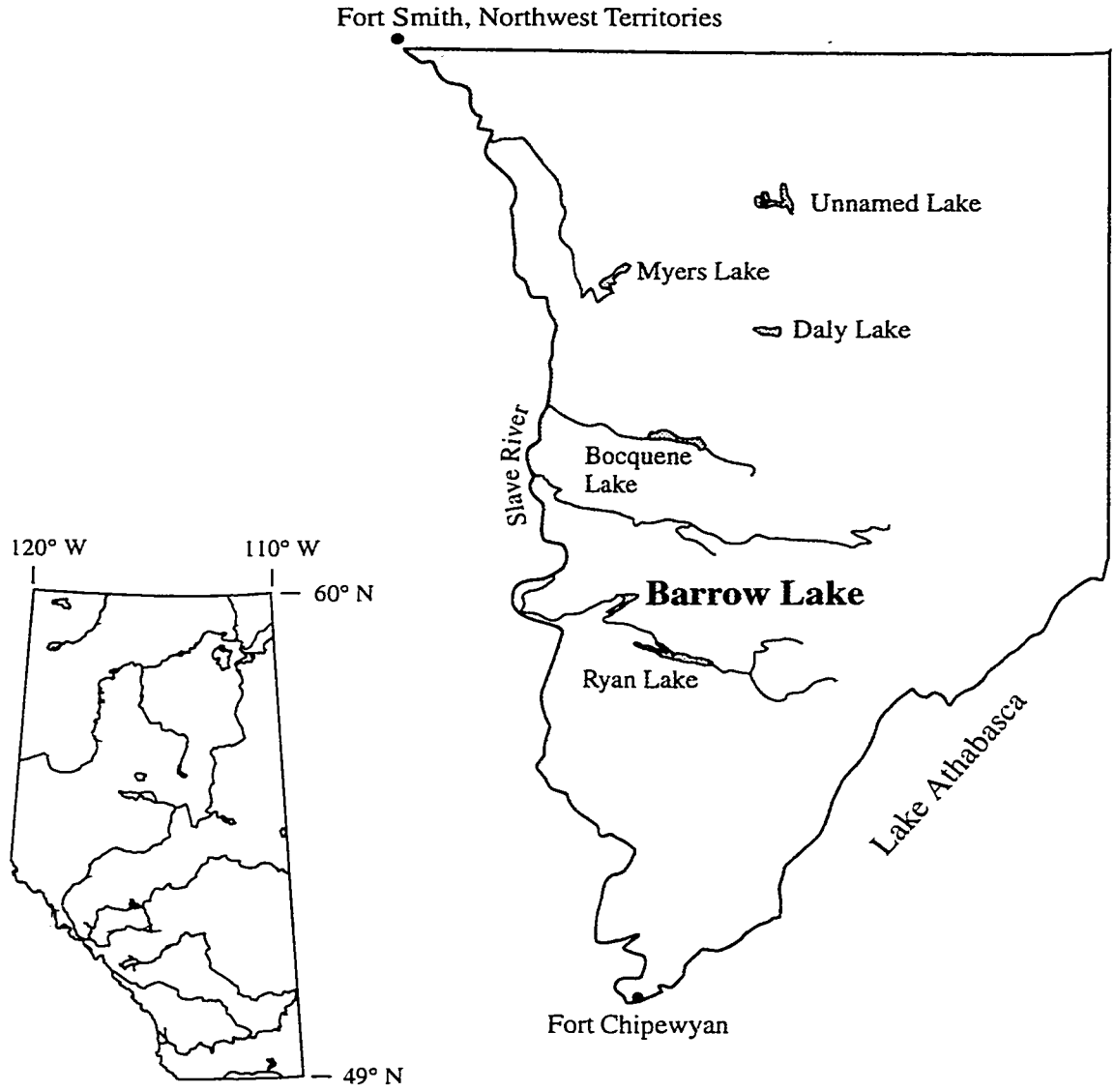

Figure 1. Location of study sites in northeastern Alberta.

draining the lake, enters the southern tip of the lake and drains to the Slave River from the northwestern tip. Ryan Creek is a shallow, slow-moving watercourse that is choked with submergent macrophytes during much of the open water season. It was not navigable by motorized craft at any time during this study. While it appears possible that ciscoes could move up and down this creek, the habitat is distinctly sub-optimal and there is probably little, if any, cisco immigration or emigration. Ryan Creek connects Barrow Lake to Ryan Lake (approximately 15 km distance) and there is no evidence of exchange of cisco forms between these lakes. Ryan Creek also appears unsuitable for cisco spawning due to the soft, detritus-covered bottom and thick submergent vegetation. Direct evidence of spawning sites in the main body of the lake was not found in this study nor by Turner (1967a) but the latter study suggested few suitable spawning sites of appreciable size.

Lake basin morphometry data from all six lakes surveyed in this study are summarized in Table 2. Myers and Daly lakes are uniformly shallow compared to Barrow, Bocquene, Ryan, and Unnamed lakes. The latter include substantial regions of deeper water (≥20 m).

Water temperature profiles revealed the establishment of a thermocline at about 7-8 m depth in all lakes except Myers Lake. Dissolved oxygen data (not shown) revealed oxygen depletion (O_2 concentrations <1ppm) in the bottom strata of lakes sampled in mid-August (Daly Lake and Unnamed Lake) and in early October (Barrow Lake). Samples taken in July (Ryan Lake, Myers Lake, and Barrow Lake) showed some O_2 decrease with depth but values never dropped below 3.5 ppm.

Water chemistry data for all of the lakes surveyed in this study are presented in Table 3. Data represent three replicates of a single temporal sample from each site. Since samples were taken in different years and at different times during the open water season, inter-lake comparisons of most parameters are not valid. However, a few trends are

Table 2. Summary of lake basin morphometry for the six lakes surveyed in this study. Data from unpublished reports for Alberta Department of Lands and Forests, Fish and Wildlife Division.

Lake	Lat./long.	Surface area (km^2)	Max. length (km)	Max. width (km)	Mean width (km)	Max. depth (m)	Mean depth (m)	Depth distribution
Barrow (Turner 1967a)	59° 15'N, 111° 14' W	3.81	4.99	1.6	0.75	21.9	11.0	15% < 3.0 m 27% < 6.1 m 58% > 9.1 m
Bocquene (Anon. c. 1966)	59° 28'N, 111° 07'W	7.14	8.53	1.45	0.84	24.7	9.3	40% < 3.0 m 48.3% < 6.1m 57.3% < 9.1 m
Daly (Anon. c. 1975a)	59° 37'N, 110° 50'W	2.59	7.52	3.27	0.34	11.6	4.2	45% < 3.0 m 70.5% < 6.1 m
Myers (Turner 1967b)	59° 41'N, 111° 15'W	5.36	5.63	2.01	0.95	7.3	3.7	37% < 3.0 m
Ryan (Anon. c. 1975b)	59° 10'N, 111° 03'W	5.83	12.6	0.87	0.47	23.5	6.43	36% < 3.0 m 69.3% < 6.1 m
Unnamed (Anon. c. 1975c)	59° 48'N, 110° 47'W	4.58	8.85	1.06	0.51	19.2	4.5	57% < 3.0 m 78% < 6.1 m

Table 3. Water chemistry of the six lakes surveyed in this study. Samples were taken from the midpoint of the euphotic zone (zone of light penetration) estimated at two times the secchi disc transparency. Abbreviations: TDN – total dissolved nitrogen; PARTN – particulate nitrogen; TP – total phosphorus; PARTC – particulate carbon; CHL A – chlorophyll *a*; COND – conductance; ALK – alkalinity; HCO3 – bicarbonate.

SITE	DATE	NO.	DEPTH (m)	SECCHI (mm)	TDN (µg/l)	PARTN (µg/l)	TP (µg/l)	PARTC (µg/l)	CHL A (µg/l)	COND (µS/cm)	PH	ALK (mg/l as CaCO3)	HCO3 (mg/l)
Barrow	07/28/96	1	11	310	538.3	70.4	13.1	521	1.41	67.0	7.14	24.13	29.41
Barrow	07/28/96	2	20	290	474.1	69.4	13.3	524.7	1.84	67.0	7.16	23.0	28.04
Barrow	07/28/96	3	4	290	485.3	77.4	14.8	1125.2	2.13	67.0	7.17	23.75	28.96
Bocquene	07/15/97	1	22	320	550.02	88.0	18.93	841.05	2.97	120.8	7.64	49.22	60.01
Bocquene	07/15/97	2	5	285	549.23	86.4	17.4	685.88	2.70	121.1	7.79	50.38	61.43
Bocquene	07/15/97	3	25	N/A	506.12	88.85	20.02	645.95	4.08	120.6	7.75	49.85	60.78
Daly	08/19/97	1	15	225	592.5	113.2	18.8	1213.2	4.33	100.0	7.23	45.72	55.74
Daly	08/19/97	2	8	200	614.83	115.6	25.8	1209.0	4.83	99.5	7.41	48.19	58.75
Daly	08/19/97	3	N/A	N/A	650.37	132.0	22.1	1438.0	3.76	100.4	7.47	47.65	58.09
Myers	07/22/96	1	8	235	438.9	114.2	20.6	629.5	2.05	70.0	7.20	32.25	39.32
Myers	07/22/96	2	7	180	446.5	83.0	19.5	515.7	1.73	71.0	7.18	31.38	38.25
Myers	07/22/96	3	5	150	426.7	76.0	19.0	493.6	2.09	72.0	7.26	31.75	38.71
Ryan	06/16/96	1	20	310	490.9	51.4	12.4	401.0	1.18	59.0	7.19	23.75	28.96
Ryan	06/16/96	2	19	320	468.9	50.0	15.0	382.4	2.11	60.0	7.16	23.63	28.80
Ryan	06/16/96	3	5	280	494.4	45.8	15.2	336.4	1.24	58.0	7.14	23.13	28.19
Unnamed	08/18/97	1	12	469	577.59	130.8	17.5	1912.8	2.56	76.0	7.28	31.3	38.16
Unnamed	08/18/97	2	20	465	568.97	122.8	12.6	2120.8	2.5	75.8	7.32	31.28	38.13
Unnamed	08/18/97	3	21	425	501.71	99.2	12.0	1750.0	2.5	75.9	7.36	31.02	37.82

apparent from samples taken at approximately the same time. Based on chlorophyll *a* concentrations (Mitchell and Prepas 1990), Daly Lake is more eutrophic than Unnamed Lake. Secchi disk transparency was lower in Myers Lake than in Barrow, Bocquene, or Unnamed Lake (and probably Ryan Lake) and is similar to Daly Lake. Since secchi readings are mainly affected by the amount of algae in the water and algal growth is considered a rough index of fertility (Mitchell and Prepas 1990), the data suggest Myers and Daly lakes are more eutrophic than the other four lakes. This is expected given the depth distribution of each lake. It is interesting to note that sympatric forms of cisco were found in all of the deeper, more oligotrophic lakes (≥20 m maximum depth and >250 mm secchi transparency) and in none of the shallower, more eutrophic lakes.

Specimen Acquisition

Cisco were collected with monofilament gill nets arranged in gangs of 20 m X 2 m, 38, 63.5, and 89 mm stretched mesh panels. Three such gangs were deployed at each lake. A stratified random design was used to select sampling sites. Bathymetric maps were used to divide each lake into three approximately equal-sized zones based on depth. Grids were placed over these maps and cells within each zone numbered. Using a random number table, five "sites" were chosen in each zone for a total of 15 sites on each lake. Depth of net placement was also chosen randomly from a choice of five depth strata (surface, midway between surface and midpoint of water column, midpoint, midway between midpoint and bottom, and bottom). Nets were deployed at each site for 12 hours (during the day) and checked every four hours. Specimens to be retained were euthanized in MS222. All fish were measured (fork length) and weighed, and muscle and liver samples were excised from most. These were immediately frozen on dry ice. All specimens were fixed in 10% buffered formalin in the field and transferred to 70% ethanol after approximately 3-4 weeks.

Morphometrics and Meristics

The following counts and measurements were taken as indicated below. Twenty-three measurements represented elements of a truss network (Fig. 2) (Strauss and Bookstein 1982). Measurements were made on the left side of the body with dial calipers and recorded to the nearest 0.1mm. Gillrakers were counted under 20 X magnification after dissecting the first, left epibranchial from its dorsal attachment and pinning the out-stretched gill arch to the side of the body. The ceratobranchial was not detached but a small slit was made in the gill membrane to expose all rudimentary rakers on the anterior portion of this bone. This procedure resulted in excellent visibility of all gillrakers while eliminating the danger of loss of the taxonomically important gill arch in museum specimens. Pyloric caeca were counted after removal of surrounding adipose tissue. Each outpocket was marked with a spot of dye applied with a fine-tipped pen. This ensured that every caecum was counted and none was re-counted without resorting to destruction of this structure in museum specimens.

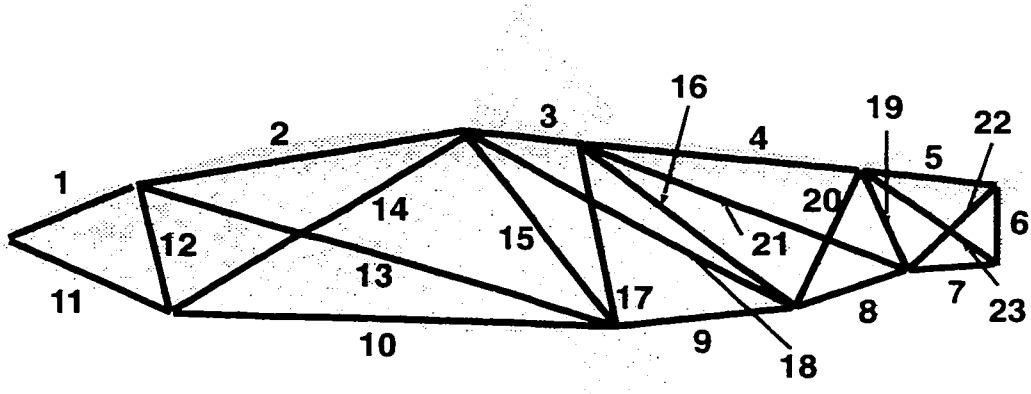

Figure 2. Elements of the truss network.

Traditional Measurements

1) Standard length: tip of premaxilla to caudal flexure

2) Head length: tip of premaxilla to posterior margin of opercle (excluding opercular membrane)

3) Snout length: tip of premaxilla to anterior fleshy margin of eye

4) Orbit: dorsal margin of infraorbital at ventral notch vertically to dorsal margin of orbit at posterior tip of supraorbital 1.

5) Upper jaw length: median suture of premaxillae to posterior tip of maxilla

6) Length of gillraker 1: anterolateral origin to tip of first gillraker entirely on first ceratobranchial (immediately anterior to raker on ceratobranchial-epibranchial joint)

7) Adipose fin base: origin of adipose fin to posterior margin of fin base

8) Adipose fin length: origin to posterior margin of adipose fin

Truss Measurements (Fig. 2)

1) Tip of premaxilla to tip of supraccipital crest exposed by dissection

2) Tip of supraccipital crest to origin of dorsal fin

3) Dorsal fin base

4) Terminus of dorsal fin base to origin of adipose fin

5) Origin of adipose fin to origin of first dorsal procurrent ray

6) Origin of first dorsal procurrent ray to origin of first ventral procurrent ray

7) Origin of first ventral procurrent ray to posterior terminus of anal fin base

8) Anal fin base

9) Origin of anal fin to posterior terminus of pelvic fin base

10) Posterior terminus of pelvic fin base to anteroventral tip of cleithrum exposed by dissection

11) Anteroventral tip of cleithrum to tip of premaxilla

12) Tip of supraccipital crest to anteroventral tip of cleithrum

13) Posterior terminus of pelvic fin base to tip of supraoccipital crest

14) Origin of dorsal fin to anteroventral tip of cleithrum

15) Posterior terminus of pelvic fin base to origin of dorsal fin

16) Origin of anal fin to posterior terminus of dorsal fin base

17) Posterior terminus of pelvic fin base to posterior terminus of dorsal fin base

18) Dorsal fin origin to anal fin origin

19) Posterior terminus of anal fin base to origin of adipose fin

20) Origin of anal fin to origin of adipose fin

21) Posterior terminus of dorsal fin base to posterior terminus of anal fin base

22) Posterior terminus of anal fin base to base of first dorsal procurrent ray

23) Origin of adipose fin to base of first ventral procurrent ray

Counts

1) Upper gillrakers: number of gillrakers, including all rudiments, on first, left epibranchial and including the raker on the ceratobranchial-epibranchial joint

2) Lower gillrakers: number of gillrakers, including all rudiments, on first, left ceratobranchial

3) Total gillrakers: sum of upper and lower gillrakers

4) Lateral line scales: all pored lateral line scales. (Scale pockets were counted if scales were lost. For all specimens used in this analysis, the last pored scale was intact.)

5) Total dorsal fin rays: all rays in the dorsal fin including rudimentary rays.

6) Principal dorsal fin rays: branched or unbranched rays extending at least 3/4 of the way to the dorsal margin of the fin.

7) Pectoral fin rays: all rays in pectoral fin

8) Principal pelvic fin rays: branched or unbranched rays extending at least 3/4 of the way to the dorsal margin of the fin.

9) Anal fin rays: all anal fin rays

10) Pyloric caeca: all outpockets visible after dissection and removal of surrounding adipose tissue.

Character Independence and Redundancy

Independent evolution of characters is an important assumption in taxonomic analysis. However, functional interdependence is rarely tested empirically by examination of the relationship between specific character states in a wide range of taxa. It is difficult to prove whether characters in a well-integrated phenotype are functionally correlated and therefore redundant or whether they are phyletically correlated (based on the same ancestral gene complex) and representative of taxonomically valuable character complexes. Mayr and Ashlock (1991) note that some phyletically correlated characters may have originated as functionally correlated complexes that have subsequently broken down because of a change in function of some of the components. If the original genetic integration is maintained, however, these character complexes can be of great taxonomic significance. However, only after a careful functional analysis is it possible to consider with confidence the functional relationships among characters.

Experimental proof of obligatory dependencies or covariation among characters, and the genetic basis for these, was beyond the scope of this study. Only in a few cases were inferences made regarding functional correlations. Upper and lower gillraker counts were presumed to be functionally dependent and were found to be highly correlated with total gillraker number (correlation between upper and total count r^2=.854, P=1.2 x 10^{-201}; correlation between lower and total count r^2=.936, P=2.7 x 10^{-287}; n=480). Only total gillraker number was used in subsequent analyses. Scale counts were limited to the number of pored scales in the lateral line on the assumption that scale number is largely a function of scale size and scale size is a general feature typically affecting all parts of

the body. Therefore, similarly sized fishes with small scales might be expected to have higher scale counts (predorsal, above lateral line, below lateral line, etc.) than individuals with large scales. Considering each count separately would distort estimates of similarity (Mayr and Ashlock 1991). Since only a single scale count was taken, the assumption of correlation among scale counts was not tested statistically.

Redundancy in the Truss Network

The objective of truss analysis (Strauss and Bookstein 1982) is to archive the position of landmark points on an organism, or part thereof, to permit later reconstruction of the form. This is achieved by mapping the set of distances among landmarks. Some advantages of this procedure in comparative morphological analyses include a thorough and even coverage of the entire body form and the use of homologous, precisely definable anatomical landmarks as opposed to "extremal" measures defined by some minimum or maximum distances (Jardine 1969). The redundancy inherent in truss analysis is used to assess measurement error, to mathematically "flatten the truss" to improve the accuracy of body form reconstruction (Strauss and Bookstein 1982), and to facilitate a multivariate definition of shape (Humphries et al. 1981). When considered individually, however, truss measurements based on the same internal landmark are correlated and cannot be considered independent. As one landmark is displaced, as many as five measurements (for internal nodes) may change significantly. This redundancy will lead to inflated estimates of the number of divergent or unique characters among taxa and may bias multivariate analyses.

The intent in this study was to achieve the two advantages of truss measurements outlined above (even coverage of form and use of homologous landmarks), not to perform the full mathematical body form reconstruction (Strauss and Bookstein 1982). Therefore, to avoid redundancy in the analysis of multiple characters, it was necessary

to carefully select measurements from any set of informative measurements derived from any one landmark. When multiple, significantly different characters were based on the displacement of the same landmark point (i.e., only one character actually changed), the measurement that exhibited the greatest difference among the taxa being considered (the lowest value of *P*) was chosen as the most informative. Redundant characters were, therefore, removed from subsequent multivariate analyses.

Statistical Analyses

As samples were added to the analysis and statistics (t-tests) recomputed, it was found that some characters alternated between significance and non-significance at the 5% level. Characters with means that are well separated in relation to their variances (i.e., highly significantly different in t-tests or ANOVAS) are generally considered the best for taxonomic purposes (Sneath and Sokal 1973). In the interest of selection of clearly discriminating traits for further analysis, the significance level for determination of informative characters was set at $P<.01$.

The variability of each morphometric character was assessed by simple linear regression of each untransformed variable on standard length. The correlation coefficient (r) of each bivariate plot was used as an index of data dispersion for each dependent variable. While high within group variance is undesirable in a quantitative character, its usefulness as a discriminating trait depends, in part, on the magnitude of the mean difference between populations. Both univariate and multivariate statistical procedures consider the within and between group variances as well as mean differences when calculating probabilites of significance. Thus, highly variable characters will often show insignificant differences in univariate tests and be low contributors in multivariate analyses. However, they should not be dismissed before the appropriate tests have been performed.

Plots of all raw variables on standard length were examined for evidence of non-linearity.

A linear relationship between character size and overall body size is assumed in data transformation techniques based on linear regression (Reist 1985, 1986). An ontogenetic shift in growth rate of a body part relative to overall size (or other body parts) may result in a curvilinear relationship between traits. Such a relationship could confound interpretations of size and shape differences among populations and bias regression transformation results. Empirical data have shown that most morphometric traits in fishes are linearly related to overall size (J. Reist pers. comm.) but data plots should be examined for significant deviations from linearity.

Estimation of allometry

Allometry is defined as unequal growth rates between body parts or between these parts and the body as a whole (Gould 1966, Mayr and Ashlock 1991). The slope of the linear regression of the $\log_{10}$ of standard length on the $\log_{10}$ of each dependent variable can be used to estimate the degree of allometry in individual characters (Gould 1966). Variation in allometric relationships can be a useful indicator of taxonomic differences. However, allometry can also confound the elucidation of evolutionarily significant morphological differences between populations when samples include a range of sizes and ontogenetic stages. Care must be taken to distinguish differences in relative proportions (shape) of characters due to growth from differences representing evolutionary change.

Weiner and Thomas (1992) have demonstrated that allometries measured from statistical summaries of differently sized specimens (allomorphosis) are not necessarily reflections of the growth trajectories of individuals. However, while it is acknowledged that allometric growth is best assessed by repeated measurements from individuals throughout ontogeny, this is not practical or possible in many taxonomic studies – especially those based on museum specimens. An analysis of individuals of various sizes and growth stages often must serve as an estimator of the average amount of allometry displayed by each character in that sample.

The equation of simple allometry is $y=bx^a$ (Gould 1966) where y is a variable whose proportions are dependent on a size estimator x, b is the intercept of the regression of y on x, and a is the slope of this regression (or the ratio of the growth rate of y and x). Log transformation of the equation results in linearity of this relationship. When growth rates of two body parts are exactly the same, the slope of the logx/logy regression = 1. While no hard and fast rules exist, slopes of characters that deviate by 0.1 (10%) or less from 1 can be considered essentially isometric (J. Reist pers. comm.).

Sexual Dimorphism

T-tests of the difference between means of size-transformed character values were computed for subsamples of males and females when sufficient numbers (n>10) of each were available. A general lack of sexual dimorphism has been found in most other studies on coregonine life history and taxonomy (Lindsey 1963, Schweitzer 1968, Clarke 1973, but see Hile 1937).

Removal of the effect of body size

Systematic studies employing morphometric data should consider the maximum available information including both the variation in the absolute size and in the shape (relative size) of body parts in the organisms under investigation. When analyzing relative body proportions in organisms with indeterminate growth, such as fishes, it is necessary to remove the magnitude effect of size to facilitate comparisons of individuals of different body lengths. Measuring only specimens of the same length would circumvent this problem but this is rarely feasible in taxonomic studies where examination of a wide range of populations, ontogenetic stages, and sexes is essential or where sample sizes are limited.

The use of ratios (e.g., body part/standard length) has been widely employed as a means of creating size-free shape variates but these are fraught with statistical problems. Ratios

are not only ineffective in removal of size effects (Atchley et al. 1976 , Albrecht 1978, Dodson 1978) but their use in subsequent data analysis may degrade the power of statistical tests, increasing the probability of Type II errors and masking differences between samples (Atchley 1978 and references therein, Pimental 1979). Therefore, they are not recommended in taxonomic studies for other than cursory data examination.

Logarithmic transformations have also been widely used but these simply alter the limits of size variation and do not remove it. They are especially inappropriate when size differences are great and may result in nonlinearity of data (Reist 1985). Logs of ratios (log X/Y) have been suggested as appropriate by some authors (Middleton 1962, Blackith and Reyment 1971, Schuessler 1974, Hills 1978) but their use is still considered inferior to regression analysis for maximizing the removal of size effects (Atchley 1978).

Regression-related techniques derive a shape measure from the relationship between body parts. This technique has been suggested by Gould (1966), Atchley et al. (1976), Atchley (1978), and Reist (1985). The algorithm followed in this study is that recommended by Reist (1985, 1986). He provides an excellent empirical evaluation of many size adjustment techniques currently in use by systematists and concludes that the regression residual transformation protocol is superior to most other techniques. For each character, a regression line was calculated from an Analysis of Covariance (SPSS ver. 8.0) with standard length as the independent variable and population as the fixed factor. This generated a regression slope common to all populations (common-within groups slope) and hence a common standard from which to compare the relative body sizes of all populations combined. Residuals from the common-within groups regression line were adjusted by subtracting the difference of the estimated marginal mean of the dependant variable for each population (as calculated by the ANCOVA) and the grand mean of each dependant variable across all populations. The resulting adjusted residuals

were used as character values for all subsequent analyses.

The efficacy of size removal using this algorithm was tested by regressing the adjusted shape variates on standard length. An insignificant correlation indicates independence of size and shape (i.e., effective removal of the effect of size). The results of this evaluation, using the Barrow Lake high gillraker cisco as the test population, are shown in Table 4. Correlation coefficients (r values) were all very low but were significant for five measurements. Despite a small residual size component in a few characters, this procedure was still considered the most appropriate given its overall effectiveness, desirable statistical properties, and relative simplicity.

The intra-population frequency distributions of transformed variates were examined for evidence of non-normality. 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. The Kolmogorov-Smirnov D statistic was used to evaluate deviations of the sample data from a normal distribution.

Multivariate Analysis

Principal Components Analysis (PCA) and Discriminant Function Analysis (DF) were used at various stages of this study to examine and visualize morphometric differences among populations based on combinations of characters. Principal Components Analysis requires no prior knowledge of grouping structure, and few assumptions with respect to data distribution and variance homogeneity among populations. The procedure examines the major underlying sources and directions of variation in a single sample and allows

Table 4. Efficacy of size removal using regression residual transformation. The test sample was the Barrow Lake high gillraker (*C. artedi*) population (n=74). Significant correlations ($P<.05$) between transformed character values and standard length, shown in bold, suggest less effective removal of the magnitude effect of size.

Character	r
Gillraker length	.134
Orbit diameter	.176
Upper jaw	.122
Head	.187
Snout	.055
Truss 1	.114
Truss 2	.272
Truss 3	**.263**
Truss 4	.063
Truss 5	.100
Truss 6	**.257**
Truss 7	.077
Truss 8	.207
Truss 9	.114
Truss 10	.045
Truss 11	.026
Truss 12	.045
Truss 13	.266
Truss 14	.089
Truss 15	.283
Truss 16	.055
Truss 17	.302
Truss 18	**.327**
Truss 19	**.424**
Truss 20	**.385**
Truss 21	.138
Truss 22	.032
Truss 23	.089

for the discovery of groups (Humphries et al. 1981). Discriminant Function Analysis is designed to separate populations and to permit allocation of unknowns to one or another of these populations. A discriminant function is a linear combination of objectively weighted characters that maximizes the separation among pre-determined groups relative to the variation within each group (Reyment et al. 1984). *A priori* grouping criteria must be considered carefully prior to application of this algorithm.

The main objective of this study was to determine if the two previously reported sympatric ciscoes in Barrow Lake were distinct. Analyses were intended to support or refute the null hypothesis of a single population. Theoretically, no prior assumptions could be made regarding groups since the search for data structure (e.g., multivariate bimodality) was the purpose of this phase of the investigation. Gillraker number, the character used by Paterson (1969) to separate the two forms in Barrow Lake, might be considered a valid, biologically meaningful grouping criterion. However, gillraker number was not used in multivariate analyses to permit testing of the efficacy of discrimination by other independent characters. Therefore, Principal Components Analysis was chosen as the appropriate multivariate technique for this portion of the study.

Both principal components and discriminant functions were used initially as tools in the determination of the specific identity of the Barrow Lake low gillraker cisco. The interpretation of ordination patterns of principal component and discriminant function scores were similar for both techniques. Analysis of variance (ANOVA) revealed significant variance heterogeneity (Levene's statistic) among populations for some characters. Because Discriminant Function Analysis assumes homogeneity of within group dispersion matrices (Reyment et al. 1984), and since both PCA and DF produced similar results, it was decided to present the results in terms of the less statistically restrictive Principal Components Analysis.

Ageing of Specimens

Specimens were aged by examination of otoliths. To improve resolution of annuli, otoliths were polished and immersed for 10 seconds in a 20% hydrochloric acid bath (Mackay et al. 1990, Stevensen and Campana 1992). Annuli were counted under magnification using reflected light. Ages were not validated so absolute values are subject to measurement error. Accuracy was considered sufficient for determination of relative length at age for the purpose of *a priori* estimation of population boundaries. All age groups were combined in the analyses. The youngest specimens used were in their second summer (I+) and all exceeded 125 mm SL.

Stomach Content Analysis

Stomach contents from 46 Barrow Lake ciscoes (19 low gillraker and 27 high gillraker specimens), 40 Ryan Lake ciscoes (12 low gillraker and 28 high gillraker specimens), and 14 Barrow Lake *C. clupeaformis* (lake whitefish) were examined. The esophagus and stomach were removed from preserved specimens, slit lengthwise, and the contents flushed into a petri dish with 70% ethanol. The dish was marked with a grid of 1cm x 1 cm squares. Food particles were mixed thoroughly and allowed to settle. The contents were examined under magnification to locate and identify all prey types. Except in the case of *Mysis relicta*, no attempt was made to identify prey to species. Order- or Family-level identifications were considered sufficient to discriminate between planktonic (Copepoda, Cladocera) and benthic (Chironomidae, Pelecypoda) organisms. When more than one species was present, the proportion of each prey type was estimated from the relative surface area of the dish occupied by each. Settled volume estimates were also attempted but, because of greatly disparate prey sizes in most mixed assemblages, were felt to grossly underestimate the significance of the planktonic component.

Environmental Data

Water samples were collected with a drop-sleeve water bottle, stored on ice for a maximum of 48 hours in acid washed nalgene bottles and analyzed by staff of the limnology section, Department of Biological Sciences, University of Alberta. Samples for chlorophyll *a* determination were filtered in the field and stored on dry ice until analyzed. Dissolved oxygen concentrations were determined in the field with a Hach kit.

Genetic Analysis

Mitochondrial DNA sequencing followed procedures outlined in Bodaly et al. (1998) and Reist et al. (1998). Analyses were conducted by staff of the Freshwater Institute, Department of Fisheries and Oceans Canada, Winnipeg, Manitoba.

Results

Comparison of Barrow Lake Ciscoes

Three hundred and fifty one ciscoes were collected in Barrow Lake during July 22-27, 1996, July 4-9, 1997 and October 1-3, 1997. Nineteen of these specimens were determined to represent the low gillraker form (putative *Coregonus zenithicus*). These 19 specimens and a random sample of 74 high gillraker specimens (*C. artedi*) were used in most morphological analyses. Gillrakers were counted on 195 individuals.

Informative Morphological Characters

Discrimination of sympatric forms was estimated *a priori* by a combination of gillraker number and body size. The low gillraker (lgr) form had a modal gillraker count of 40 (38-43) and a mean standard length of 228 mm. The high gillraker (hgr) form had a modal gillraker count of 49 (42-52) and a mean standard length of 187 mm. In the field, the low gillraker form was also reliably distinguishable from the high gillraker form by a smaller eye, longer maxilla, and shallower head (Plates 1 and 2). The gillraker number frequency distribution was bimodal although the modes were not discontinuous (Fig. 3). The exact gillraker number demarcation point between groups was determined by visual examination of the relationship between gillraker number and upper jaw and gillraker lengths. Scatter plots (Fig. 4A & B) demonstrated a distinct shift in the relative sizes of these characters between specimens with 43 and 44 gillrakers. Therefore, 43 or fewer gillrakers was used initially to delimit the low gillraker group, and 44 or more gillrakers to delimit the high gillraker group. Subsequent multivariate analyes revealed one *C. artedi* specimen with 43 gillrakers – the rest had 44 or more. All *C. zenithicus* specimens had 43 or fewer gillrakers.

The data from 28 morphometric characters were examined for variability and linearity

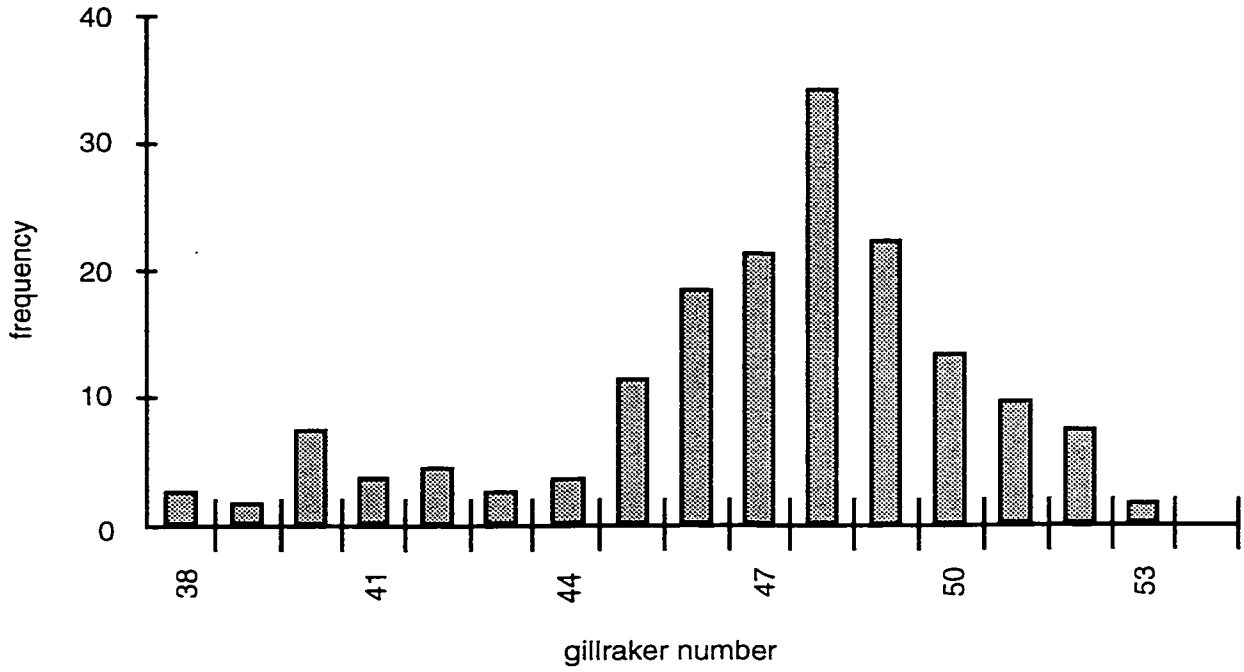

Figure 3. Gillraker number frequency distribution for Barrow Lake ciscoes.

of raw measurements and normality of regression transformed values (Table 5). All measurements were significantly correlated with standard length ($P<.01$) and visual examination of the bivariate plots revealed no evidence of non-linearity. Gillraker length, truss 7, truss 8, and truss 22 displayed the greatest data dispersion about the mean. Truss measurements 7 and 22 both use the origin of the procurrent caudal fin rays as landmarks (see Fig. 2). These points appear to be either inherently variable or subject to excessive measurement error. Determination of the precise location where the first procurrent ray becomes fully exposed can be influenced by the presence or absence (due to capture, handling, etc.) of a scale that partially covers the base of this structure. This undoubtedly contributed to the error variance in these characters. Univariate statistics (t-tests) detemined if variance was sufficient to mask inter-population differences thus rendering characters uninformative.

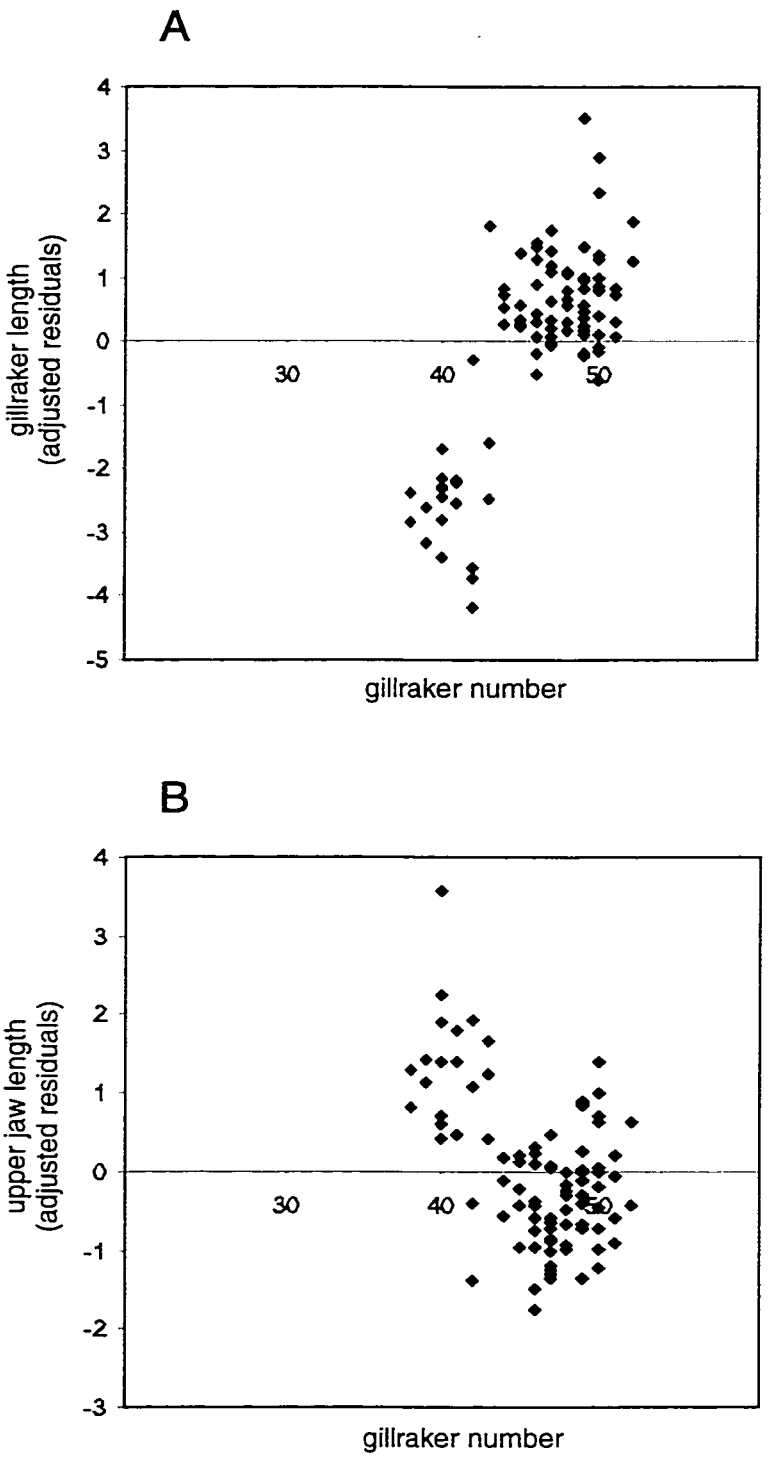

Figure 4. Plots of gillraker number versus gillraker length (A) and upper jaw length (B) for Barrow Lake ciscoes. A discontinuity in these characters between most 43 and 44 gillraker specimens was useful in discriminating between forms.

Table 5. Parameters of Barrow Lake low gillraker (lgr) and high gillraker (hgr) cisco morphometric data. The correlation coefficient (r) of the untransformed variables on standard length provides an indication of data variation. All correlations were significant ($P<.01$). Visual examination of data plots revealed no suggestion of non-linearity. Values in bold highlight those characters that are particularly allometric. Kolmogorov-Smirnov D values indicate normality of regression transformed variables ($P>.05$).

Character	Lgr form			Hgr form			Allometric Relationship
	r	Slope of log/log Regression	D	r	Slope of log/log Regression	D	
gillraker 1	.957	**1.250**	.159	.827	1.070	.090	**+ allometry in lgr form**
upper jaw	.988	0.970	.126	.953	1.003	.057	
orbit	.981	**0.751**	.171	.889	**0.813**	.119	**- allometry**
head	.990	0.916	.151	.971	0.992	.046	
snout	.964	1.004	.129	.852	**1.309**	.083	**+ allometry in hgr form**
Truss 1	.989	0.947	.115	.958	0.94	.086	
Truss 2	.985	1.06	.181	.965	1.11	.109	
Truss 3	.973	1.115	.133	.880	0.95	.103	
Truss 4	.992	1.04	.096	.917	1.07	.139	
Truss 5	.969	0.892	.123	.878	1.08	.075	
Truss 6	.987	1.12	.124	.930	0.951	.142	
Truss 7	.935	0.934	.100	.730	0.984	.193	
Truss 8	.970	0.95	.123	.788	**0.74**	.091	**- allometry in hgr form**
Truss 9	.993	**1.189**	.143	.906	1.08	.051	**+ allometry in lgr form**
Truss 10	.996	1.05	.154	.957	1.000	.078	
Truss 11	.985	0.873	.154	.931	0.995	.096	
Truss 12	.990	1.046	.119	.934	1.067	.092	
Truss 13	.996	1.04	.097	.977	1.06	.161	
Truss 14	.995	1.11	.158	.977	1.04	.053	
Truss 15	.987	1.15	.138	.957	1.01	.125	
Truss 16	.997	1.17	.102	.961	1.15	.075	
Truss 17	.989	1.15	.174	.921	0.975	.090	
Truss 18	.997	1.16	.130	.983	1.07	.074	
Truss 19	.991	1.17	.153	.942	0.979	.164	
Truss 20	.986	1.12	.131	.932	0.969	.097	
Truss 21	.998	1.05	.188	.972	0.98	.054	
Truss 22	.986	1.04	.228	.840	0.990	.171	
Truss 23	.992	1.04	.211	.896	1.03	.115	

Results of univariate comparisons of the 38 morphometric and meristic characters examined are shown in Table 6. The means of 13 morphometric and six meristic characters differed between forms (t-tests, $P<.01$). The low gillraker form can be characterized by shorter gillrakers, longer upper jaw, smaller eye, longer snout to occiput (truss 1), shallower head (truss 12), shorter distance from head to dorsal fin (truss 2), longer dorsal fin base (truss 3), and an adipose fin relatively farther forward (truss 5 and 23) than the sympatric *C. artedi*.

Allometry

Slopes of the log/log regression of each morphometric character on standard length (Table 5) were used to assess if allometry was likely to confound the interpretation of inter-population differences for informative characters. Orbit diameter was negatively allometric in both populations (i.e., larger fish have proportionally smaller eyes). This relationship has been established in a wide range of fish species and in vertebrates generally (Hubbs 1926, Koelz 1929, Gould 1966). Since it was found that the larger form of cisco in Barrow Lake (the low gillraker form) had smaller eyes (Table 6), a relationship consistent with the predicted allometric relationship, the taxonomic validity of this character was suspect. It could be interpreted as representing the outcome expected if the smaller form grew to the size of the larger form. The length of the first gillraker on the ceratobranchial was found to be positively allometric in the low gillraker form. However, in this case, the observed relationship between forms - the larger low gillraker form having proportionally shorter gillrakers than the smaller high gillraker form - is the opposite of what would be predicted from the allometric relationship. Thus, this character appears to show a distinctive difference between forms and remains highly significant despite the diluting effect of allometry. Consistent positive allometry in truss measurements 14 through 20 in the low gillraker form suggests these individuals may become relatively deeper-bodied as they grow.

Table 6. Inter-population comparison of Barrow Lake low gillraker (lgr) and high gillraker (hgr) cisco morphometrics and meristics. Characters in bold are significantly different between forms ($P<.01$).

Character	Relationship	*P*	
standard length	**lgr > hgr**	**<.0001**	**means 228 (lgr) & 197 (hgr) mm**
gillraker 1	**lgr < hgr**	**<.0001**	
upper jaw	**lgr > hgr**	**<.0001**	
orbit	**lgr < hgr**	**<.0001**	
head	lgr = hgr	>.05	
snout	lgr = hgr	>.01	
Truss 1	**lgr > hgr**	**<.01**	
Truss 2	**lgr < hgr**	**<.01**	
Truss 3	**lgr > hgr**	**<.0001**	
Truss 4	**lgr < hgr**	**<.0001**	
Truss 5	**lgr > hgr**	**<.001**	
Truss 6	lgr = hgr	>.05	
Truss 7	lgr = hgr	>.05	
Truss 8	lgr = hgr	>.05	
Truss 9	lgr = hgr	>.05	
Truss 10	lgr = hgr	>.05	
Truss 11	**lgr < hgr**	**<.0001**	
Truss 12	**lgr < hgr**	**<.0001**	
Truss 13	lgr = hgr	>.05	
Truss 14	**lgr < hgr**	**<.01**	
Truss 15	lgr = hgr	>.05	
Truss 16	lgr = hgr	>.05	
Truss 17	lgr = hgr	>.05	
Truss 18	lgr = hgr	>.01	
Truss 19	lgr = hgr	>.05	
Truss 20	lgr = hgr	>.05	
Truss 21	lgr = hgr	>.05	
Truss 22	lgr = hgr	>.05	
Truss 23	**lgr > hgr**	**<.0001**	
upper gillrakers	**lgr < hgr**	**<.0001**	**modes 15 (lgr) and 18 (hgr)**
lower gillrakers	**lgr < hgr**	**<.0001**	**modes 25 (lgr) and 30 (hgr)**
total gillrakers	**lgr < hgr**	**<.0001**	**modes 40 (lgr) and 49 (hgr)**
dorsal fin rays	**lgr > hgr**	**<.0001**	**modes 15 (lgr) and 14 (hgr)**
pelvic fin rays	lgr = hgr	>.05	modes 11 (lgr) and 11 (hgr)
anal fin rays	lgr = hgr	>.05	modes 15 (lgr) and 15 (hgr)
pectoral fin rays	**lgr > hgr**	**<.01**	**modes 16 (lgr) and 16 (hgr)**
lateral line scales	**lgr > hgr**	**<.0001**	**modes 74 (lgr) and 68 (hgr)**

Most of the other characters that exhibited some degree of allometry were only slightly over the 0.1 threshold level. Measurements that were positively allometric in one form and negatively allometric in the other may reflect some biological inter-population differences but may also be an artifact of a small sample size. In particular, values for the low gillraker form were based on a sample of only 19 individuals.

Sexual Dimorphism

All characters were examined for evidence of sexual dimorphism (Table 7). Females were larger than males in the smaller, high gillraker form ($P<.005$) but no differences were apparent in the low gillraker form. Of the 34 traits examined (excluding standard length), only one was significantly different between sexes. Truss 11 (the distance from the tip of the premaxilla to the antero-ventral tip of the cleithrum) was slightly larger in females than males ($P<.05$) of both populations. Overall, sexual dimorphism does not appear to be a confounding factor so the sexes were pooled in all analyses.

Multivariate Analysis

A Principal Components Analysis of 13 morphometric traits (Table 8) demonstrated complete separation of Barrow Lake forms on axis 1 (Fig. 5). No morphological intermediates (possible hybrids) were apparent in the sample suggesting little successful interbreeding between forms. Variability on component 1 largely reflected the contrast of gillraker length against upper jaw length and dorsal fin base length (truss 3) (Table 8).

Mitochondrial DNA Analysis.

Nucleotide sequence variability in an approximately 321 base pair (bp) segment of the mitochondrial DNA control region (d-loop) revealed no significant differences between the sympatric ciscoes in Barrow Lake (Table 9). Two variants were found, differing at

Table 7. Summary of sexual dimorphism in Barrow Lake ciscoes. Characters in bold are significantly different (s. d.) between sexes ($P<.05$).

Character	High Gillraker Form		Low Gillraker Form	
	P	Relationship	*P*	Relationship
Standard length	**<.005**	**females bigger**	>.05	no s.d.
Gillraker 1	>.05	no s.d.	>.05	no. s.d.
Upper jaw	>.05	no s.d.	>.05	no s.d.
Orbit	>.05	no s.d.	>.05	no s.d.
Head	>.05	no s.d.	>.05	no s.d.
Snout	>.05	no s.d.	>.05	no s.d.
Truss 1	>.05	no s.d.	>.05	no s.d.
Truss 2	>.05	no s.d.	>.05	no s.d.
Truss 3	>.05	no s.d.	>.05	no s.d.
Truss 4	>.05	no s.d.	>.05	no s.d.
Truss 5	>.05	no s.d.	>.05	no s.d.
Truss 6	>.05	no s.d.	>.05	no s.d.
Truss 7	>.05	no s.d.	>.05	no s.d.
Truss 8	>.05	no s.d.	>.05	no s.d.
Truss 9	>.05	no s.d.	>.05	no s.d.
Truss 10	>.05	no s.d.	>.05	no s.d.
Truss 11	**<.05**	**females bigger**	**<.05**	**females bigger**
Truss 12	>.05	no s.d.	>.05	no s.d.
Truss 13	>.05	no s.d.	>.05	no s.d.
Truss 14	>.05	no s.d.	>.05	no s.d.
Truss 15	>.05	no s.d.	>.05	no s.d.
Truss 16	>.05	no s.d.	>.05	no s.d.
Truss 17	>.05	no s.d.	>.05	no s.d.
Truss 18	>.05	no s.d.	>.05	no s.d.
Truss 19	>.05	no s.d.	>.05	no s.d.
Truss 20	>.05	no s.d.	>.05	no s.d.
Truss 21	>.05	no s.d.	>.05	no s.d.
Truss 22	>.05	no s.d.	>.05	no s.d.
Truss 23	>.05	no s.d.	>.05	no s.d.
total gillrakers	>.05	no s.d.	>.05	no s.d.
total dorsal fin rays	>.05	no s.d.	>.05	no s.d.
pelvic fin rays	>.05	no s.d.	>.05	no s.d.
anal fin rays	>.05	no s.d.	>.05	no s.d.
pectoral fin rays	>.05	no s.d.	>.05	no s.d.
lateral line scales	>.05	no s.d.	>.05	no s.d.

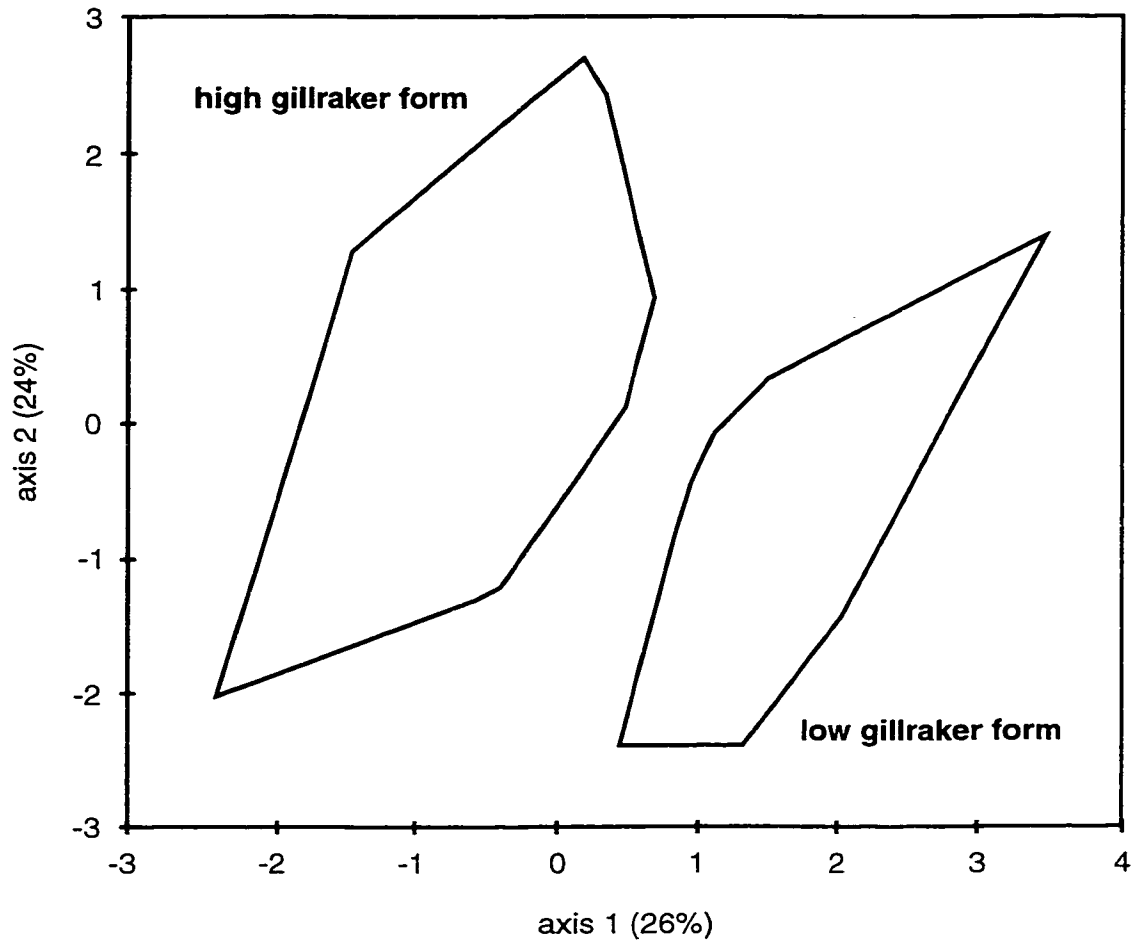

Figure 5. Principal component scores for Barrow Lake ciscoes based on 13 morphometric characters

only one nucleotide position (301), but these were not congruent with the morphological variation. Minimal and inconsistent differences were also found between the Barrow Lake samples, six *C. artedi* haplotypes reported by Bodaly et al. (1998), and a single haplotype found in 12 specimens of *C. artedi* reported by Reist et al. (1998). *C. artedi* and *C. zenithicus* sequences deposited in GenBank by Reed et al. (1998) also showed no consistent interspecific differences within this segment. These data may reflect close taxonomic affinity between these species or they may simply mean that the d-loop region is of limited value in discriminating among cisco taxa.

Table 8. Eigenvalues and eigenvectors of the first two principal components based on 13 morphometric characters from Barrow Lake ciscoes.

Eigenvalue	1	2
% of variability.	26	24
Cumulated %	26	50
Vectors :	1	2
truss 1	0.631	0.554
truss 3	0.763	-0.113
truss 5	0.389	-0.360
truss 6	0.520	0.275
truss 8	0.186	0.073
truss 9	-0.385	-0.353
truss 11	-0.185	0.760
truss 12	-0.250	0.847
truss 14	-0.306	0.559
upper jaw	0.840	0.152
gillraker 1	-0.702	0.540
head	0.310	0.727
snout	0.506	0.264

Ecology

Age Structure

Length-at-age plots (Fig. 6) suggested the Barrow Lake low gillraker cisco grows more rapidly than the high gillraker form especially in the first three or four years of life. It was also clear that the small high gillraker form did not represent a young stage of the larger low gillraker form. Paterson (1969) conceded that this was a possibility in his sample that included smaller (high gillraker) specimens ranging from 2–4 years of age and larger (low gillraker) individuals ranging from 5–11 years of age. Based on the data in the present study, this suggestion can be dismissed.

Diet

Results of stomach content analyses of Barrow Lake ciscoes are summarized in Figure 7. *Mysis relicta* comprised 96% of the diet of the low gillraker form. Eleven of the 15 individuals with non-empty stomachs (73%) had fed exclusively on *Mysis relicta* and

Table 9. Variable positions in a 321 bp segment of the mitochondrial DNA d-loop from *C. artedi* and *C. zenithicus* specimens examined in this study and by Bodaly et al. (1998), Reist et al. (1998), and Reed et al. (1998). The reference form is the Bering race of *C. clupeaformis*. Two Barrow Lake varieties, differing at position 301, are not congruent with the morphological variation (high gillraker versus low gillraker forms).

Variable nucleotide position			1	57	80	81	106	123	162	163	206	220	241	261	279	301
Sample	No.	Var.														
Reference			T	A	A	C	C	T	G	G	A	T	A	G	C	T
Barrow Lake																
HGR	42420	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
LGR	42430	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
LGR	42432	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
LGR	42433	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
LGR	42434	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
HGR	42423	1	-	-	-	-	-	-	-	T	-	-	-	A	-	-
HGR	42421	2	-	-	-	-	-	-	-	T	-	-	-	A	-	C
LGR	42431	2	-	-	-	-	-	-	-	T	-	-	-	A	-	C
LGR	42435	2	-	-	-	-	-	-	-	T	-	-	-	A	-	C
Bodaly et al. (1998)																
C. artedi	Cr13		-	-	-	-	-	-	-	-	-	-	-	A	-	-
C. artedi	Cr 24		A	-	-	-	-	-	-	-	-	-	-	A	-	-
C. artedi	Cr 15		-	-	-	-	-	-	-	-	-	-	-	A	-	C
C. artedi	Cr 19		A	-	-	-	-	-	-	T	-	-	-	A	-	-
C. artedi	Cr 16		A	-	-	-	-	-	-	T	-	-	-	A	-	C
C. artedi	Cr 20		A	-	-	-	-	-	-	-	-	-	-	A	-	C
Reist et al. (1998)																
C. artedi (n=12)			A	-	-	-	-	-	-	-	-	-	-	A	-	C
Reed et al. (1998)																
C. artedi	282-5		-	-	-	T	-	-	-	-	-	-	-	-	-	-
C. artedi	410-1		-	-	-	-	-	-	-	T	-	-	-	A	-	-
C. artedi	004-1		-	-	-	-	-	-	A	-	-	-	-	A	-	-
C. artedi	256-4		-	-	-	T	-	-	-	T	-	-	-	A	-	-
C. artedi	412-2		-	-	-	-	-	-	-	T	-	-	-	A	-	-
C. artedi	016-1		-	-	G	-	T	-	-	T	-	-	-	A	-	-
C. zenithicus	420-2		-	-	-	-	-	-	-	-	-	-	-	A	-	-
C. zenithicus	421-A		-	-	-	-	-	-	-	-	-	-	-	A	G	-
C. zenithicus	106-2		-	-	-	-	-	-	-	T	G	-	-	A	-	-
C. zenithicus	122-2		-	-	-	-	-	-	-	T	-	C	-	A	-	-
C. zenithicus	271-1		-	G	-	-	-	C	-	-	-	-	-	A	-	-
C. zenithicus	273-2		-	-	-	-	-	-	-	T	-	-	G	A	-	-

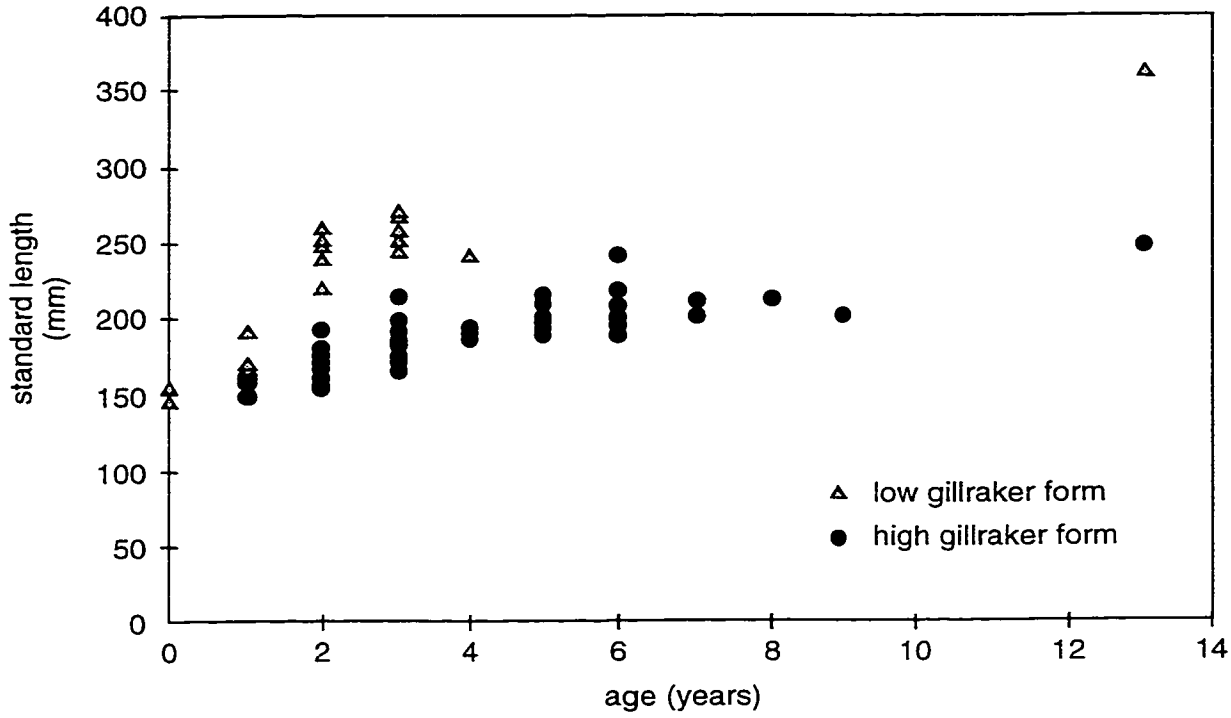

Figure 6. Age-length relationship for Barrow Lake ciscoes.

this prey item predominated in four of the other fish examined. One immature specimen had consumed approximately 40% cladocerans. Other items recovered included two chironomid pupae, one amphipod, and one pelecypod, all from different individuals. In the high gillraker form, 75% of the diet was comprised of *Mysis relicta*; the other 25% included almost equal proportions of cladocerans and copepods. Fifteen of the 21 individuals from which food items were recovered (71%) had fed exclusively on *Mysis relicta*.

For comparison, stomach contents from a sample of Barrow Lake *C. clupeaformis* were analysed to investigate if there were any similarities between the diet of a known benthivore and either of the two forms of cisco. A summary of the stomach contents from 14 *C. clupeaformis* specimens, collected over the same time period as the ciscoes examined, is shown in Figure 8. The majority of the diet was composed of chironomid pupae

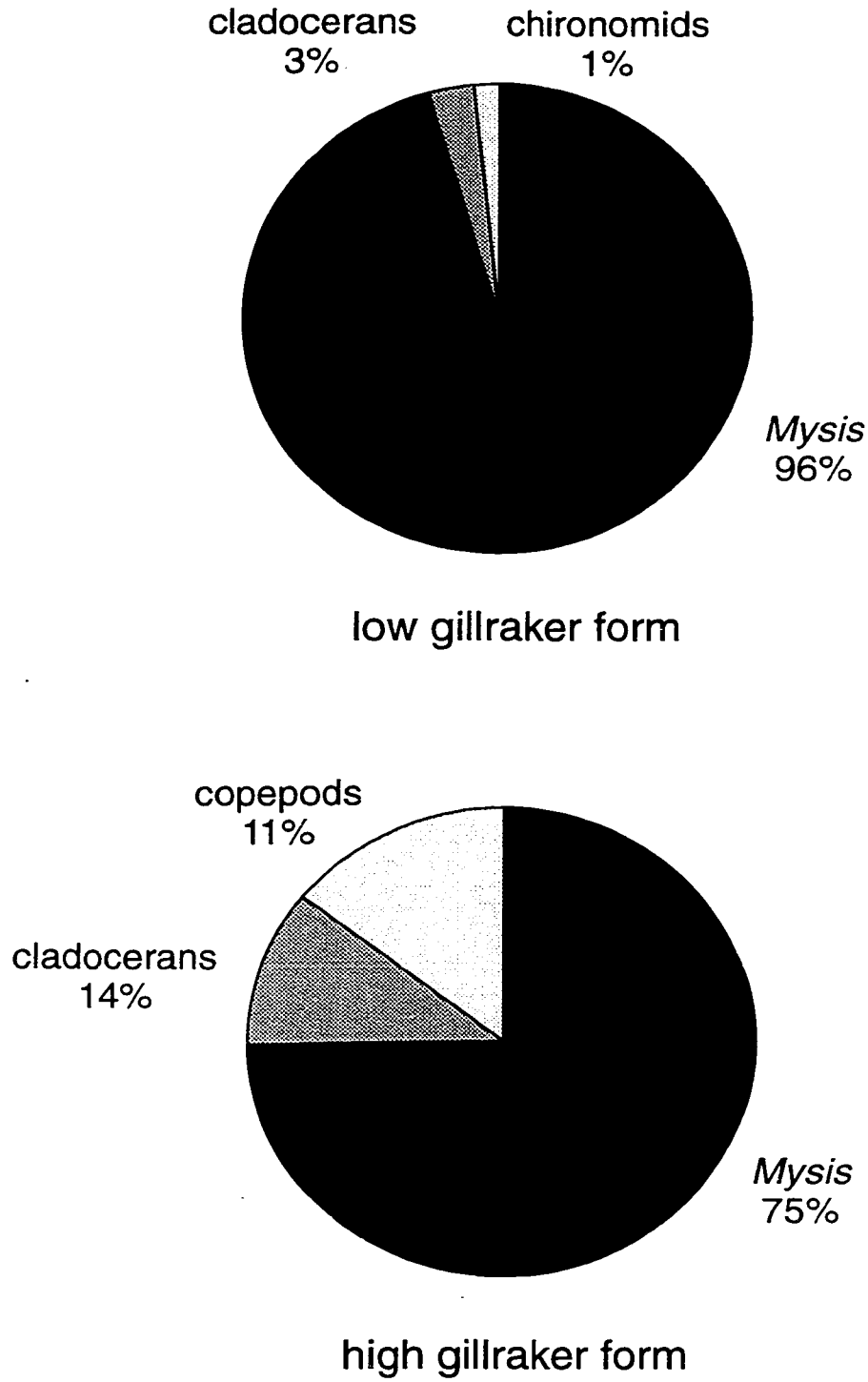

Figure 7. Approximate proportion of prey items in stomach contents of Barrow Lake ciscoes based on surface area estimation (described in Methods section). Both forms (low gillraker form n=15; high gillraker form n=21) fed predominantly on *Mysis relicta* throughout the open water season.

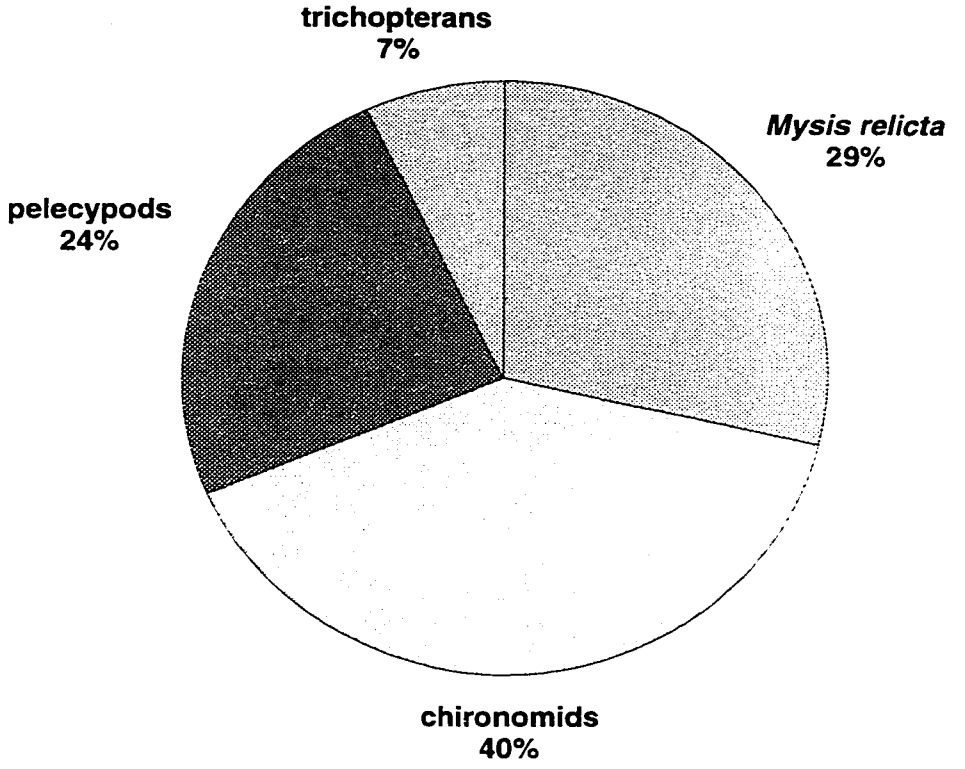

Figure 8. Approximate proportion of prey items in stomach contents of Barrow Lake *C. clupeaformis* (lake whitefish) based on surface area estimation

with the bulk of the remainder consisting of almost equal proportions of *Mysis relicta* and pelecypods. This is quite different from the diet of either form of cisco and demonstrates selection of a higher proportion of benthic prey items.

Spatial Distribution

The Barrow Lake high gillraker cisco was common throughout the lake including the deepest regions (24 m depth) (Fig. 9). In contrast, no low gillraker specimens (putative *C. zenithicus*) were collected in water greater than 16 m deep, either in surface, midwater, or bottom sets. Paterson (1969) also found *C. zenithicus* only in shallow water (2-5 m) in August 1966. Overall, the ranges of the low and high gillraker forms appeared to overlap broadly through the open water season.

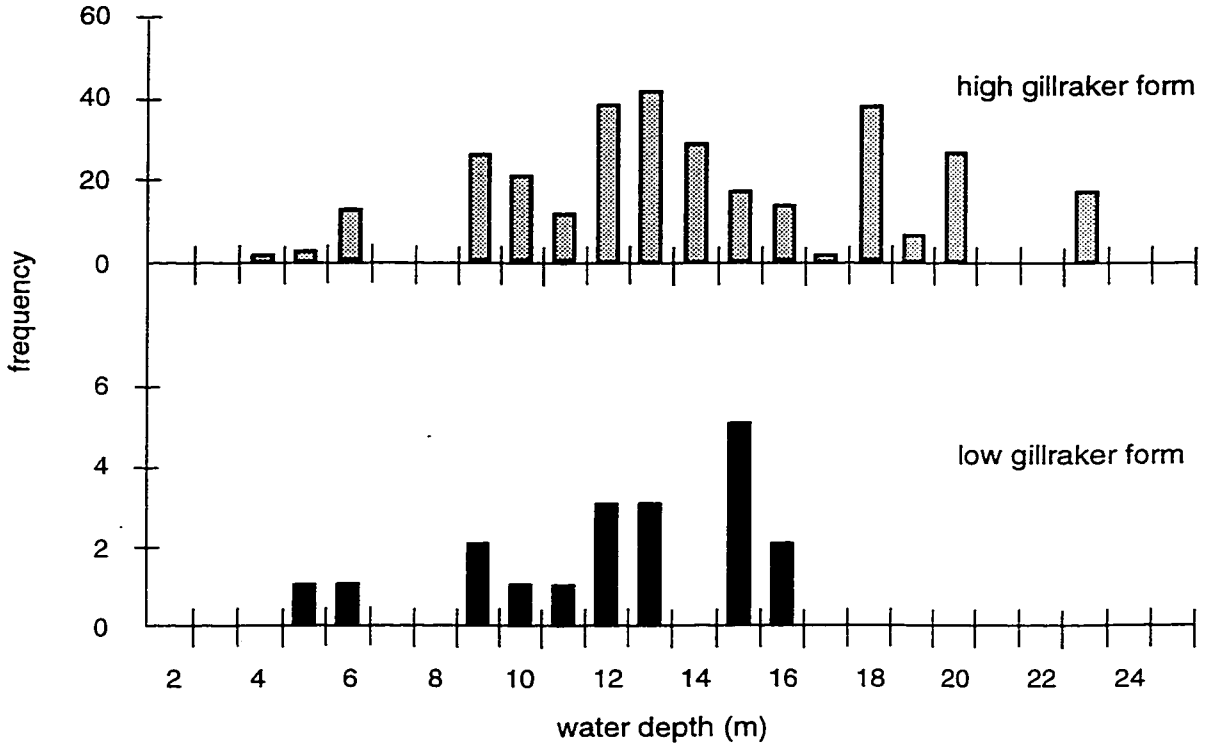

Figure 9. Water depth at point of capture of Barrow Lake ciscoes. No low gillraker specimens were captured in water deeper than 16 m.

Specific Identity of Barrow Lake Low Gillraker Cisco.

Principal Components Analysis of 19 morphometric characters from the nine northeastern Alberta cisco populations examined in this study showed the putative *C. zenithicus* in Barrow Lake was morphologically distinct in this sample (Fig. 10). Gillraker length, orbit diameter, and position of the adipose fin (truss 5) contributed most to the separation on the main axis of inter-taxon variation (axis 3) (Table 10). Multiple pairwise comparison of nine characters among all populations (from ANOVA using the Tamhane multiple comparison correction factor) showed significantly ($P<.05$) shorter gillrakers, smaller orbit, and longer upper jaw in the Barrow Lake low gillraker ciscoes than all other Alberta populations (Appendix 1). This population also had a longer adipose fin origin to caudal origin (truss 5) and longer snout than any other population except the Ryan Lake high gillraker form.

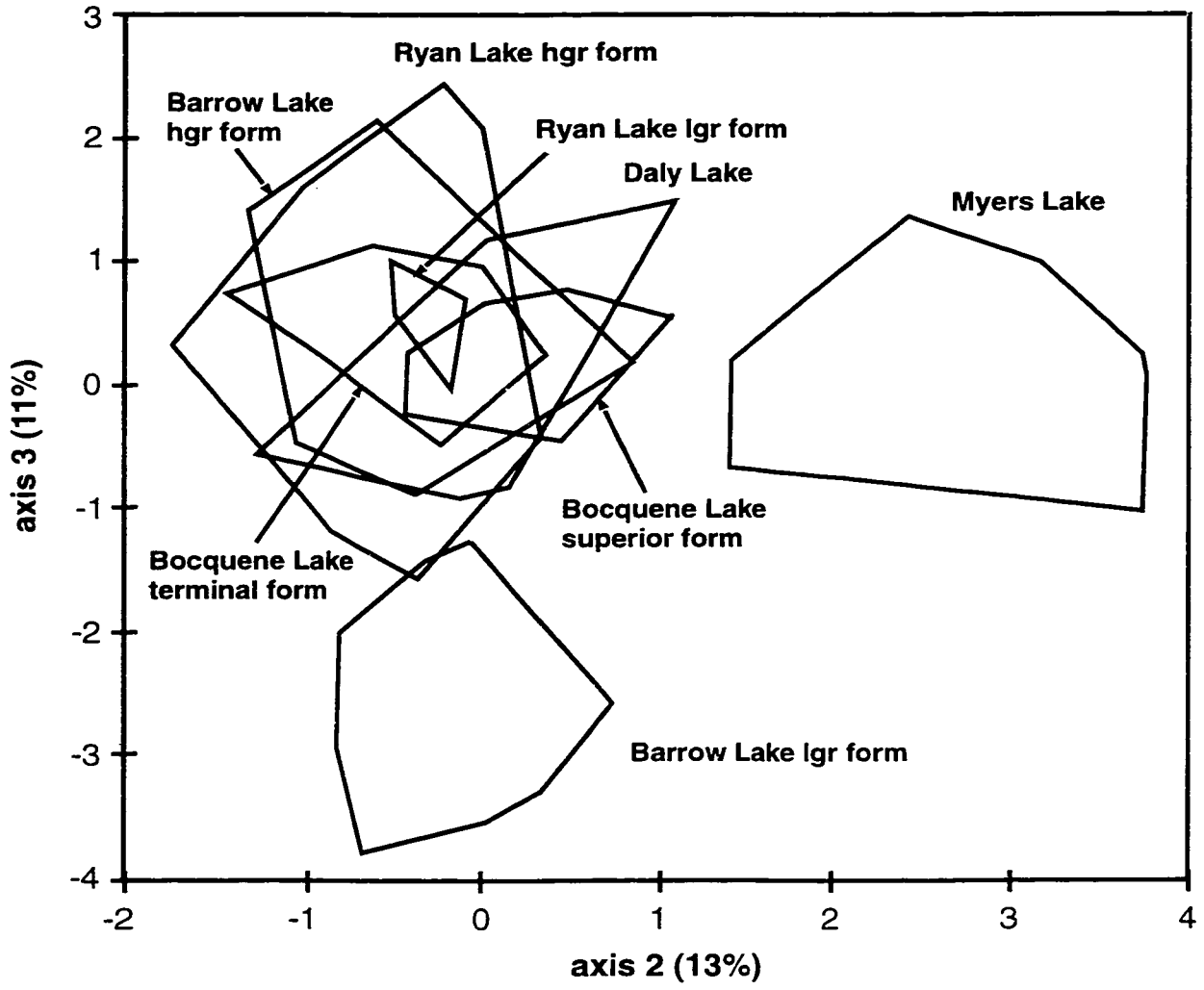

Figure 10. Principal component scores for all Alberta cisco populations examined based on 19 morphometric characters.

Table 10. Eigenvalues and eigenvectors from principal components 2 and 3 based on 19 morphometric characters from all Alberta ciscoes examined.

Eigenvalue	2	3
% of variability.	13	11
Cumulated %	13	24
Vectors :	2	3
truss 1	-0.250	-0.157
truss 2	0.057	0.304
truss 3	0.514	-0.298
truss 4	0.271	0.424
truss 5	-0.053	-0.578
truss 6	0.524	-0.053
truss 7	-0.032	-0.357
truss 8	0.572	0.103
truss 9	0.619	-0.055
truss 10	0.136	-0.120
truss 11	-0.292	0.199
truss 12	0.009	0.190
truss 14	0.201	0.216
truss 17	0.615	-0.025
upper jaw	-0.432	-0.378
g.r. 1	-0.276	0.719
head	-0.361	-0.011
snout	-0.462	-0.196
orbit	-0.127	0.572

A subset of measurements from 87 individuals representing eight populations of *C. zenithicus* was taken from specimens in the collection of the Royal Ontario Museum to examine the resemblance between the Barrow Lake low gillraker cisco and known *C. zenithicus* populations. Specimens from the following populations were examined: Lake Superior (n=13, including paratype from California Academy of Sciences), Lake Winnipeg, Manitoba (n=11), Reindeer Lake, Saskatchewan (n=9), Basswood Lake, Ontario (n=10), Little Athapapuskow Lake, Manitoba (n=9), Great Slave Lake, Northwest Territories (n=8), Sandy Lake, Ontario (n=11), and Lake Nipigon, Ontario (n=16). The following measurements and counts were taken: length of first gillraker on certatobranchial, upper jaw length, orbit diameter, truss 1, truss 3, truss 5, truss 11, truss

12, upper gillraker number, lower gillraker number, total gillraker number, principal dorsal fin rays, pectoral fin rays, and pored lateral line scales. A complete set of counts and measures was taken from the *C. zenithicus* paratype (cat. no. SU 13084).

The holotypes of *Leucichthys macrognathus*, *L. entomophagus*, and *L. athabascae* (Harper and Nichols 1919), in the collection at the Canadian Museum of Nature, were examined by Dr. J. S. Nelson. These specimens were synonymized with *C. zenithicus* by Dymond (1943) but questions regarding their identity persist (Clarke 1973, McPhail and Lindsey 1970, Scott and Crossman 1973). A morphological comparison of these specimens with known *C. zenithicus* and *C. artedi* samples is given in Table 11. Based on gillraker counts, all three "species" could represent *C. zenithicus.* It is probably no longer possible to obtain an accurate gillraker count from the *L. athabascae* specimen because the gill arch has been cut short and the specimen is in generally poor condition. This individual apparently has abnormally short or damaged rakers. *L. macrognathus* falls within the range of overlap of gillraker number for known *C. artedi* and *C. zenithicus* (Scott and Crossman 1973). It resembled *C. artedi* in its relatively long gillrakers and short upper jaw but was more *zenithicus*-like in its short dorsal fin base and shallow head. The number and length of the gillrakers in *L. entomophagus* suggested similarity to *C. zenithicus*. However, the short upper jaw, long dorsal fin base, and deep head were more *artedi*-like. The data presented here do not permit conclusive taxonomic allocation of these specimens. Therefore, they were not included in the sample of "known" *C. zenithicus* used in comparisons with the Barrow Lake population.

The mean, range, and standard deviation of morphometric variation in a combined set of all "known" *C. zenithicus* and *C. artedi* samples was compared with the Barrow Lake low gillraker form (Figure 11). The arrows indicate the values of the respective characters in the *C. zenithicus* paratype. This figure illustrates the extensive morphometric variation and overlap within and between these species. For all traits except dorsal fin base length, the

Table 11. Comparison of the holotypes of *L. macrognathus*, *L. athabascae*, and *L. entomophagus* (Harper and Nichols 1919) with known *C. zenithicus* and *C. artedi*. Morphometric values (means and standard deviations [S.D.]) are based on ratios of body parts to standard length.

Species	mean gillraker no. (range)	mean gillraker length (S.D.)	mean upper jaw length (S.D.)	mean truss 3 (S.D.)	mean truss 5 (S.D.)	mean truss 12 (S.D.)
C. zenithicus	39.05 (30-46)	26.397 (3.361)	10.003 (1.013)	9.208 (.734)	8.417 (.742)	6.364 (.367)
C. artedi	49.86 (42-62)	23.169 (3.508)	11.001 (.768)	7.857 (.715)	8.564 (.737)	6.231 (.499)
L. macrognathus	40-41	24.096	11.111	9.091	8.511	7.407
L. athabascae	38**	41.515*	11.810	9.320	9.320	6.782
L. entomophagus	36-37	26.863	12.060	8.303	N/A	6.089

* This gillraker is apparently damaged or aberrant.
** The gill arch in this specimen has been cut short and some rakers are undoubtedly missing (J. S. Nelson pers. comm.).

Barrow Lake low gillraker form more closely resembled *C. zenithicus* than *C. artedi*. Although gillraker length in the Barrow Lake low gillraker cisco overlapped broadly with *C. zenithicus*, the former exhibited the shortest gillrakers of all populations examined. A striking exception to the overall similarity between the Barrow Lake low gillraker form and *C. zenithicus* was the large dorsal fin base in the Barrow Lake population. In this respect it more closely resembled *C. artedi*. The *C. zenithicus* paratype had the shortest dorsal fin base of any specimen examined.

Means, modes, and ranges of several meristic characters for all populations are shown in Table 12. The Barrow Lake low gillraker form was clearly aligned with *C. zenithicus* in number of gillrakers. Mean differences in lateral line scale and principal dorsal fin ray counts were significant between species (t-test, $P<.0001$) but extensive overlap in the ranges of these characters precluded assignment of the Barrow Lake low gillraker form to either species based on these traits alone. The modal dorsal fin ray number in the Barrow Lake

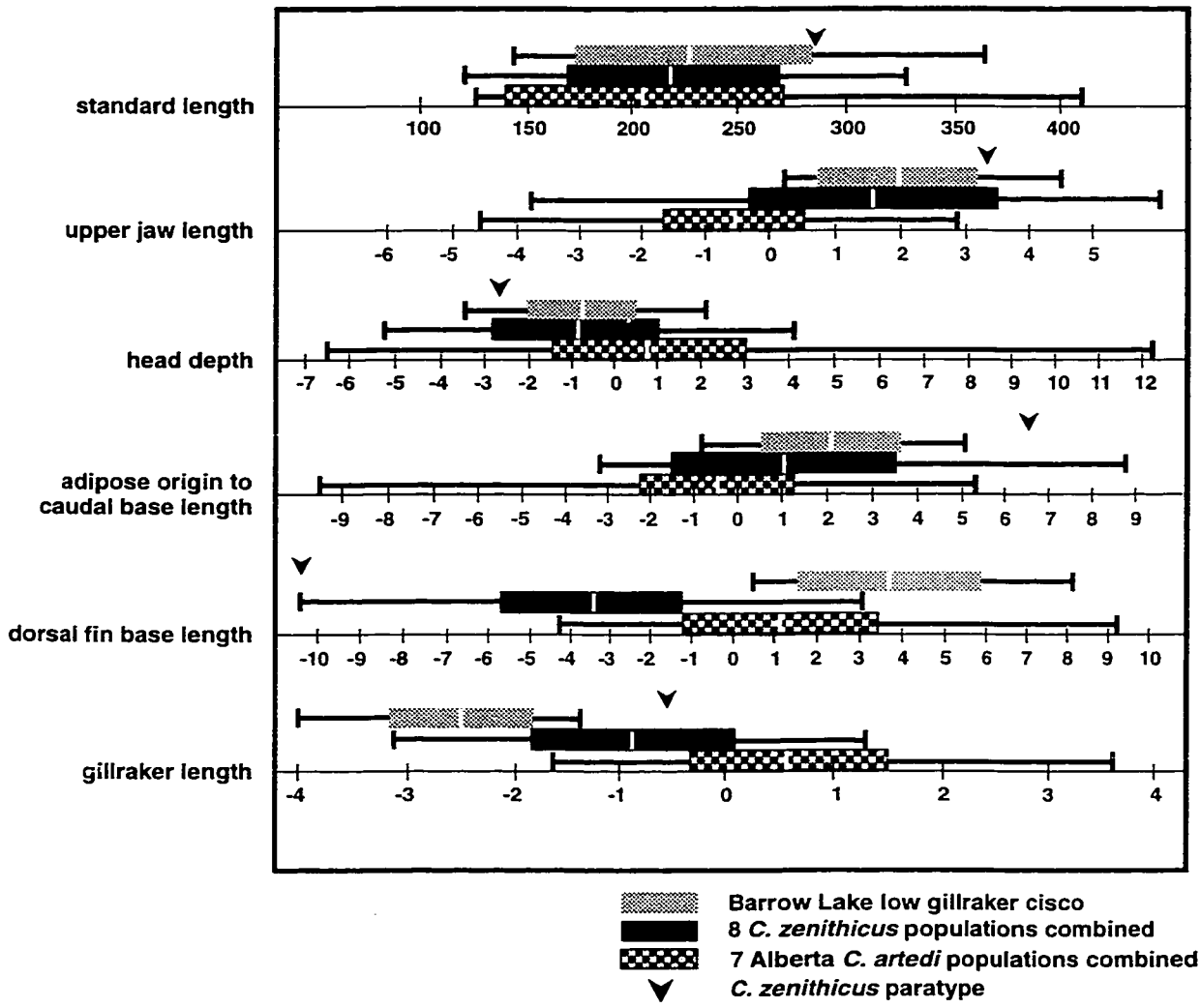

Figure 11. Means (white vertical lines), ranges (capped horizontal lines) and standard deviations (boxes) of selected morphometric characters in the Barrow Lake low gillraker ciscoes (n = 19) compared with eight *C. zenithicus* populations from across North America (n = 87) and seven Alberta *C. artedi* populations (n = 243). Values for the *C. zenithicus* paratype are indicated by arrows. All values except standard length are dimensionless adjusted regression residuals.

Table 12. Meristic comparison of *C. zenithicus* and *C. artedi* populations examined.

	Lake	Gillrakers			Lateral Line Scales			Pectoral Fin Rays			Principal Dorsal Fin Rays		
		mean	mode	range	mean	mode	range	mean	mode	range	mean	mode	range
C. zenithicus	Superior (n = 12)	41.9	42	37-45	78.6	80	73-84	16.5	17	15-18	10.2	11	9-11
	Winnipeg (n = 11)	38.4	37	36-41	66.9	67	61-73	15.5	15	14-17	10.2	10	9-11
	Reindeer (n = 9)	37.9	37	34-46	75.8	74	73-79	16.8	16	16-18	10.3	10	9-11
	Basswood (n = 10)	33.2	32	30-37	71.1	71	67-78	15.9	16	15-18	9.8	9	9-11
	Little Athapap. (n = 8)	39.1	36	36-43	69.8	-	64-77	16.6	17	15-18	10.6	10	10-12
	Great Slave (n = 8)	41.6	43	37-44	72.6	74	68-78	16.3	16	15-17	10.5	10	10-11
	Sandy (n = 7)	42.7	42	42-44	72.3	71	70-75	15.7	16	15-16	9.3	9	9-10
	Nipigon (n = 12)	36.7	35	35-39	70.5	71	66-74	16.1	16	15-17	10.5	11	9-11
	All populations combined (n = 87)	**38.7**	**42**	**30-46**	**71.7**	**71**	**61-84**	**16.1**	**16**	**14-18**	**10.2**	**10**	**9-12**
	Barrow lgr (n = 19)	40.5	40	38-43	72.6	74	66-79	16.0	16	15-17	11.9	12	10-13
C. artedi	Barrow hgr (n = 75)[1]	47.8	49	42-52	67.6	68	61-76	15.5	16	14-17	11.0	11	10-12
	Bocquene[2] (n = 31)	52.8	53	49-57	66.6	69	59-76	15.8	16	14-17	11.0	11	10-12
	Daly (n = 21)	52.3	51	48-57	69.5	70	63-75	16.2	16	15-17	11.3	11	10-12
	Myers (n = 21)	50.2	51	45-53	67.7	66	59-75	15.8	16	15-17	11.4	11	10-12
	Ryan lgr (n = 13)	46.0	45	44-48	63.5	64	61-70	16.1	16	15-17	11.1	11	10-12
	Ryan hgr (n = 37)	54.7	56	49-62	67.2	70	57-72	16.7	17	16-18	10.7	11	8-13
	Unnamed (n = 45)	48.2	47	42-55	70.6	73	63-83	16.1	16	14-18	10.7	11	10-12
	All populations combined (n = 243)	**50.1**	**50**	**42-62**	**68.0**	**70**	**57-83**	**16.0**	**16**	**14-18**	**11.0**	**11**	**8-13**

[1] Gillraker number n = 169; other counts n = 75.

[2] Includes only Bocquene Lake "terminal" mouth form believed to be *C. artedi*. The sympatric "superior" mouth form may be *C. sardinella* so is excluded from this comparison.

low gillraker cisco was higher than any other population examined and, therefore, more like *C. artedi*. Pectoral fin ray counts did not differ significantly between species ($P>.05$).

The results of one-way ANOVAs performed on each morphometric character across all populations are shown in Appendix 2. In post-hoc pairwise comparisons of means for each population, the Tamhane's correction of significance level for multiple comparisons was used if sample variances were heterogeneous and the Bonferroni correction used if variances were not significantly different. The Levene's statistic revealed variance homogeneity for all characters except truss 5 ($P<.05$). Bold values in Appendix 2 are statistically significant ($P<.05$).

Morphological generalities with respect to each *C. zenithicus* population, based on the pairwise comparisons, are summarized below (a similar comparison among Alberta *C. artedi* populations is presented later in this section).

Lake Superior *C. zenithicus*: modal gillraker count 42 (37-45). This population had a short dorsal fin base. The paratype, taken from Lake Superior, had the shortest dorsal fin base of any specimen examined.

Lake Winnipeg *C. zenithicus*: modal gillraker count 37 (36-41). This population had a relatively small upper jaw and short cranium.

Reindeer Lake *C. zenithicus*: modal gillraker count 37 (34-46). This population had a relatively short cranium.

Basswood Lake *C. zenithicus*: modal gillraker count 32 (30-37). This population had few and short gillrakers and a large eye.

Little Athapapaskow Lake *C. zenithicus*: modal gillraker count 36 (36-43). This population had a long upper jaw and long cranium.

Great Slave Lake *C. zenithicus*: modal gillraker count 43 (37-44). This population had the shortest upper jaw of all populations examined, a short cranium, slender head, and a relatively large dorsal fin base.

Sandy Lake *C. zenithicus*: modal gillraker count 42 (42-44): This population exhibited relatively long gillrakers and a long upper jaw.

Lake Nipigon *C. zenithicus*: modal gillraker count 35 (35-39): This population had a relatively small dorsal fin base and shallow head.

Barrow Lake *C. zenithicus*: modal gillraker count 40 (38-43): This population had the shortest gillrakers and longest dorsal fin base of all populations examined.

Several trends emerge from an examination of the pairwise comparisons of all *C. zenithicus* and *C. artedi* populations combined.

1) *C. zenithicus* has a longer upper jaw than *C. artedi*. The only exception to this is the Great Slave Lake *C. zenithicus*, which has a mean upper jaw length significantly shorter than all other *C. zenithicus* populations except Lake Winnipeg and not significantly different from any *C. artedi* populations.

2) Most *C. zenithicus* populations have shorter gillrakers than most *C. artedi* populations, although the differences were not always significant at the 5% level. The Barrow Lake putative *C. zenithicus* has significantly shorter gillrakers than all *C. artedi* populations

and four of the *C. zenithicus* populations. Basswood Lake specimens also have notably short gillrakers, a finding reported by Todd (in press).

3) Most *C. zenithicus* have a significantly shorter dorsal fin base (truss 3) than *C. artedi*. The only exception to this is the Great Slave Lake population which is not significantly different from most *C. artedi* populations. Barrow Lake putative *C. zenithicus* have a longer dorsal base than any other *C. zenithicus* population and, in fact, any *C. artedi* population except Myers Lake. The Lake Superior form of *C. zenithicus* has a shorter dorsal fin base than any other population, and the paratype (from Lake Superior) has the shortest dorsal fin base of all specimens examined. There may be a weak suggestion here of a latitudinal or northwest-southeast trending gradient (small in the southeast, large in the northwest), which would negate any comparisons made with samples taken only from a restricted geographic region. More populations from across the range of *C. zenithicus* must be examined to test this hypothesis.

4) The distance from the origin of the adipose fin to the base of the first dorsal procurrent ray (truss 5) tends to be larger in *C. zenithicus* although few inter-population differences were significant.

5) *C. zenithicus* has a shallower head than *C. artedi*. Great Slave Lake and Lake Nipigon specimens had the shallowest heads of all *zenithicus* populations examined. The Bocquene Lake "superior" form of cisco (putative *C. sardinella*) had the slenderest head (and body) of all populations examined and the Ryan Lake *C. artedi* the deepest.

A Principal Components Analysis of six morphometric characters was conducted for all populations (Figs. 12 & 13). Eigenvalues and eigenvectors for the first three principal components are shown in Table 13. A plot of scores on components 1 and 2 (Fig. 12) clusters

the Barrow Lake putative *C. zenithicus* with the known *C. zenithicus* and demonstrates reasonably good separation of the two species on component 2. Gillraker length and dorsal fin base length contributed most to this axis of variation (Table 13). Figure 13 shows the Barrow Lake putative *C. zenithicus* separated on component 3 from most other populations (except the Myers Lake *C. artedi*) based primarily on the influence of dorsal fin base length (Table 13).

Other Sympatric Alberta Cisco Populations

Ryan Lake (59° 10' N 111° 03' W)

Informative Morphological Characters

Two forms of cisco were found in Ryan Lake. As in Barrow Lake, *a priori* estimation of groups was based on body size and gillraker number. In Ryan Lake, the larger form had more gillrakers - the opposite relationship to that found in Barrow Lake. Plates 3 and 4 show typical members of each form. Mean standard length of the larger, high gillraker specimens was 305 mm (n=35); that of the low gillraker form 160 mm (n=15). The high gillraker form had a modal gillraker count of 56 (range 50 - 62); the low gillraker form a modal count of 45 (range 44 - 51). The gillraker frequency distribution (Fig. 14) was bimodal but not disjunct. Twelve of the 15 low gillraker specimens had 48 or fewer gillrakers. Three individuals assigned originally to the high gillraker group were later reallocated to the low gillraker (dwarf) group based on morphometric and length at age data. These specimens had 49, 50, and 51 gillrakers.

Twenty-eight morphometric characters were examined for variability and linearity of raw values, and normality of regression transformed variates (Table 14). All measurements were significantly correlated with standard length ($P<.01$) and bivariate plots revealed no evidence of non-linearity. Snout length, truss 5, and truss 7 exhibited the

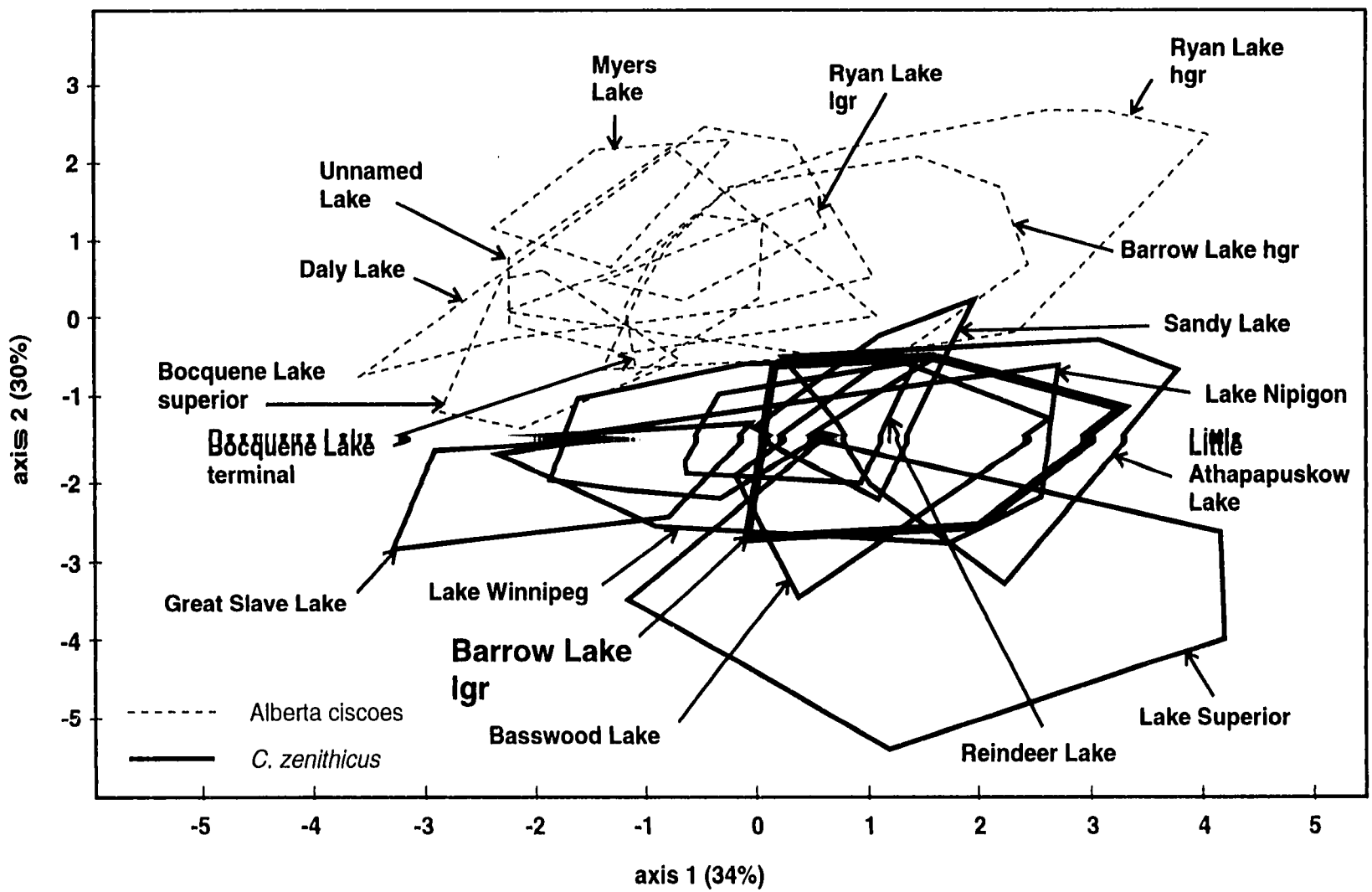

Figure 12. Scores on principal components 1 and 2 for nine Alberta cisco populations and eight *C. zenithicus* populations from across North America. The Barrow Lake low gillraker (lgr) form clusters with *C. zenithicus*.

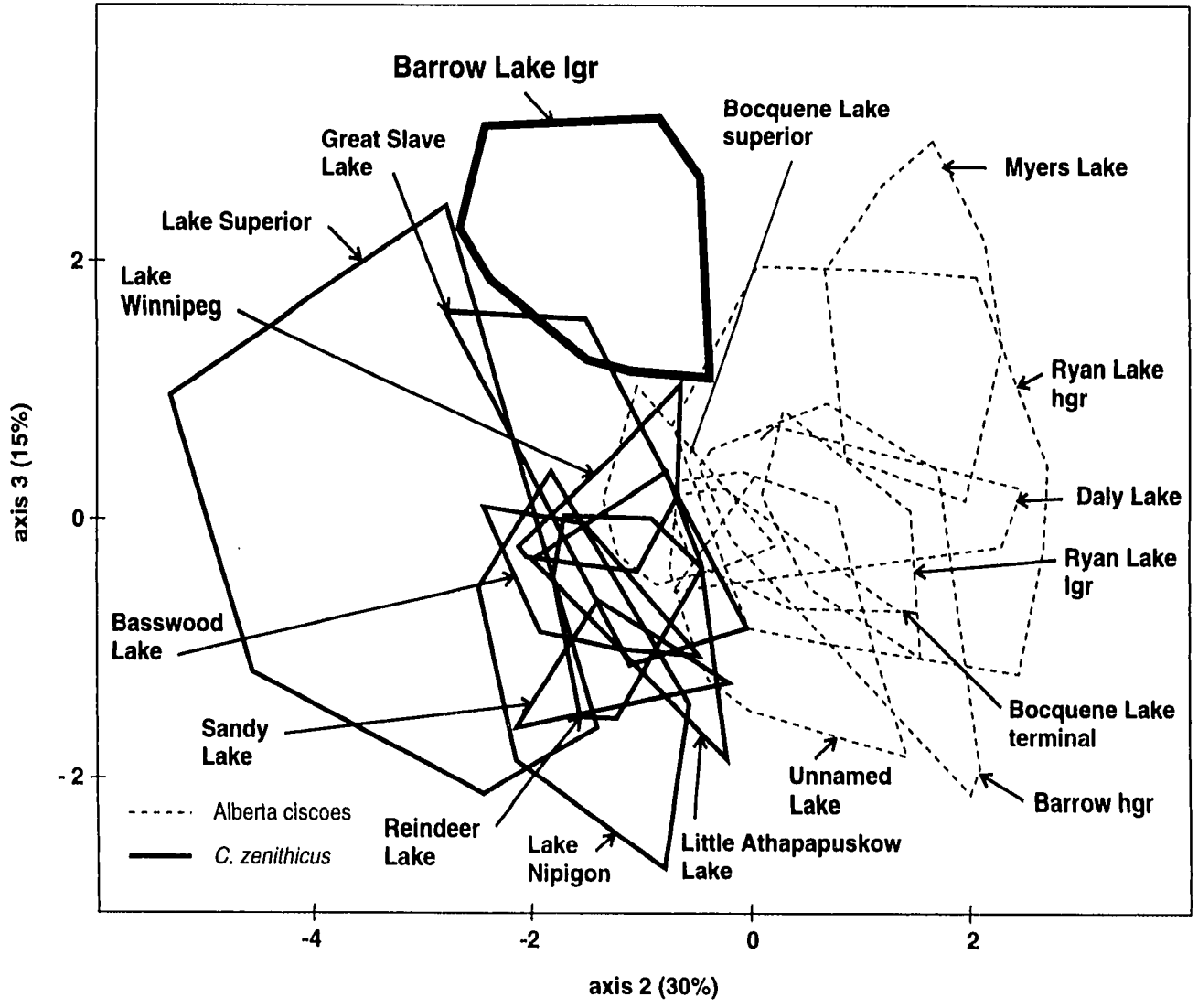

Figure 13. Scores on principal components 2 and 3 for nine Alberta cisco populations and eight *C. zenithicus* populations from across North America.

Table 13. Eigenvalues and eigenvectors of the first three principal components based on six morphometric characters from all *C. zenithicus* and *C. artedi* populations.

Eigenvalues	1	2	3
Value	2.0607	1.7909	0.9201
% of variability.	0.3434	0.2985	0.1534
Cumulated %	0.3434	0.6419	0.7953
Vectors :	1	2	3
truss 5	0.1450	-0.4493	0.4555
truss 1	0.6603	-0.0046	-0.0024
truss 3	0.0199	0.5087	0.6789
truss 12	0.4848	0.4077	0.1498
upper jaw	0.5475	-0.3375	-0.1904
g.r.l	0.0887	0.5092	-0.5224

greatest variability. Difficulties associated with consistent measurement of the latter two characters were discussed earlier. Variability in snout length was likely due to inconsistencies in determining a point representing the most anterior fleshy margin of the eye.

A summary of morphometric and meristic differences between cisco forms in Ryan Lake is presented in Table 15. Seventeen of 29 morphometric and five of eight meristic characters showed significant differences between the two populations based on univariate analysis (t-test; $P<.01$). The large, high gillraker form had a longer upper jaw and snout, a longer and deeper caudal peduncle, an overall deeper body, more pectoral fin rays, and more lateral line scales than the small, low gillraker form. Despite a large inter-population difference in gillraker number (modes 45 and 56), no difference in gillraker length was observed. The often cited correlation between raker number and length (e.g., fewer and shorter) does not apply in Ryan Lake ciscoes.

Allometry

Values of the log/log regression of standard length on each morphometric character for the Ryan Lake forms are shown in Table 14. Fifteen of the 28 characters examined

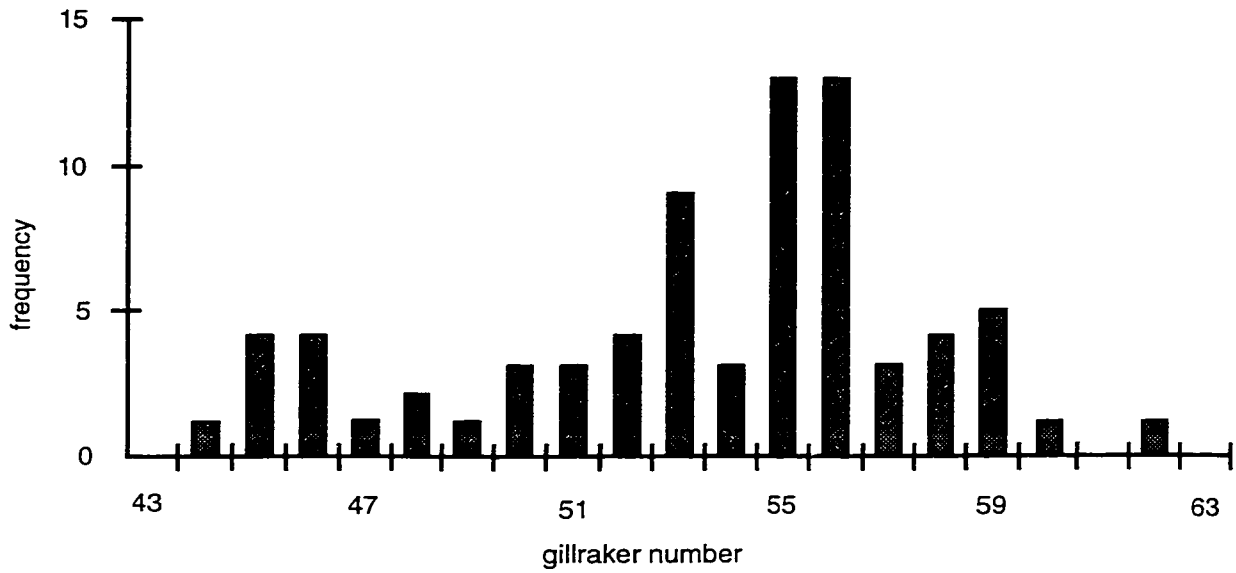

Figure 14. Gillraker number frequency distribution for Ryan Lake ciscoes.

exhibited allometry exceeding the 0.1 deviation criteria in at least one of the populations. Most of these represented deviations only slightly greater than the 0.1 level and probably have little biological meaning. Orbit diameter showed the most significant allometry of all characters examined. Based on the negative allometry observed, the larger form might be expected to have relatively smaller eyes, as in the Barrow Lake ciscoes. In Ryan Lake, however, the difference in eye size was not significant at the 99% confidence level adopted here (P=.03). However, at the 95% confidence level, the large form had larger eyes than the small form - the opposite of the predicted allometric relationship. This inverse condition was also found in truss measurements 2 and 5 which showed highly significant differences between groups despite the "diluting" effect of allometry. In general, the extreme size difference between Ryan Lake forms, and the potential for significant allometric effects, does not seem to be a major factor in explaining the morphological distinctiveness observed.

Table 14. Parameters of Ryan Lake cisco morphometric data. The correlation coefficient (r) of the untransformed variables on standard length provides an indication of data variation. All correlations were significant ($P<.01$). Visual examination of data plots revealed no suggestion of non-linearity. Values in bold highlight those characters that are particularly allometric. Kolmogorov-Smirnov D values indicate normality of regression transformed variables ($P>.05$).

Character	Hgr form			Lgr form			Allometric Relationship
	r	Slope of log/log regression	D	r	Slope of log/log regression	D	
gillraker 1	.863	**1.222**	.087	.930	**0.834**	.142	**+ and - allometry**
upper jaw	.973	.919	.101	.965	0.935	.222	
orbit	.896	**0.667**	.091	.957	**0.685**	.110	**- allometry**
head	.954	**0.783**	.095	.987	0.923	.185	**- allometry in lgr form**
snout	.760	.990	.084	.914	1.03	.129	
truss 1	.942	**0.808**	.082	.987	0.902	.129	**- allometry in lgr form**
truss 2	.992	**1.351**	.110	.991	1.14	.153	**+ allometry in hgr form**
truss 3	.955	0.863	.080	.976	1.04	.139	
truss 4	.972	1.040	.128	.984	0.989	.105	
truss 5	.872	**0.740**	.120	.954	**0.79**	.110	**- allometry**
truss 6	.914	1.000	.084	.985	1.12	.164	
truss 7	.763	1.020	.098	.943	**0.82**	.164	**- allometry in hgr form**
truss 8	.975	1.025	.107	.966	1	.234	
truss 9	.977	1.021	.117	.986	0.992	.193	
truss 10	.996	1.092	.121	.990	1.11	.169	
truss 11	.920	**.799**	.109	.989	1.01	.123	**- allometry in hgr form**
truss 12	.951	.963	.112	.983	1.11	.130	
truss 13	.994	1.125	.120	.995	1.12	.122	
truss 14	.985	1.149	.056	.991	1.14	.070	
truss 15	.958	1.030	.045	.978	1.08	.088	
truss 16	.949	1.021	.086	.981	1.06	.107	
truss 17	.950	1.006	.113	.974	1.04	.152	
truss 18	.974	.983	.060	.989	1.06	.167	
truss 19	.914	.916	.068	.976	0.99	.116	
truss 20	.964	1.057	.112	.983	1.04	.169	
truss 21	.981	.950	.074	.989	0.99	.224	
truss 22	.955	0.890	.080	.986	0.969	.108	
truss 23	.939	.995	.091	.981	0.935	.213	

Table 15. Inter-population comparison of Ryan Lake cisco morphometrics and meristics. Characters in bold are significantly different between forms ($P<.01$)

Character	Relationship	*P*	
standard length	**hgr > lgr**	**<.0001**	**means 305 (hgr) & 160 (lgr) mm**
gillraker 1	hgr = lgr	>.05	
upper jaw	**hgr > lgr**	**<.001**	
orbit	hgr = lgr	>.01	
head	hgr = lgr	>.05	
snout	**hgr > lgr**	**<.0001**	
truss no. 1	hgr = lgr	>.05	
truss no. 2	**hgr < lgr**	**<.0001**	
truss no. 3	hgr = lgr	>.05	
truss no. 4	hgr = lgr	>.05	
truss no. 5	**hgr > lgr**	**<.0001**	
truss no. 6	hgr = lgr	<.05	
truss no. 7	**hgr > lgr**	**<.01**	
truss no. 8	hgr = lgr	>.05	
truss no. 9	hgr = lgr	>.05	
truss no. 10	**hgr < lgr**	**<.0001**	
truss no. 11	hgr = lgr	>.05	
truss no. 12	hgr = lgr	>.05	
truss no. 13	**hgr < lgr**	**<.001**	
truss no. 14	hgr = lgr	>.01	
truss no. 15	**hgr > lgr**	**<.01**	
truss no. 16	**hgr > lgr**	**<.001**	
truss no. 17	**hgr > lgr**	**<.01**	
truss no. 18	**hgr > lgr**	**<.001**	
truss no. 19	**hgr > lgr**	**<.0001**	
truss no. 20	**hgr > lgr**	**<.0001**	
truss no. 21	**hgr > lgr**	**<.0001**	
truss no. 22	**hgr > lgr**	**<.0001**	
truss no. 23	**hgr > lgr**	**<.0001**	
upper gillrakers	**hgr > lgr**	**<.0001**	**modes 21 (hgr) & 18 (lgr)**
lower gillrakers	**hgr > lgr**	**<.0001**	**modes 35 (hgr) & 28 (lgr)**
total gillrakers	**hgr > lgr**	**<.0001**	**modes 56 (hgr) & 45 (lgr)**
total dorsal fin rays	hgr = lgr	>.05	modes 14 (hgr) & 14 (lgr)
pelvic fin rays	hgr = lgr	>.05	modes 11 (hgr) & 11 (lgr)
anal fin rays	hgr = lgr	>.01	modes 14 (hgr) & 15 (lgr)
pectoral fin rays	**hgr > lgr**	**<.01**	**modes 17 (hgr) & 16 (lgr)**
lateral line scales	**hgr > lgr**	**<.01**	**modes 66 (hgr) & 64 (lgr)**

Sexual Dimorphism

All counts and measurements taken from the high gillraker form were examined for evidence of sexual dimorphism (Table 16). Insufficient sample sizes precluded this analysis on the low gillraker form (total n=15). Five traits exhibited significant ($P<.05$) sexual dimorphism - truss 5, 14, 15, 17, and 20. Truss 5 appears slightly larger in females ($P=.013$) and the remaining four measurements were significantly larger in males. These latter measures are either nearly vertical or have a strong vertical component (see Fig. 2) suggesting Ryan Lake male ciscoes are somewhat deeper bodied than females.

Multivariate Analysis

Several measurements were excluded from multivariate analysis due to redundancy as discussed in the Methods section. Truss 5, 19, 20, and 22 all originate at the adipose fin origin. Only truss 5 was used in subsequent analyses as this was deemed the most easily interpretable character. The respective vectors of the other measurements could be influenced by a combination of several morphological changes including an overall increase in depth of the mid and posterior regions of the body. It was assumed here that truss 5 represents primarily an anterior shift of the adipose fin base in the high gillraker form. Truss 13 was found to be highly correlated with truss 10 and so dropped from further analysis.

A plot of principal component scores based on 18 morphometric characters (Table 17) revealed substantial overlap of cisco forms in Ryan Lake (Fig. 15). However, the low gillraker form clustered at the negative extreme of component 2. This axis largely contrasted truss 2, 10, and 14 with truss 5 and 7 (Table 17) suggesting the larger high gillraker form is relatively shorter anteriorly and has a longer caudal peduncle than the small low gillraker form. It appears the Ryan Lake ciscoes, despite being greatly divergent in size and gillraker number, are less distinctive overall than the Barrow Lake ciscoes.

Table 16. Summary of sexual dimorphism in Ryan Lake high gillraker ciscoes. Characters in bold are significantly different between sexes ($P<.05$).

Character	*P*	Relationship
standard length.	>.05	no s.d.
gillraker 1	>.05	no s.d.
upper jaw	>.05	no s.d.
orbit	>.05	no s.d.
head	>.05	no s.d.
snout	>.05	no s.d.
truss no. 1	>.05	no s.d.
truss no. 2	>.05	no s.d.
truss no. 3	>.05	no s.d.
truss no. 4	>.05	no s.d.
truss no. 5	**<.05**	**female bigger**
truss no. 6	>.05	no s.d.
truss no. 7	>.05	no s.d.
truss no. 8	>.05	no s.d.
truss no. 9	>.05	no s.d..
truss no. 10	>.05	no s.d.
truss no. 11	>.05	no s.d.
truss no. 12	>.05	no s.d.
truss no. 13	>.05	no s.d.
truss no. 14	**<.05**	**males bigger**
truss no. 15	**<.05**	**males bigger**
truss no. 16	>.05	no s.d.
truss no. 17	**<.05**	**males bigger**
truss no. 18	>.05	no s.d.
truss no. 19	>.05	no s.d.
truss no. 20	**<.01**	**males bigger**
truss no. 21	>.05	no s.d.
truss no. 22	>.05	no s.d.
truss no. 23	>.05	no s.d.
total gill rakers	>.05	no s.d.
total dorsal fin rays	>.05	no s.d.
pelvic fin rays	>.05	no s.d.
anal fin rays	>.05	no s.d
pectoral fin rays	>.05	no s.d.
lateral line scales	>.05	no s.d.

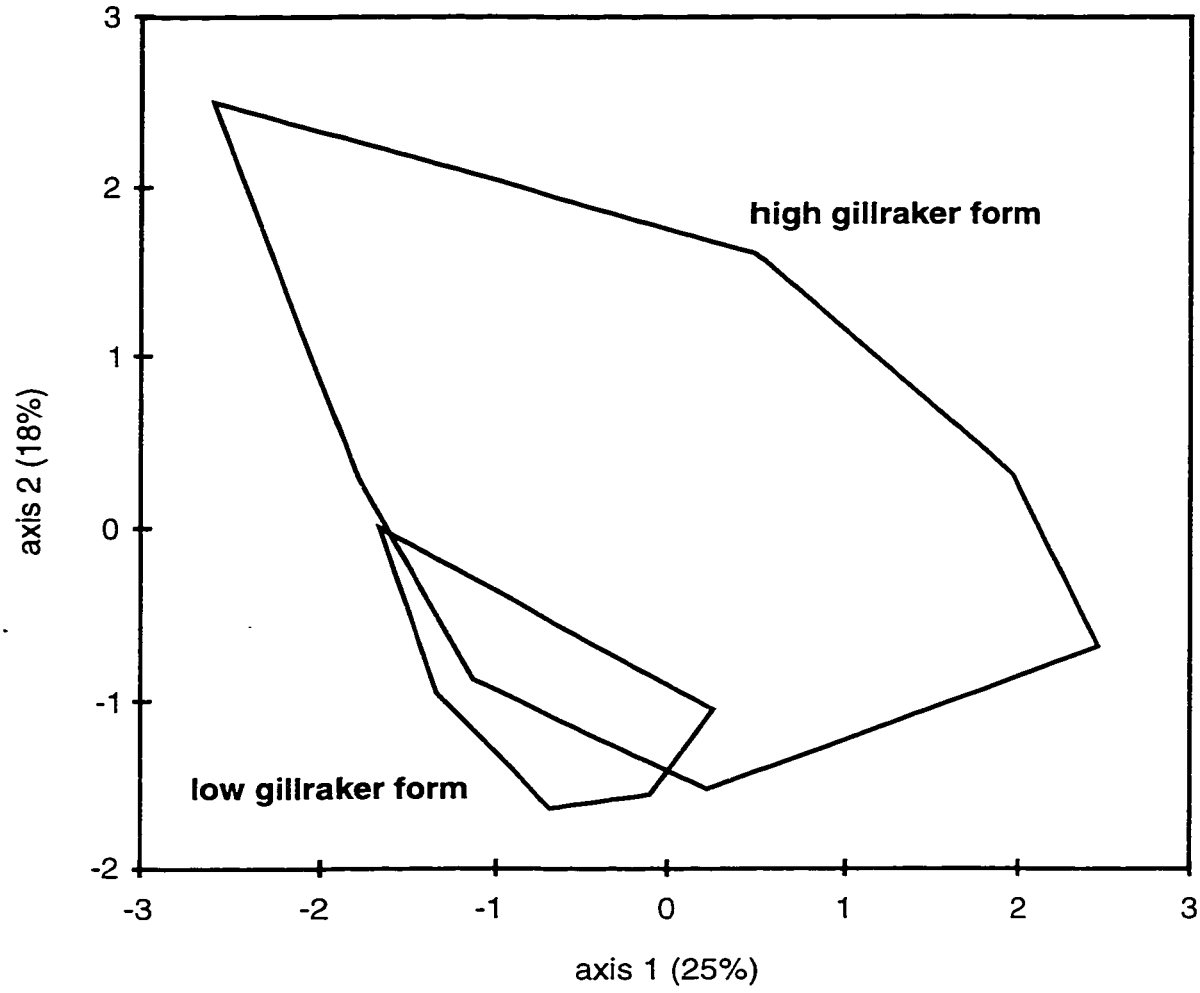

Figure 15. Scores on principal components 1 and 2 for Ryan Lake ciscoes based on 18 morphometric characters.

Table 17. Eigenvalues and eigenvectors from the first two principal components based on 18 morphometric characters from Ryan Lake ciscoes.

Eigenvalues	1	2
% of variability.	25	18
Cumulated %	25	43
Vectors :	1	2
truss 1	0.880	-0.171
truss 2	-0.305	-0.664
truss 3	0.395	0.010
truss 4	0.008	0.206
truss 5	0.036	0.672
truss 6	0.886	0.036
truss 7	-0.035	0.684
truss 8	0.087	-0.049
truss 9	-0.319	0.164
truss 10	0.061	-0.717
truss 11	0.519	0.395
truss 12	0.638	-0.276
truss 14	0.456	-0.787
truss 17	0.713	-0.271
upper jaw	0.632	0.292
gillraker 1	0.392	0.281
snout	0.675	0.346
orbit	0.370	0.034

PCA of all Alberta populations (Fig. 10) demonstrated considerable overlap between the Ryan Lake ciscoes and other Alberta *C. artedi*.

Ecology

Diet

The Ryan Lake low gillraker cisco consumed approximately 53% copepods, 25% cladocerans, and 22% *Mysis relicta* (Fig. 16). Stomachs of the high gillraker form contained 67% copepods, 7% cladocerans, and 26% *Mysis relicta*. If copepods and cladocerans are considered collectively as pelagic prey, the proportion of large bentho-pelagic (*Mysis*) to small pelagic food was essentially the same in both forms.

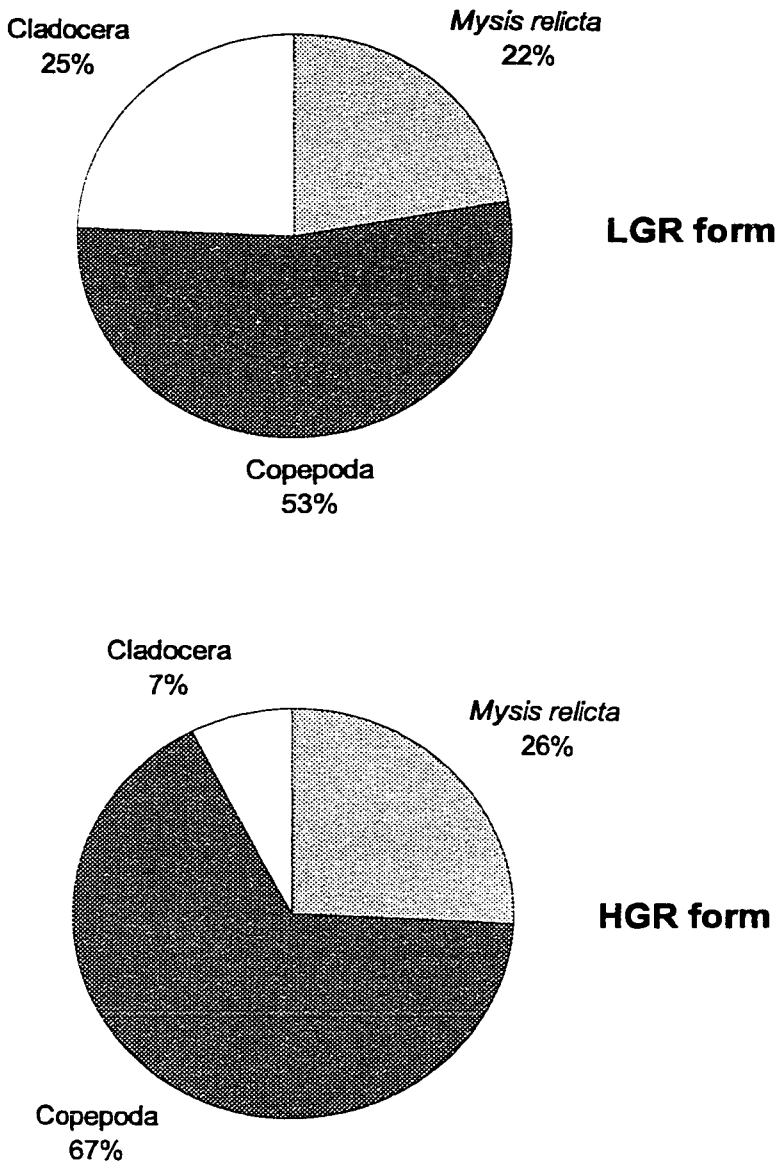

Figure 16. Approximate proportion of prey items in stomach contents of Ryan Lake ciscoes collected mid-June, 1996. Both forms fed predominantly on plankton (copepods and cladocerans).

Spatial Distribution

No differences in water depth at point of capture were found between the Ryan Lake ciscoes (Fig. 17). Where encountered, the rare low gillraker form was always collected along with many of the abundant high gillraker specimens. These data suggest no spatial separation of forms over the time period sampled.

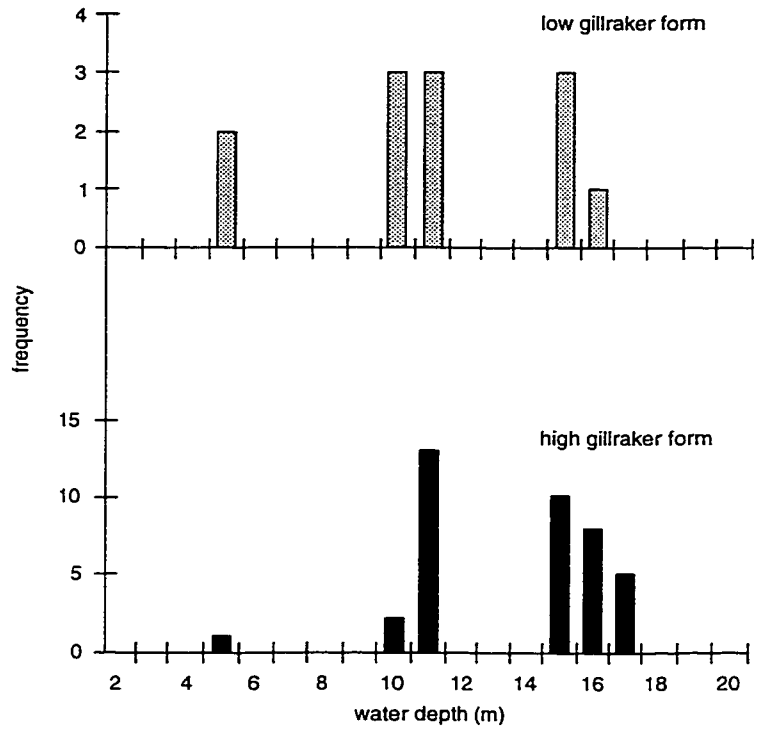

Figure 17. Water depth at point of capture of Ryan Lake ciscoes. Both forms were captured most frequently in 10 to 15 m of water.

Conclusion

Both ciscoes in Ryan Lake fall within the gillraker range of *C. artedi* and cluster on principal component plots with other *C. artedi* populations. These forms likely represent intralacustrine divergence of an ancestral *C. artedi* population. The lack of clear discontinuity between forms in PCA plots suggests some gene flow is probably still occurring between ecotypes. Positive assortative mating by size might be predicted to be an important incipient pre-zygotic isolating mechanism between these populations.

Bocquene Lake (59° 28' N 111° 07' W)

Two forms of cisco, identifiable in the field by the shape and position of the mouth, were found in Bocquene Lake. One form (modal gillraker number=49, range 45-53; n=27) exhibited a curved (upturned) dentary which consistently protruded beyond the upper jaw (Plate 5). This form was labelled the "superior" form for its superior mouth.

The other form (modal gillraker number = 53, range 49-57; n=30) had a more typical jaw structure with a terminal mouth (labelled "terminal" form) in which the lower jaw most often was included within the upper (Plate 6). Extensive overlap in gillraker number between forms resulted in weak evidence of a bimodal frequency distribution (Fig. 18).

Examination of plots of untransformed variables on standard length revealed consistently high data variance (Table 18). Unusually low correlations of most characters with standard length may be due in part to a disproportionately large influence of absolute measurement error in samples from a limited range of body sizes. In particular, the range of standard lengths in the sample of the terminal form was 34 mm (144-178 mm SL). Correlation coefficients in this group were consistently lower than in the superior form where the length range was 77 mm (141-218 mm SL). Both of these ranges were much smaller than in any other populations studied. Examination of the plots of the raw values of character size on standard length provided no evidence of a relationship that is

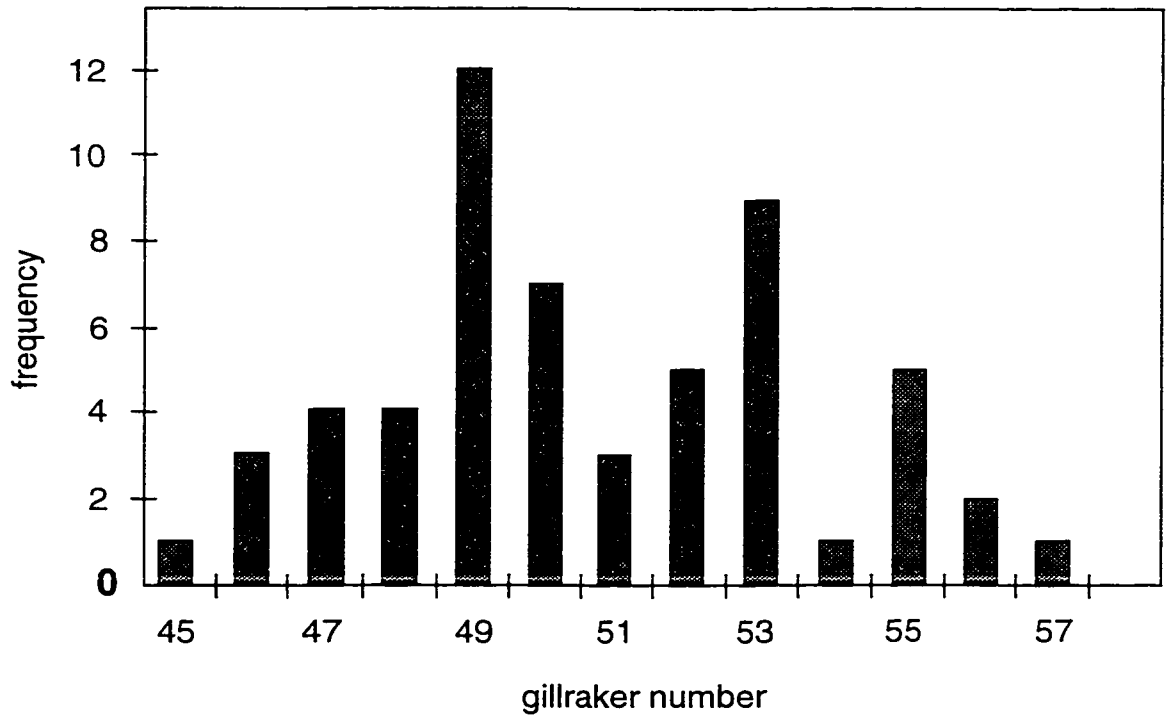

Figure 18. Gillraker number frequency distribution for Bocquene Lake ciscoes.

Table 18. Parameters of Bocquene Lake cisco morphometric data. Correlation coefficients (r) of the untransformed variables on standard length provide an indication of data variation. All correlations were significant ($P<.05$) except gillraker length in the terminal form. Visual examination of data plots revealed no suggestion of non-linearity. Values in bold highlight those characters that were particularly allometric. Kolmogorov-Smirnov D values indicate no significant deviation of regression transformed variables from normality ($P>.05$).

Character	Superior form			Terminal form			Relationship
	r	Slope of log/log regression	D	r	Slope of log/log regression	D	
gillraker 1	.751	**0.772**	.080	.174	?	.104	**- allometry in superior form**
upper jaw	.788	**0.721**	.174	.693	**0.827**	.105	**- allometry**
orbit	.853	**0.649**	.081	.478	**0.524**	.148	**- allometry**
head	.899	**0.731**	.125	.861	0.982	.176	**- allometry in superior form**
snout	.533	**0.612**	.089	.517	**1.170**	.131	**- allometry in superior form**
interorbital	.802	**0.690**	.118	.766	**1.390**	.065	**- and + allometry**
truss 1	.889	**0.722**	.144	.811	0.896	.080	**- allometry in superior form**
truss 2	.922	0.950	.065	.903	**1.390**	.089	**+ allometry in terminal form**
truss 3	.869	1.060	.121	.725	1.160	.110	
truss 4	.919	0.887	.078	.661	0.967	.209	
truss 5	.854	**0.751**	.113	.659	0.891	.099	**- allometry in superior form**
truss 6	.923	1.040	.071	.761	**1.380**	.116	**+ allometry in terminal form**
truss 7	.711	**0.830**	.088	.425	0.970	.074	**- allometry in superior form**
truss 8	.890	1.120	.100	.581	0.888	.127	
truss 9	.929	0.945	.115	.492	**0.664**	.145	**- allometry in terminal form**
truss 10	.942	0.994	.106	.839	**0.825**	.086	**- allometry in terminal form**
truss 11	.744	**0.706**	.174	.717	1.060	.118	**- allometry in superior form**
truss 12	.750	**0.565**	.118	.707	**0.816**	.116	**- allometry**
truss 13	.967	1.010	.086	.916	0.940	.082	
truss 14	.961	0.980	.089	.867	1.060	.164	
truss 15	.915	1.060	.120	.534	**0.746**	.086	**- allometry in terminal form**
truss 16	.927	**0.790**	.085	.696	0.910	.103	**- allometry in superior form**
truss 17	.915	1.130	.108	.437	**0.675**	.090	**- allometry in terminal form**
truss 18	.963	**0.850**	.091	.809	0.900	.146	**- allometry in superior form**
truss 19	.883	0.940	.085	.507	**0.720**	.109	**- allometry in terminal form**
truss 20	.875	1.010	.085	.660	**0.840**	.101	**- allometry in terminal form**
truss 21	.961	**0.850**	.114	.769	**0.860**	.106	**- allometry**
truss 22	.858	1.050	.082	.663	1.020	.089	
truss 23	.896	0.910	.109	.660	0.910	.117	

other than linear nor of any hidden pattern suggesting further subdivision of this group. The distributions were always a "shotgun" pattern suggesting high relative measurement error or high inherent character variability. It seems unlikely that this population exhibits high variability in the same characters that show tight correlations with standard length in all other populations examined. Until further evidence suggests otherwise, it is, therefore, assumed that the poor correlations with standard length are not biologically based but reflect the reduced statistical ability to predict y from x over a small range of x given a consistent magnitude of variation about the mean of y (measurement error and variation).

Morphometric and meristic differences between the Bocquene Lake forms are summarized in Table 19. Nineteen of 30 morphometric and all eight meristic characters examined showed significant differences between forms ($P<.01$). Of particular note, the superior form had fewer and shorter gillrakers, more lateral line scales, a much narrower interorbital width, a shorter cranium, shorter dorsal fin base, longer anal fin base, and shallower head than the terminal form. In general, the entire anterior portion of the superior form was relatively shorter and the posterior portion longer than the terminal form. This results in relatively forward-positioned pelvic fins in the superior form (tip of snout to pelvic origin is shorter than pelvic origin to caudal flexure). This feature is diagnostic of *C. sardinella* (McPhail and Lindsey 1970).

Allometry

Accurate assessment of allometric relationships is hampered in both of these populations by the narrow size range of the specimens in the sample. However, the size similarity of these two forms minimized concerns regarding the potential confounding effect of allometry in assessing inter-group morphological differences. Compared to the other sympatric populations studied, coefficients of allometry in Bocquene Lake ciscoes were

Table 19. Inter-population comparison of Bocquene Lake cisco morphometrics and meristics. Forms are designated by mouth orientation. Superior form (s.) = putative *C. sardinella;* terminal form (t.) = *C. artedi.* Characters in bold are significantly different between forms.

Character	Relationship	*P*	
standard length	**superior > terminal**	**<.01**	**means 164 (s.) & 154 (t.) mm**
gillraker length	**superior < terminal**	**<.0001**	
upper jaw	superior = terminal	>.05	
orbit	**superior > terminal**	**<.001**	
head	**superior < terminal**	**<.0001**	
snout	superior = terminal	>.05	
interorbital	**superior < terminal**	**<.0001**	
truss 1	**superior < terminal**	**<.0001**	
truss 2	**superior < terminal**	**<.001**	
truss 3	**superior < terminal**	**<.0001**	
truss 4	**superior > terminal**	**<.0001**	
truss 5	**superior > terminal**	**<.0001**	
truss 6	superior = terminal	>.05	
truss 7	**superior > terminal**	**<.0001**	
truss 8	**superior > terminal**	**<.0001**	
truss 9	superior = terminal	>.05	
truss 10	superior = terminal	>.05	
truss 11	**superior < terminal**	**<.01**	
truss 12	**superior < terminal**	**<.0001**	
truss 13	**superior < terminal**	**<.0001**	
truss 14	**superior < terminal**	**<.05**	
truss 15	superior = terminal	>.05	
truss 16	**superior > terminal**	**<.001**	
truss 17	superior = terminal	>.05	
truss 18	superior = terminal	>.05	
truss 19	superior = terminal	>.05	
truss 20	**superior > terminal**	**<.0001**	
truss 21	**superior > terminal**	**<.0001**	
truss 22	superior = terminal	>.05	
truss 23	**superior > terminal**	**<.01**	
upper gillrakers	**superior < terminal**	**<.0001**	**modes 18 (s.) and 19 (t.)**
lower gillrakers	**superior < terminal**	**<.0001**	**modes 31 (s.) and 34 (t.)**
total gillrakers	**superior < terminal**	**<.0001**	**modes 49 (s.) and 53 (t.)**
dorsal fin rays	**superior < terminal**	**<.0001**	**modes 13 (s.) and 14 (t.)**
pelvic fin ray	**superior > terminal**	**<.01**	**modes 12 (s.) and 11 (t.)**
anal fin rays	**superior > terminal**	**<.001**	**modes 15 (s.) and 14 (t.)**
pectoral fin rays	**superior < terminal**	**<.0001**	**modes 15 (s.) and 16 (t.)**
lat line scales	**superior > terminal**	**<.0001**	**modes 71 (s.) and 69 (t.)**

sympatric populations studied, coefficients of allometry in Bocquene Lake ciscoes were considered a less important criterion in character selection for multivariate analysis.

The length-at-age plot shown in Figure 19 suggests slow growth of both populations and little evidence for two different growth rates. Slopes of the log/log regressions of morphometric characters on standard length are given in Table 18. Many characters in both forms appeared to exhibit significant allometry. As in all cisco populations examined, the size of the orbit was consistently negatively allometric. In the superior form, it appeared that all characters associated with the head region were negatively allometric as were traits associated with the caudal portion of the body (e.g., truss 5 and 7). In general, it seems growth in the middle portion of the body in this form was essentially isometric. In the terminal form, most characters associated with the head, excluding the eye, were more nearly isometric or positively allometric (especially the interorbital

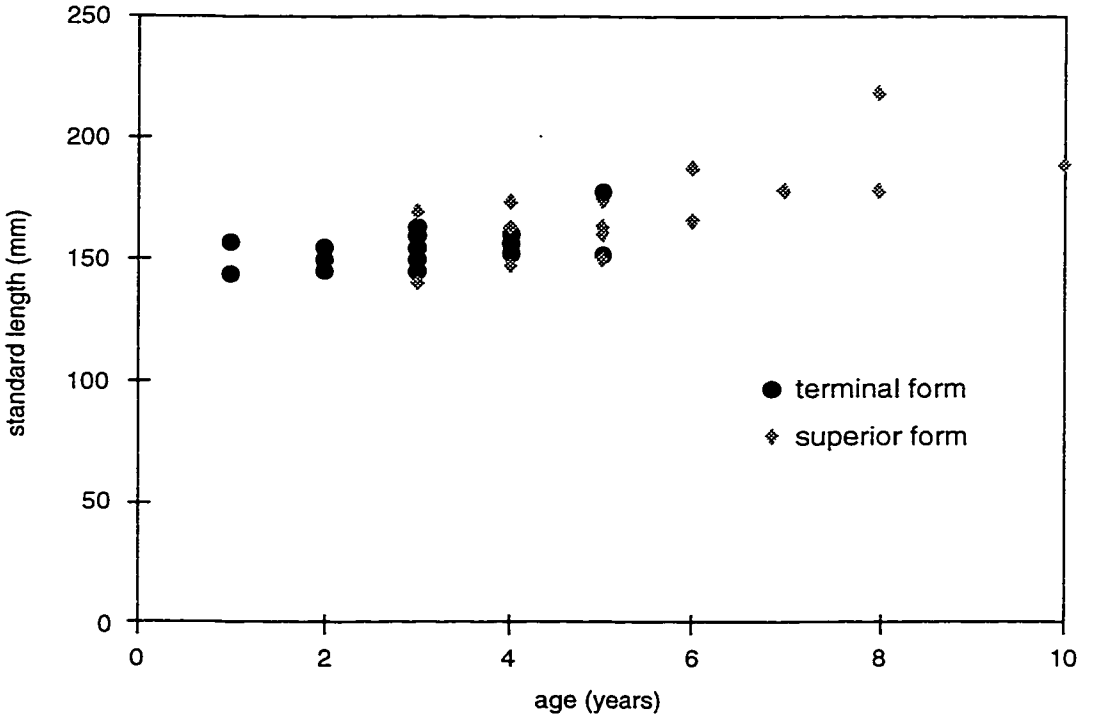

Figure 19. Length-at-age plot for Bocquene Lake ciscoes.

width and snout length). Characters that reflect body depth tended to show negative allometry in this form (e.g., truss 12, 15, 17, and 19). The exception to this was truss 6 (roughly equivalent to caudal peduncle depth) which was larger in large individuals.

Sexual Dimorphism

The terminal form of cisco in Bocquene Lake was examined for evidence of sexual dimorphism. The sample consisted of 16 females and 12 males (the superior form was not analysed because there were only six males in the sample of 27). Five characters showed significant ($P<.05$) sexual dimorphism (Table 20). Females appeared to have a slightly longer head (as represented by truss 1 and 11), a wider interorbital width, and a smaller anal fin (truss 8 and 21).

Multivariate Analysis

Characters chosen for multivariate analysis were based on the minimum redundancy criteria described for the Barrow and Ryan lake populations. A principal components plot of 21 morphometric characters showed almost complete separation of forms on axis 1 (Fig. 20). Eigenvalues and eigenvectors for components 1 and 2 are given in Table 21. Component 1 largely contrasts the overall length of the anterior portion of the body (e.g., head and truss 1) with the length of the posterior portion (e.g., truss 4, 5, 7 and 8).

Conclusion

The superior form of cisco in Bocquene Lake exhibits a number of characters that appear unique among all of the ciscoes examined in this study. The slim body, superior mouth with distinctly curved dentary, and relatively forward-positioned pelvic fins suggest this may represent a population of the small, non-migratory form of *C. sardinella* (McPhail and Lindsey 1970, Scott and Crossman 1973). The range of gillraker counts in this population (45-53) falls within the range known for *C. sardinella* (McPhail and Lindsey 1970); however, further work is required to confirm this identification.

Table 20. Summary of sexual dimorphism in Bocquene Lake ciscoes. Characters in bold are significantly different between sexes ($P<.05$).

Character	*P*	Relationship
standard length	>.05	
gillraker 1	>.05	
upper jaw	>.05	
orbit	>.05	
head	>.05	
snout	>.05	
interorbital	**<.05**	**females larger than males**
truss 1	**<.05**	**females larger than males**
truss 2	>.05	
truss 3	>.05	
truss 4	>.05	
truss 5	>.05	
truss 6	>.05	
truss 7	>.05	
truss 8	**<.01**	**females smaller than males**
truss 9	>.05	
truss 10	>.05	
truss 11	**<.01**	**females larger than males**
truss 12	>.05	
truss 13	>.05	
truss 14	>.05	
truss 15	>.05	
truss 16	>.05	
truss 17	>.05	
truss 18	>.05	
truss 19	>.05	
truss 20	>.05	
truss 21	**<.05**	**females smaller than males**
truss 22	>.05	
truss 23	>.05	
total gillrakers	>.05	
total dorsal fin rays	>.05	
pelvic fin ray	>.05	
anal fin rays	>.05	
pectoral fin rays	>.05	
lat line scales	>.05	

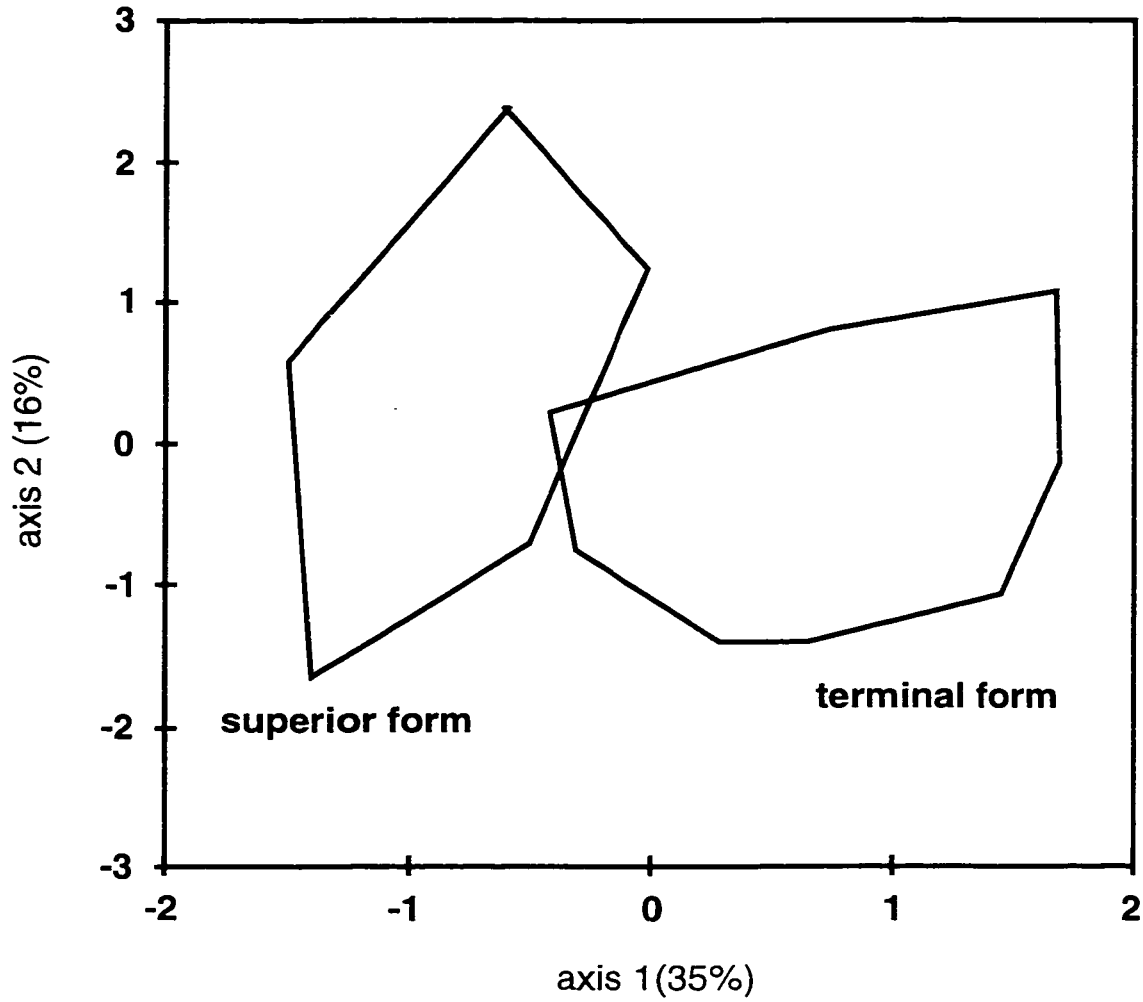

Figure 20. Scores on principal components 1 and 2 for Bocquene Lake ciscoes based on 21 morphometric characters.

Table 21. Eigenvalues and eigenvectors from the first two principal components based on 21 morphometric characters from Bocquene Lake ciscoes.

Eigenvalues	1	2
% of variability.	35	16
Cumulated %	35	51
Vectors :	1	2
truss 1	0.924	0.125
truss 2	0.487	0.131
truss 3	0.728	0.224
truss 4	-0.749	0.387
truss 5	-0.548	0.067
truss 6	-0.160	0.602
truss 7	-0.622	0.387
truss 8	-0.631	0.536
truss 9	-0.281	-0.096
truss 10	0.226	0.219
truss 11	0.579	0.187
truss 12	0.779	0.182
truss 14	0.393	0.520
truss 17	0.156	0.624
truss 20	-0.461	0.801
g.r. 1	0.758	0.001
head	0.881	0.252
snout	0.479	0.449
interorbit	0.852	-0.110
orbit	-0.110	0.715
upper jaw	0.417	0.321

Unnamed Lake (59° 48' N 110° 48' W)

Based on a plot of standard length versus age, it appeared that two forms of cisco occurred in Unnamed Lake (Fig. 21). A similar suggestion was made by staff of Alberta Fish and Wildlife (Anon. c. 1975). In that survey 134 "dwarf" (162.3–187 mm FL) specimens and one "normal" (281 mm FL) individual were collected in late August of 1974. Groups of dwarfs and normals were estimated *a priori* based on length at age data. Only those specimens clearly assignable to one or the other size-at-age group were included in the initial analyses. Morphometric and meristic comparisons (primarily gillraker number) allowed subsequent allocation of all but six of the 45 specimens to one or other of the groups.

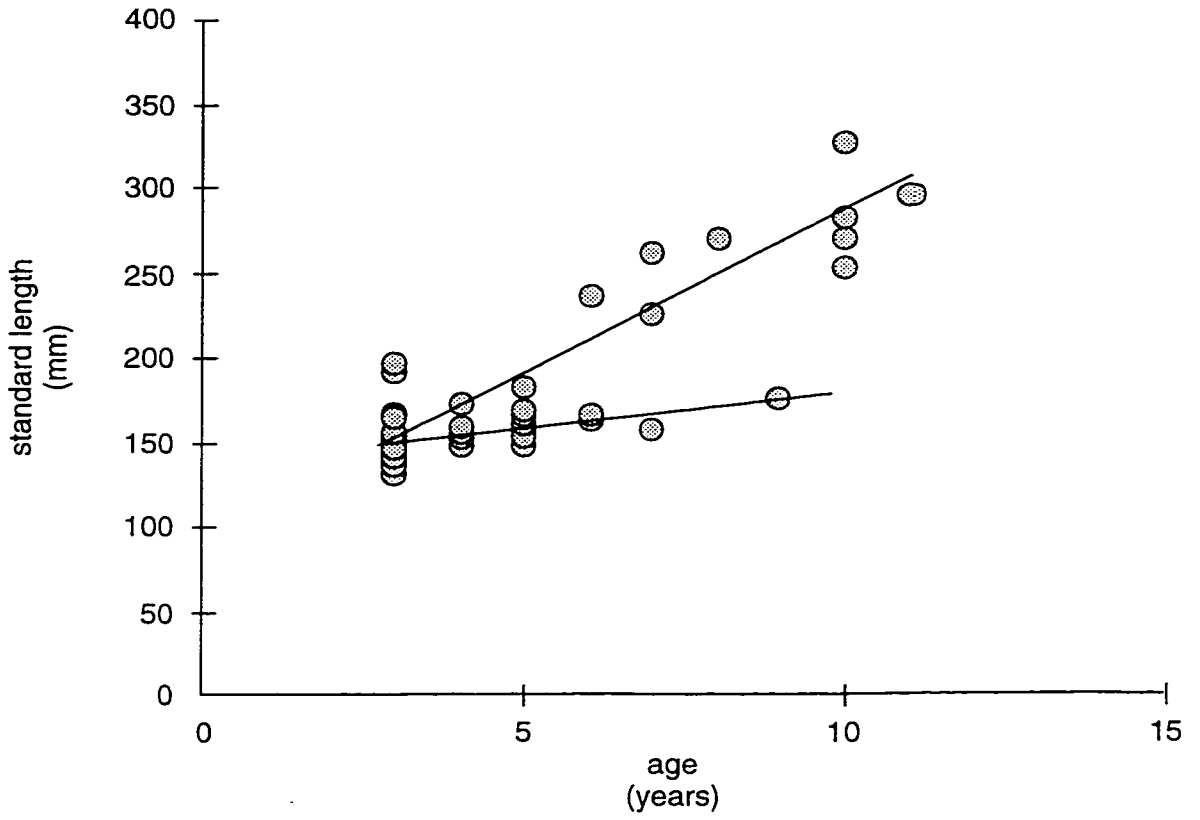

Figure 21. Length at age plot for Unnamed Lake ciscoes. Lines of eyeball fit suggest a small, slow-growing (dwarf) and a large, faster-growing (normal) form.

Data variability as represented by the correlation coefficients of each untransformed character on standard length, show high apparent variability in the dwarf form but much less variance in the large form (Table 22). This is undoubtedly an artifact of the small overall size range in the dwarf sample (range 44 mm,133-177 mm; n=26) compared to the normal sample (range 193 mm, 165-358; n=13). Bivariate plots exhibited no evidence of non-linearity between quantitative traits and standard length.

Morphometric and meristic differences between members of a subset of specimens classifiable *a priori* into a normal, fast-growing group and dwarf, slow-growing group are shown in Table 23. Eight morphometric characters and one meristic character differed significantly between forms ($P<.01$). A comparison of gillraker number between these

Table 22. Parameters of Unnamed Lake cisco morphometric data. The correlation coefficient (r) of the untransformed variables on standard length provides an indication of data variation. All correlations were significant ($P<.01$). Visual examination of data plots revealed no suggestion of non-linearity. Values in bold highlight those characters that are particularly allometric. Kolmogorov-Smirnov D values indicate normality of regression transformed variables ($P>.05$).

Character	dwarf form			normal form			Relationship
	r	Slope of log/log regression	D	r	Slope of log/log regression	D	
g.r. 1	.715	1.120	.112	.971	1.030	.101	
upper jaw	.884	1.116	.123	.986	**0.791**	.151	**- allometry in normal form**
orbit	.854	1.060	.142	.988	**0.668**	.158	**- allometry in normal form**
head	.894	1.050	.221	.992	**0.819**	.116	**- allometry in normal form**
snout	.791	**1.230**	.080	.915	**0.797**	.152	**+ and - allometry**
truss 1	.884	1.020	.128	.995	**0.834**	.187	**- allometry in normal form**
truss 2	.959	**1.430**	.142	.979	0.970	.166	**+ allometry in dwarf form**
truss 3	.680	0.890	.054	.957	1.020	.162	
truss 4	.837	0.938	.141	.980	0.951	.130	
truss 5	.519	**0.573**	.082	.972	0.932	.136	**- allometry in dwarf form**
truss 6	.698	0.910	.122	.986	1.120	.220	
truss 7	.622	0.983	.144	.913	0.966	.091	
truss 8	.714	0.935	.145	.959	0.930	.082	
truss 9	.728	**0.755**	.124	.982	0.918	.137	**- allometry in dwarf form**
truss 10	.842	0.935	.103	.987	0.920	.159	
truss 11	.764	0.890	.090	.971	**0.820**	.182	**- allometry in normal form**
truss 12	.621	**0.643**	.067	.971	0.950	.194	**- allometry in dwarf form**
truss 13	.937	1.010	.074	.991	0.970	.126	
truss 14	.956	1.163	.105	.990	0.960	.142	
truss 15	.744	**0.668**	.077	.988	1.090	.128	**- allometry in dwarf form**
truss 16	.848	**0.858**	.141	.990	1.020	.118	**- allometry in dwarf form**
truss 17	.735	**0.662**	.087	.989	1.060	.113	**- allometry in dwarf form**
truss 18	.910	0.969	.138	.992	0.995	.134	
truss 19	.733	**0.733**	.099	.984	1.040	.180	**- allometry in dwarf form**
truss 20	.804	**0.813**	.114	.988	0.990	.140	**- allometry in dwarf form**
truss 21	.922	0.904	.085	.991	0.950	.135	
truss 22	.704	**0.777**	.075	.986	0.941	.168	**- allometry in dwarf form**
truss 23	.777	**0.828**	.138	.987	1.015	.169	**- allometry in dwarf form**

Table 23. Inter-population comparison of Unnamed Lake cisco morphometrics and meristics. Characters in bold are significantly different between forms. (n.) = normal form; (d.) = dwarf form.

Character	Relationship	*P*	
standard length	**normal > dwarf**	**<.0001**	**means 250 (n.) and 151 (d.) mm**
gillraker 1	normal = dwarf	>.05	
upper jaw	normal = dwarf	>.01	
orbit	**normal > dwarf**	**<.01**	
head	normal = dwarf	>.01	
snout	normal = dwarf	>.05	
truss 1	normal = dwarf	>.05	
truss 2	normal = dwarf	>.01	
truss 3	**normal > dwarf**	**<.001**	
truss 4	normal = dwarf	>.05	
truss 5	**normal < dwarf**	**<.0001**	
truss 6	normal = dwarf	>.01	
truss 7	**normal < dwarf**	**<.01**	
truss 8	normal = dwarf	>.05	
truss 9	normal = dwarf	>.05	
truss 10	normal = dwarf	>.05	
truss 11	normal = dwarf	>.05	
truss 12	normal = dwarf	>.05	
truss 13	normal = dwarf	>.05	
truss 14	normal = dwarf	>.05	
truss 15	**normal > dwarf**	**<.01**	
truss 16	**normal > dwarf**	**<.01**	
truss 17	normal = dwarf	>.01	
truss 18	**normal > dwarf**	**<.01**	
truss 19	normal = dwarf	>.01	
truss 20	**normal > dwarf**	**<.001**	
truss 21	normal = dwarf	>.05	
truss 22	normal = dwarf	>.05	
truss 23	normal = dwarf	>.05	
total gillrakers	**normal > dwarf**	**<.0001**	**modes 46 (n.) & 53 (d.)**
total dorsal fin rays	normal = dwarf	>.05	modes 13 (n.) & 13 (d.)
pelvic fin rays	normal =dwarf	>.05	modes 12 (n.) & 12 (d.)
anal fin rays	normal = dwarf	>.05	modes 15 (n.) & 14 (d.)
pectoral fin rays	normal = dwarf	>.05	modes 17 (n.) & 16 (d.)
lateral line scales	normal = dwarf	>.05	modes 69 (n.) & 68 (d.)

groups demonstrated a highly significant difference between means ($P<.0001$). Modal gillraker counts were 47 (42-50) for the "dwarf" form (n=26) and 52 (49-53) for the "normal" form (n=13). However, the gillraker frequency distribution for the entire sample (n=45 - including unclassifiable specimens) does not exhibit bimodality (Fig. 22). Morphometrics suggested the normal form has a deeper body (truss 15, 16, 18, and 20), a shorter caudal peduncle (truss 5 and 7), a longer dorsal fin base (truss 3), and a larger eye than the dwarf form. Other than total gillraker number, none of the meristic characters was significantly different between forms.

Allometry

Slopes of the log/log regressions of morphometric characters on standard length are shown in Table 22. The overall allometry patterns were distinct between forms. The normal form was negatively allometric around the head region while remaining essentially

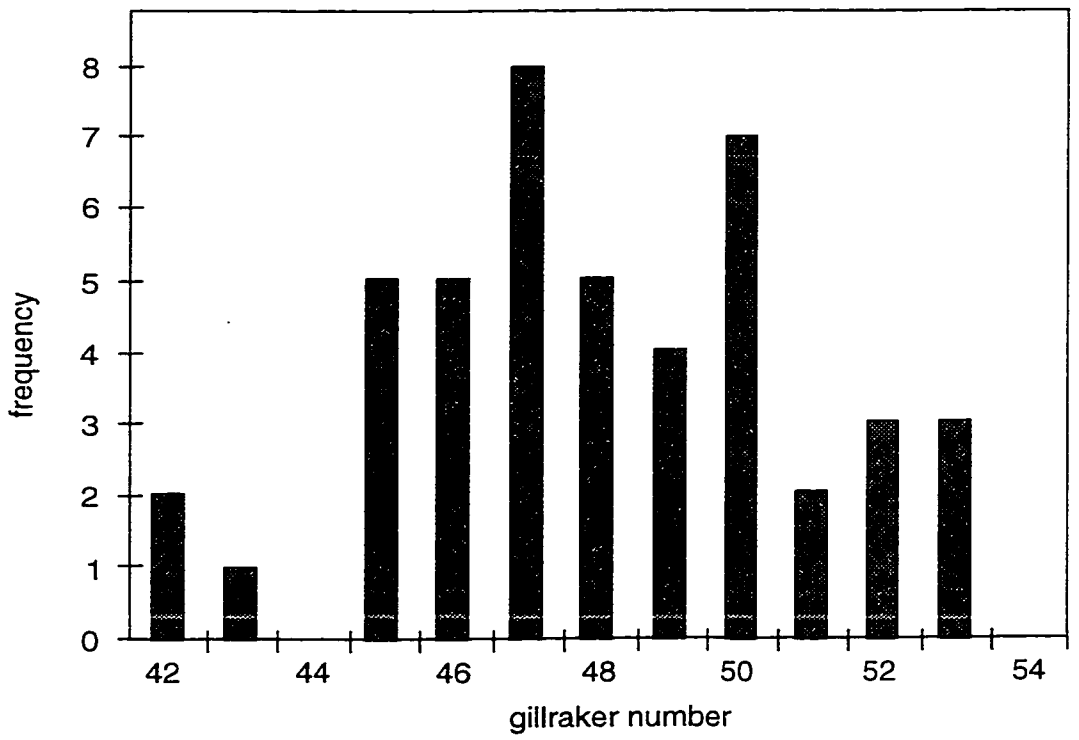

Figure 22. Gillraker number frequency distribution for Unnamed Lake ciscoes.

isometric throughout the remainder of the body. This is the common condition observed in many species of fishes. The dwarf form, on the other hand, was nearly isometric or positively allometric anteriorly (including orbit size) but negatively allometric with respect to characters related to body depth. This suggests the dwarf form becomes proportionally more slender as it grows. The negative allometry in orbit size of the normal form was not reflected in the differences between the dwarf and normal populations; the normal form had significantly larger eyes than the dwarf. This was considered a taxonomically useful character and used in multivariate analyses. However, truss 5 appeared negatively allometric in the dwarf form, and was indeed found to be smaller in the population of normal individuals. This consistency with the allometric relationship renders this character of questionable taxonomic value.

Sexual Dimorphism

Three of the characters examined showed statistically significant sexual dimorphism ($P<.05$) (Table 24). All of these (truss 19, 20, and 22), in combination with a not quite significant difference in truss 6, suggested that males have a deeper caudal peduncle than females.

Multivariate Analysis

A Principal Components Analysis was conducted using 19 measurements (Table 25). Plots of individual component scores on axes 1 and 2 demonstrated incomplete separation of forms on axis 1 (Fig. 23). Eigenvectors for axes 1 and 2 are shown in Table 25.

Conclusion

The two forms of cisco in Unnamed Lake are rather similar morphologically. While eight morphometric characters were found to differ between forms, the significance levels were much lower in these populations than in other populations examined. Gillraker

Table 24. Summary of sexual dimorphism in Unnamed Lake ciscoes (both forms combined). Characters in bold are significantly different between sexes ($P<.05$).

Character	*P*	Relationship
standard length	>.05	
gillraker 1	>.05	
upper jaw	>.05	
orbit	>.05	
head	>.05	
snout	>.05	
truss 1	>.05	
truss 2	>.05	
truss 3	>.05	
truss 4	>.05	
truss 5	>.05	
truss 6	>.05	
truss 7	>.05	
truss 8	>.05	
truss 9	>.05	
truss 11	>.05	
truss 12	>.05	
truss 13	>.05	
truss 14	>.05	
truss 15	>.05	
truss 16	>.05	
truss 17	>.05	
truss 18	>.05	
truss 19	**0.02**	**females smaller**
truss 20	**0.01**	**females smaller**
truss 21	>.05	
truss 22	**0.03**	**females smaller**
truss 23	>.05	
total gillrakers	>.05	
total dorsal fin rays	>.05	
pelvic fin rays	>.05	
anal fin rays	>.05	
pectoral fin rays	>.05	
lateral line scales	>.05	

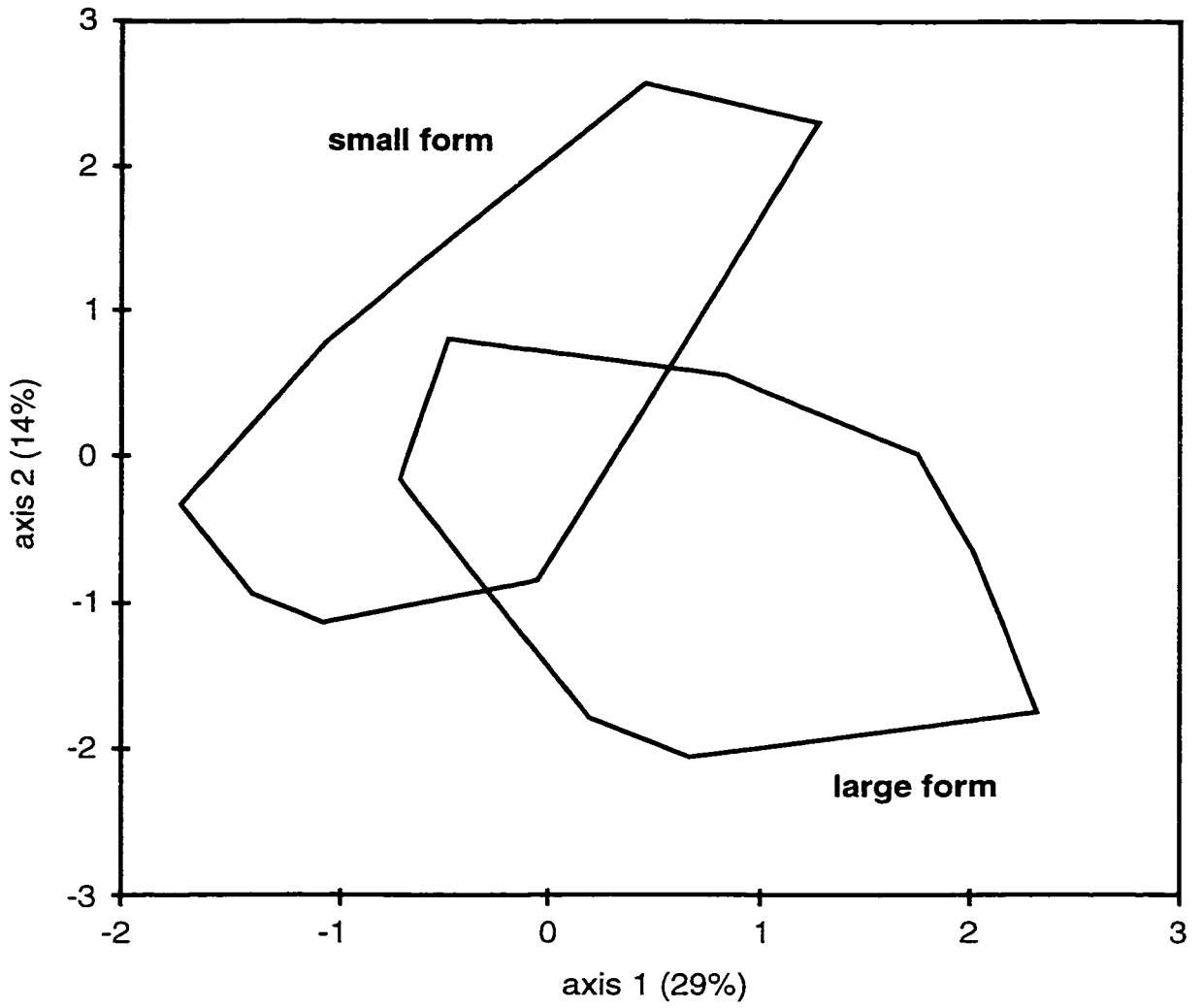

Figure 23. Scores on principal components 1 and 2 for Unnamed Lake ciscoes based on 19 morphometric characters.

Table 25. Eigenvalues and eigenvectors from the first two principal components based on 19 morphometric characters from Unnamed Lake ciscoes.

Eigenvalue	1	2
% of variability.	29	14
Cumulated %	29	43
Vectors :	1	2
truss 1	0.766	0.451
truss 2	-0.494	0.722
truss 3	0.711	-0.385
truss 4	-0.380	0.339
truss 5	-0.424	0.156
truss 6	0.488	-0.198
truss 7	-0.539	-0.129
truss 8	0.329	0.008
truss 9	-0.059	-0.351
truss 10	-0.393	0.166
truss 11	0.736	-0.054
truss 12	0.639	-0.069
truss 14	-0.244	0.727
truss 15	0.513	-0.323
truss 20	0.662	-0.293
gillraker 2	0.269	0.456
upper jaw	0.728	0.441
snout	0.218	0.345
head	0.778	0.490

counts for all specimens were well within the range of *C. artedi.* The extensive overlap in gillraker number suggests intermediate forms were common and reproductive isolation is probably incomplete. It appears likely that these populations represent an early stage of intralacustrine divergence of an ancestral *C. artedi* population. It is also possible that the disruptive selection pressures that drive sympatric divergence may be relaxed in this lake due to dynamics of food abundance, niche heterogeneity, and population size. The latter may be affected by predator abundance as this is the only lake studied that contained *Salvelinus namaycush* (lake trout).

Morphological Overview of all Northeastern Alberta Cisco Populations Examined

Characters useful for characterizing the morphology of each Alberta cisco population were apparent from the ANOVA pairwise comparisons shown in Appendix 1. Gillraker length and orbit diameter were significantly smaller and upper jaw significantly longer in the Barrow Lake low gillraker ciscoes than in any other population. The Bocquene Lake superior form (putative *C. sardinella*) had the shortest snout to occiput length (truss 1) and shallowest head (truss 12) of any population. The Ryan Lake high gillraker form had the deepest head (truss 12). Daly Lake ciscoes had the shortest distance from the base of the adipose fin to the first dorsal procurrent ray. Myers Lake specimens had the shortest upper jaw length and the greatest distance between the origin of the anal fin and the anterior base of the pelvic fin. Following is a brief summary of some of the key features of each population.

Myers Lake (Plate 9)

This form had a modal gillraker count of 49 (45-56; n=85). There was no evidence of bimodality in gillraker number frequency in this population (Fig. 24). Myers Lake ciscoes were moderately sized (mean SL=230.5 mm; max=273 mm) with a small upper jaw, short cranium, large dorsal fin base, large pelvic to anal fin distance, and an overall deep body.

Ryan Lake high gillraker form (Plate 3)

This form had a modal gillraker count of 56 (50-62; n=62), the highest of all populations examined. This was also the largest form encountered (mean SL=316 mm; max=413 mm). It was characterized by a long and deep head (premaxillary to posterior margin of operculum) and overall deep body. This form closely matches the description of *Leucichthys nipigon* (Koelz 1929), a species now synonymized with *C. artedi* (Scott

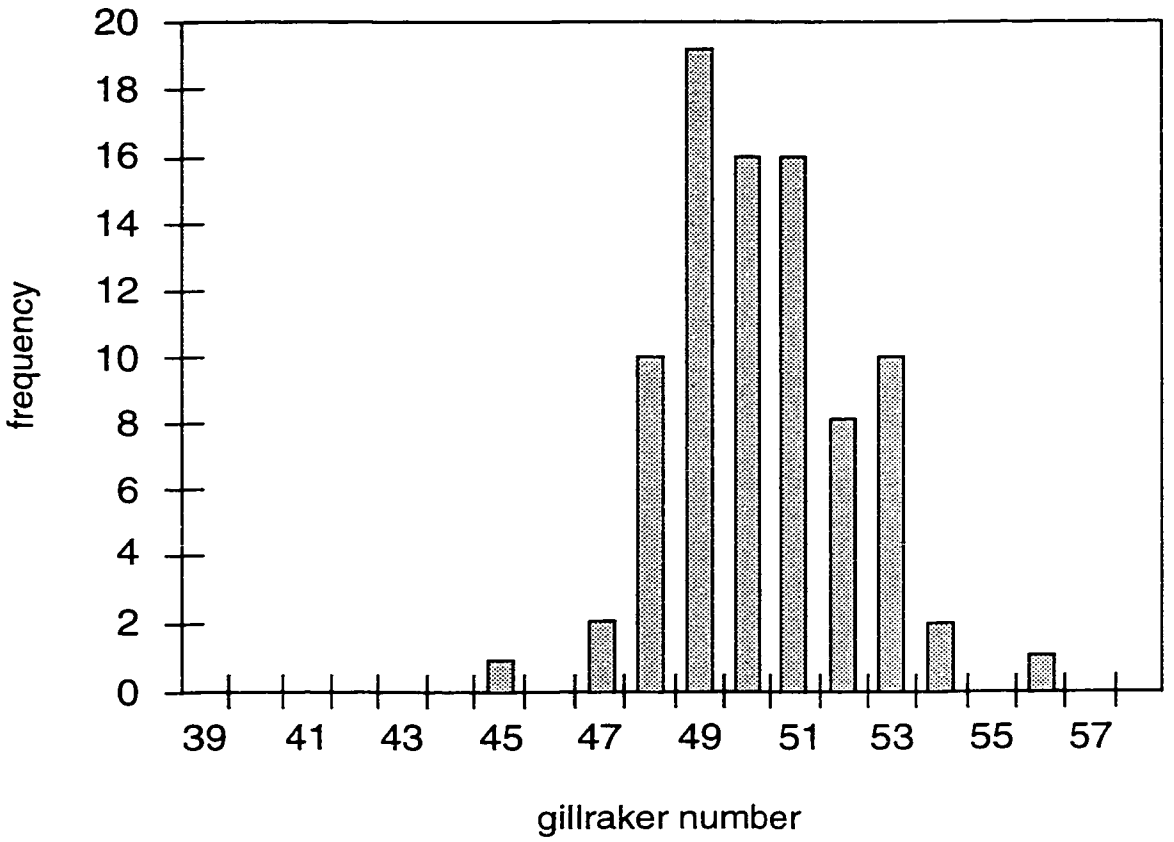

Figure 24. Gillraker number frequency distribution for Myers Lake ciscoes.

and Crossman 1973). Koelz (1929) described *C. nipigon* as the largest of all "species" of *Leucichthys* (the largest specimen observed was 447 mm with specimens over 300 mm common) with 54-66 gillrakers, a deep, compressed body, and long head.

Ryan Lake low gillraker form (Plate 4)

This form had a modal gillraker count of 45 (44-51; n=15). This is a small form (mean SL=165 mm; max=200 mm) that was unremarkable in any of the characters examined. It is interesting to note that despite differing greatly from the sympatric high gillraker form in number of gillrakers, these structures were not significantly different in length between forms.

Bocquene Lake "superior" form (Plate 5)

Phenotypically, this population resembled the non-anadromous form of *C. sardinella*. Specimens examined had a modal gillraker count of 49 (45-53; n=27). They were rather small in size (mean SL=164.4 mm; max=218 mm) with a short head, slender body, and relatively short gillrakers, dorsal fin base, and upper jaw. The mouth was distinctly superior (lower jaw never included in upper) and the dentary was strongly curved along its anteroventral margin. Overall, the anterior portion of the body appeared to be shortened and the posterior portion elongated resulting in the relatively anterior-positioned pelvic fin diagnostic of *C. sardinella*. The distance from the snout to the pelvic fin base was less than the distance from the pelvic fin base to the caudal flexure (McPhail and Lindsey 1970) in 22 of 27 specimens examined (mean ratio of pre-pelvic to post-pelvic distance=.978, SD=.036). This is compared to 3 of 29 specimens of the sympatric terminal (*C. artedi*) form (mean ratio of pre-pelvic to post-pelvic distance=1.07, SD=.048). Differences between means were highly significant (t-test, $P<.0001$). Examination of comparative *C. sardinella* is needed to verify the correct taxonomic placement of this form.

Bocquene Lake "terminal" form (Plate 6)

Samples from this population exhibited a modal gillraker count of 53 (49-57; n=30). They appear to be a small (mean SL=153.7 mm; max =178mm) and slender-bodied but otherwise unremarkable form of *C. artedi*.

Daly Lake (Plate 10)

The sample of Daly Lake ciscoes had a modal gillraker count of 51 (48-57; n=21). The gillraker number frequency distribution was unimodal (Fig. 25). This morphotype was of moderate size (mean SL=204 mm; max=308 mm) with an adipose fin positioned relatively far back on the body (short truss 5) and a short pelvic fin to anal fin distance (truss 9).

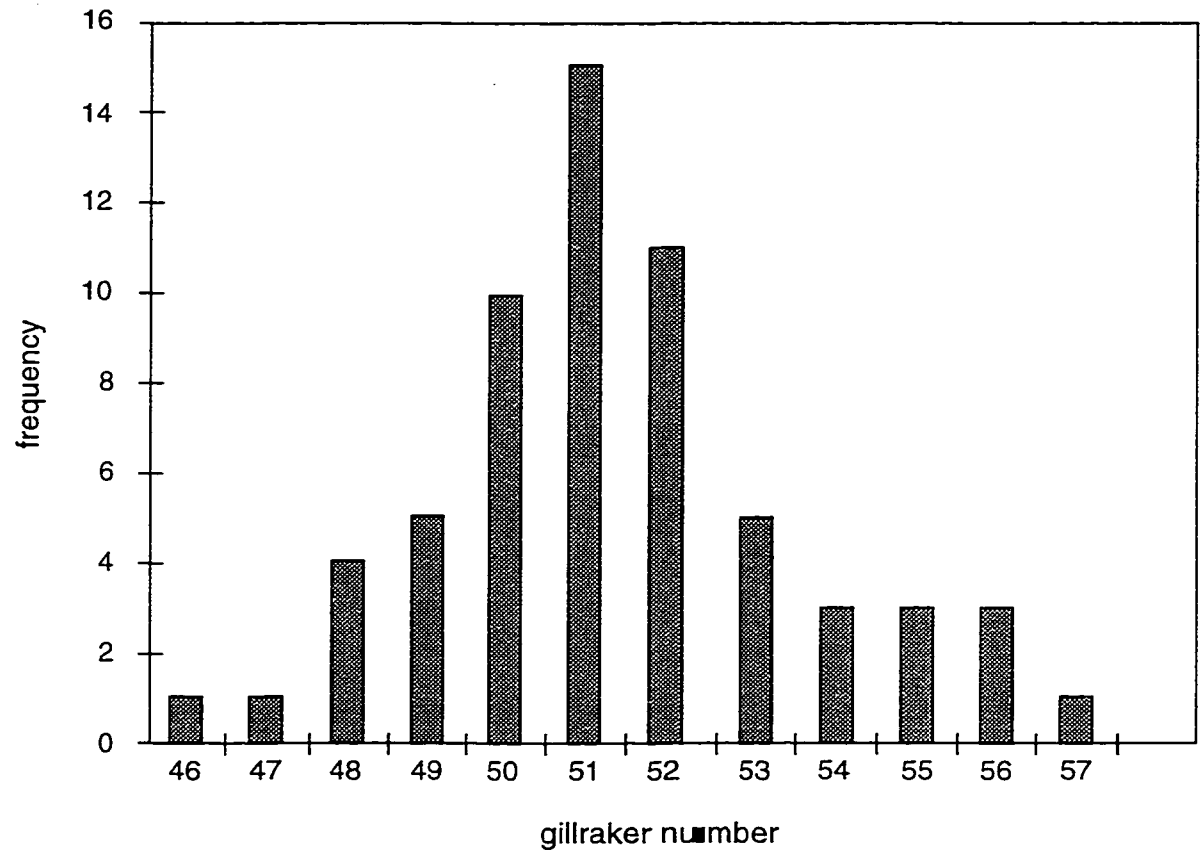

Figure 25. Gillraker number frequency distribution for Daly Lake ciscoes.

Unnamed Lake (Plates 7 and 8)

The ciscoes in this lake appeared to represent two populations, a dwarf and a normal form which, despite size at age differences, were morphologically similar. The two putative populations had modal gillraker counts of 47 ("dwarf" form) and 52 ("normal" form) but there was much overlap between forms. These populations were combined for inter-lake comparisons. Overall, the ciscoes in this lake had a slender head and body, short dorsal fin, short cranium and a small eye. Further work is required to establish the degree of reproductive isolation between these forms.

Discussion

Factors Confounding the Interpretation of Morphological Data

Phenotypic Plasticity

Estimating the relative contribution of genetic control and environmental modification of morphological characters has been a fundamental problem in coregonine taxonomy. Selecting characters that reveal the true evolutionary history of a taxon is the goal of all taxonomists. However, it can be difficult to identify those attributes resulting from identity by descent when these are confounded by the "noise" created by local adaptations and plasticity. Experimental studies in which eggs or fry of known genotype fishes were transplanted into environments different from those of their parents have been used to test for heritability of characters (Svardson 1965, Loch 1974, Todd 1998). Traditionally, gillraker number has proven relatively stable in these situations and has been considered a useful taxonomic trait. However, this character also can vary when subjected to environmental changes (Lindsey 1981, Todd 1998). The severity of these changes may explain in part the seemingly contradictory results obtained in experimental studies. Svardson (1965) and Loch (1974) studied whitefishes transplanted from one natural environment to another quite different natural environment. In these studies, no significant difference in gillraker number was found between transplants and the parent population. However, in studies where fishes have been transplanted from a natural environment to aquaria (McCart and Andersen 1967, Todd et al. 1981, Todd 1998), significant differences in gillraker number were reported, although the patterns of change within and among species are inconsistent. It may be that aquarium rearing represents an unnaturally severe environmental change that may cause modifications to a degree rarely, if ever, found in nature. While these studies provide definitive proof that a character can change without concomitant genetic change, the real questions in coregonine taxonomy are: 1) what is the magnitude of plasticity of these characters under natural

conditions, and 2) is this plasticity sufficient to mask completely the evolutionarily significant morphological differences resulting from genetic changes? The first step in addressing these questions is to understand how phenotypic plasticity works.

Mechanisms of Phenotypic Plasticity

Plasticity is defined as phenotypic variation across environments in the absence of genotypic differences. Schlichting and Pigliucci (1998) point out that this process is distinct from developmental instability which can result in variation within a single environment. Apparently distinct species may represent the results of a flexible reaction to different environmental conditions. Ultimately, the expression of the genotype (the phenotype) is a combination of the genetic background modified by complex interactions among genes and gene products and the environment to produce a viable, integrated organism. The set of phenotypes resulting from the multitude of interactions and possible outcomes has been called a "reaction norm" (Schlichting and Pigliucci 1998).

Hypotheses for the molecular basis of phenotypic plasticity across heterogeneous environments include: 1) developmental buffering as a result of heterozygosity (Lerner's homeostasis), 2) allelic sensitivity, and 3) gene regulation (Schlichting and Pigliucci 1998, Wu 1998). Lerner (1954) believed that, in a changing environment, heterozygosity results in developmental homeostasis. This developmental buffering capacity is reduced in the less genetically diverse homozygotes. Such a mechanism is particularly advantageous to organisms inhabiting unpredictable environments. The allelic sensitivity hypothesis suggests a graded response of a particular locus to changes in environmental conditions resulting in phenotypes that fluctuate with the environment. The biophysical effect of temperature on enzyme activity is an example of this type of mechanism. The regulatory gene control hypothesis is based on the epistatic action of "switch" genes. Entire, integrated phenotypes can be produced by the action of a single upstream gene

on groups of structural loci. The developmental switch is usually triggered when a threshold value for some environmental parameter (internal or external) is exceeded. This switch channels development along an alternative pathway that may involve completely different patterns of gene expression. This type of control produces discrete phenotypes that are stable over a range of environmental conditions (Smith 1990). In these cases, phenotypic variation is usually less than that predicted under a simple allelic sensitivity model. That is, the range of intermediate forms expected in a naturally fluctuating environment are absent. Under the regulatory switch model, this pattern need not imply environmental consistency from generation to generation as suggested by Kristofferson and Clayton (1990). In nature, all three genetic control mechanisms probably operate at varying levels simultaneously (Schlichting and Pigliucci 1998).

Phenotypic plasticity itself is also under genetic control and there is genetic variation, within and among species and populations, for phenotypic lability in changing environments (Schlichting and Pigliucci 1998). Models that predict the evolution of the capacity for plasticity versus the evolution of specialized phenotypes are based on the stability and predictability of the environment. When environmental conditions change frequently, with stressful conditions alternating with normal conditions, a phenotypically plastic "generalist" strategy is the optimal means of coping (Bradshaw and Hardwick 1989). Specialists are more likely to evolve in stable and predictable environments. The highly plastic coregonines appear to have adopted the former strategy probably in response to the rigors of survival in the variable arctic and temperate environments that were subjected to extreme climatic variation during the Pleistocene.

Recognizing Plasticity

Understanding that phenotypic plasticity need not be a simple, direct relationship between the magnitude and direction of environmental change and the pattern of

morphological variation makes uncovering its effects particularly difficult. Under the "traditional" allelic sensitivity model, correlations between environmental parameters and character states over space and time may reveal consistent patterns of cause and effect. Careful monitoring and analysis of morphological and environmental covariation, combined with experimental manipulation, might provide reasonable insights into the relative contribution of the environment to the morphological condition.

However, plasticity through upstream gene regulation could potentially produce two stable, phenotypically distinct morphs with almost identical genotypes. Depending on the nature of the environmentally mediated variation, there is no reason to believe these could not be reproductively isolated. With gene flow reduced or eliminated, genetic variation could begin to accrue leading eventually to species level differences. Despite this possible outcome, distinguishing morphs in the early stages of this process from genetically distinct species is problematic if based on morphology alone. Consistent patterns of phenotypic expression in specimens from a wide range of environmental conditions may be the best evidence for genetic control of morphological characters although this too may be confounded by convergence due to niche specialization (see below). Here, analysis of DNA variation is invaluable.

Developmental Instability

Rate of development has been demonstrated experimentally to be correlated with relative sizes and number of body parts (Hubbs 1926, Martin 1949, Taning 1952, Leskela and Kucharczyk 1995, Todd 1998). Generally, decreased developmental rates (resulting in prolonged embryonic development) caused by, for example, low developmental temperatures or high salinities, tend to result in an increased number of body parts such as spines, cirri, scales, and vertebrae. The opposite trend tends to occur in organisms with accelerated development (Hubbs 1926). The size and shape of structures such as

the head, eyes, and fins also appear to be effected by developmental rate (Hubbs 1926, Martin 1949). Hubbs (1926) believed that the enhancement of inhibitory developmental controls occurred concomitantly with accelerated development and, although unable to suppress very early developmental surges, these controls produced an abrupt truncation of later development. The result is greater expression of early products of differentiation and reduction or elimination of the final stages of differentiation to produce a form with juvenile characteristics (paedomorphosis). During protracted development the inhibitory controls are not accentuated and growth and differentiation proceeds farther (e.g., increased development of scales, spines, cirri, and bony plates). However, Tatarko (1968) summarized many contradictory results of studies examining temperature effects on body parts and suggested that there is no consistent relationship between morphological and meristic characters and the temperature at which the fish develops. Undoubtedly, temperature and developmental rate effect morphology but *a priori* assumptions of the magnitude and direction of these effects in nature may not be justified.

Trophic Status

Trophic status is often postulated to influence specific morphological features in a consistent and predictable manner. The relationship between gillraker number, length, and spacing, for example, has been related to prey size or the proportions of benthic versus pelagic food consumed (Clarke 1969, Kliewer 1970, Loch 1974, Bergstrand 1982). The size of the eye and mouth, depth of the body, depth of the head, length and depth of the caudal peduncle, and fin length have also been considered functionally related to trophic status (Gatz 1979, Lindsey 1981, Webb 1984, Malmquist et al. 1992, Snorrason et al. 1994). The number of gillrakers on the first branchial arch appears to be a relatively stable character and has been, and continues to be, used extensively in coregonine systematics. In his classic transplantation experiments, Svardson (1952, 1957, 1965) found no change in mean number of gillrakers in whitefishes transplanted from the Baltic Sea to small

inland lakes in Sweden over time spans of 22 to 80 years. Loch (1974) also found that gillraker number was not significantly different between parents living in a large, deep, northern Manitoba lake and their progeny transplanted as fry into a small, shallow, more southerly lake. However, others (McCart and Anderson 1967, Lindsey 1981, Todd 1998) have shown that this character does seem to change in response to the environment. The prevailing belief seems to be that gillraker number is under some genetic control but phenotypically induced variation can occur, although to a lesser extent than in most morphological characters.

Gillraker variation is usually assumed to be functionally adaptive. Traditional models of prey retention efficiency predict that gillrakers act as passive sieves with more numerous, longer, and more closely spaced rakers capable of filtering finer food particles. Only those particles larger than the inter-raker spacing will be retained by seiving (Rubenstein and Koehl 1977, Drenner et al. 1987, LaBarbera 1984). However, numerous exceptions to the predictions of seive theory have been documented in fishes. Sanderson et al. (1991) determined that the gillrakers of *Orthodon microlepidotus* (Cyprinidae) do not serve as filters at all, but rather deflect water and food particles toward the palatal organ where prey are trapped in mucus. They found that only three of 228 food particles observed through a surgically implanted endoscope were actually retained by gillrakers. Drenner et al. (1987) surgically removed the gillrakers from a test sample of *Tilapia galilaea* (Cichlidae) and found that there was no difference in prey retention efficiency or size selectivity between fish with or without gillrakers. They did not know the function of gillrakers in this species but postulated that they may be involved in mouth brooding. Langeland and Nost (1995) found that prey in stomach contents of whitefish, brown trout and Arctic charr were much smaller than the gillraker spacing and could not have been seived from the water. Seghers (1975) also showed that selection of cladoceran prey by laboratory-raised whitefish was not a function of the

mechanical sieving action of gillrakers. Kliewer (1970) was unable to explain the lack of correlation between absolute food size and absolute gillraker spacing in lake whitefish in Manitoba. He suggested that gillraker characteristics may not influence significantly the kind of food eaten but rather the method of feeding, specifically, how much water is taken in with each food particle. Koelz (1929:330) concluded after examining thousands of Great Lakes ciscoes that "...within the genus *Leucichthys* the relation between the number and form of the gillrakers and the character of the food is very loose." He found that all deepwater forms fed on *Mysis relicta* despite diagnostic differences in gillraker number and morphology. A similar lack of congruence between gillraker morphology and predominant prey was found in the present investigation.

These studies suggest the function of gillrakers in prey retention in particulate feeding fishes remains uncertain (O'Brien 1987) and variable among species. Traditional seiving models have been rejected by some researchers (Langeland and Nost 1995). LaBarbera (1984) believes that if retention efficiency does not decrease dramatically as particle sizes drop below the mesh size, seiving should be discounted as a particle capture mechanism. A more likely mechanism, called the "hydrodynamic retardation model," has been proposed by Chang (1973). This model assumes that retention sites are adhesive and through direct interception, short-range electrostatic attractive forces, and particle inertia, prey items become entrapped at the filter fibers (Rubenstein and Koehl 1977, LaBarbera 1984). Mucus secreted by epithelial cells lining the gillrakers likely plays an important role in prey capture mechanisms in many suspension feeding organisms. White and Bruton (1983) proposed that mucus lining all of the branchial structures was critical in the entrapment of particles smaller than the gillraker spacing in *Gilchristella aestuarius* (Clupeidae). Rubenstein and Koehl (1977) illustrate the flow characteristics and mechanisms of capture of particles of various sizes travelling at various velocities through filters of various densities and fiber sizes. While it might be expected that

several mechanisms operate simultaneously, equations expressing the probability of particle capture predict that, for a given particle size and velocity, only one or two filtration mechanisms predominate. As the volume fraction of fibers in a filter increases (e.g., more gillrakers), direct interception and inertial impaction of particles become the dominant capture mechanisms when intermediate particle sizes and velocities are involved (Rubenstein and Koehl 1977). This is the situation most often encountered by filter feeding fishes. Not only are these mechanisms dependent on the density of the filter but also on the size (diameter) of the fibers. This latter parameter (e.g., gillraker diameter or breadth) appears to be considered much less frequently than filter density (e.g., gillraker number or inter-raker spacing) by many biologists. However, this is an extremely important component of the prey retention models that must be invoked when seive theory is inadequate to explain the empirical results of feeding studies.

Rubenstein and Koehl (1977) enumerated the many variables that affect prey capture in suspension feeding organisms and stressed that most animals are capable of influencing retention efficiencies by altering these parameters. Selecting prey of different sizes or densities, increasing or decreasing flow rates over prey capture structures, and changing the orientation of filter fibers relative to flow lines are some of the means by which filter efficiency can be shifted. Given the complex and dynamic nature of these mechanisms, postulating a simple and consistent relationship between gillraker morphology and trophic status, particularly in the face of conflicting empirical evidence, seems unwarranted. More species-specific experimental work is needed to resolve the mechanisms of prey capture, retention, and ingestion in ciscoes. This knowledge will enhance our understanding of the adaptive pressures that may act on gillrakers to confound their usefulness as taxonomic markers.

In general, it seems imprudent to attribute morphological features solely to trophic niche

specialization based on theoretical models of body mechanics or physiology and to reject *a priori* any historical (evolutionary) component to the structure observed. Proper evaluation of the validity and taxonomic importance of characters in specific taxa requires evidence that is often beyond the scope of taxonomic studies. Careful character- and species-specific experimental manipulations, extrapolated to the natural condition, should form the basis of decisions regarding character selection and weighting. This level of analysis is often not realistic or possible, leaving characters to be judged on the basis of untested, often generalized assumptions. The studies summarized above suggest that these assumptions, and presumably the decisions derived from them, are often wrong. Therefore, in the absence of solid baseline data from which to make reasonably objective decisions, taxonomic analyses might best rely on the expression of evolutionary signal from a larger set of unweighted characters than a handful of traits prone to subjective misinterpretation.

In Barrow Lake, the majority of ciscoes sampled from both the high gillraker and low gillraker populations fed exclusively on *Mysis relicta* (71% and 73% of individuals respectively). In Ryan Lake, the ratio of bentho-pelagic to pelagic food consumed was almost identical in both the dwarf low gillraker form and the normal high gillraker population. Therefore, the data suggest little apparent correlation between adult gillraker number or length and preferred prey in these lakes. However, the data in this study is insufficient to assess the multitude of factors that could offer ecological explanations for the observed pattern of gillraker morphology. For example, food availability and capture efficiency may be most important for the vulnerable early life history stages not examined in this study. Feeding requirements of the young may determine the morphology of trophic structures that persist in the adult. Alternatively, some trophic structures may be adapted to exploit less preferred prey items or a wider range of resources - a condition that may have great survival value when food is scarce. The numerous gillrakers in

the Barrow Lake high gillraker form apparently facilitate capture of planktonic prey (25% plankton in a combined sample of stomach contents) - perhaps an option essentially unavailable to the low gillraker form (3% plankton in stomach contents). The apparent incongruence between morphology and preferred diet has been explained by this mechanism in many species of cichlids (summarized in Galis 1993). It is also possible that dietary divergence occurs between sympatric populations during a portion of the year not sampled (e.g., winter). This could select for variant morphological characters related to feeding or promote adaptive plastic responses with similar phenotypic results. Additional samples taken at regular intervals throughout the year and from all age classes are needed to acquire a fuller understanding of the trophic preferences and requirements of each population.

Interpretations of Coregonine Variation

Experimental studies have demonstrated that coregonine phenotypes can be influenced by the environment. However, the cause and effect relationships between character states, environmental conditions, and growth rates are extremely complex and general conclusions pertaining to natural populations are largely speculative. Hile (1937) found that slow-growing whitefish and cisco populations had proportionally larger body parts (e.g., longer heads and fins) than faster-growing members of the same year class at the same locality. Kozikowska (1961) noted an increase in eye size with reduced water transparency and the increased feeding depth in whitefish. Dymond and Hart (1927) found that shallow water races of fishes in Lake Abitibi, Ontario tended to have deeper, more compressed bodies and longer fins. Clarke (1973) reported that ciscoes from shallow, turbid lakes had ovate (versus terete) body profiles and more pronounced pigmentation. He also speculated that consistent differences in gillraker number, snout length, and jaw length between sympatric *Coregonus artedi* and *Coregonus zenithicus* (= his *C. prognathus*) may be related to the deep-water habitat of *C. zenithicus*.

Conversely, a lack of consistent direction of environmentally induced morphological variation was noted by Koelz (1929) in ciscoes of the Great Lakes. Turgeon et al. (1999) in a recent study of the Lake Nipigon ciscoes also found little correlation between morphology and ecology in this species flock. In their study, the most ecologically divergent forms were the most similar morphologically suggesting that predictions regarding niche parameters based on morphologic attributes are questionable. The population of *C. zenithicus* inhabiting shallow regions of Barrow Lake displayed the same character states suggested by Clarke (1973) as being related to living at great depths. These empirical data call into question proposed obligatory and predictable correlations between morphology and the environment. It seems caution must be exercised when proposing general inferences relating morphology to ecology because the relationship may reflect a substantial amount of evolutionary history.

Turgeon et al. (1999) believed the most plausible explanation for the Lake Nipigon cisco flock was secondary contact between two genetically differentiated lineages (possibly representing *C. zenithicus* and *C. artedi*) followed by extensive phenotypic plasticity in the latter. Incipient ecological speciation could not be confirmed due to a lack of evidence for strong reproductive isolation but neither could it be dismissed. A similar scenario would seem to provide the simplest explanation for the occurrence of cisco morphs in northeastern Alberta. Every population examined in the present study was unique morphologically although the degree of distinctiveness varied. The Barrow Lake low gillraker population exhibited species level differences but it is unlikely that all of the other *C. artedi*-like populations represent different species. It must be assumed that environmental differences among populations have induced local phenotypic variation through limited adaptive genetic divergence or plasticity or, most likely, a combination of both processes. Some minor (racial) genetic adaptations may have arisen in geographically or ecologically isolated populations and these have been modified by environmental

effects to produce the variety of forms observed. Evidence for some genetic divergence in sympatric conspecific populations has been found in preliminary microsatellite DNA data. Contrasts in allele frequencies at three loci revealed differences suggestive of two gene pools in Ryan Lake although both morphotypes are believed to represent *C. artedi* based on morphological criteria. Sample sizes are, as yet, insufficient for meaningful tests of statistical significance (J. Turgeon pers. comm. 1998) but further analyses may confirm that these are incipient species and perhaps permit quantification of genetic divergence and comparisons with divergence estimates among "good" species.

Simple models of adaptive radiation or phenotypic plasticity might predict that similar forms would be expected in lakes with similar environmental conditions. This was not the case in the present study. Barrow Lake and Ryan Lake, for example, have similar basin morphometry and limnology (and are only about 10 km apart) yet the ciscoes found at each site were remarkably dissimilar. The causative environmental factors inducing either genetic or "non-genetic" divergence in these ciscoes are probably numerous and interrelated in such complex ways that elucidation of specific agents is all but impossible. In natural systems, no model can accurately predict the effects of environmental change on a given species (Behnke 1992). Field experiments can provide the preliminary clues needed to narrow the list of possible interacting factors and can guide the laboratory manipulations needed to disentangle the specific causative agents. However, even when controlled experiments are conducted to test hypotheses of environmental mediation, extrapolations to the natural condition must be made cautiously.

It is clear from our current understanding of the multitude of factors affecting the expression of the genotype (epigenetic and environmental influences), that the relationship between the genotype and the phenotype is rather loose. Some believe (Behnke 1970, Lindsey 1988, Bernatchez and Dodson 1990a,b) that species level recognition of

coregonines is only possible through the use of appropriate genetic markers. Phenotypic differences or similarities may simply represent local environmental adjustments with little relation to genetic affinities (Lindsey et al. 1970, Bernatchez and Dodson 1990a, b). However, empirical evidence often demonstrates a rather high congruence in taxonomic conclusions between morphological and genetic data (Kristofferson and Clayton 1990, Reist et al. 1992, Vuorinen et al. 1993, Lu and Bernatchez 1999). This suggests that, given a sufficient number of characters, it is reasonable to expect that some genetic signal is expressed in the morphological dataset.

The Origins of Sympatric Species

Models of Speciation

Numerous models that hypothesize the requisite conditions for multiplication of species have been proposed. Some assume instantaneous speciation via massive genetic changes such as chromosomal rearrangement (stasipatric speciation). While these processes are likely of great importance in the early evolution of the tetraploid salmonids, they are of less theoretical interest here than are mechanisms that promote divergence in the absence of extraordinary genetic events.

Speciation is generally explained by variations on one of three models (Bush 1975). The allopatric model assumes related lineages evolve independently in geographically separate areas. Reproductive isolating mechanisms evolve in each lineage as byproducts of adaptive divergence in the respective isolated habitats. If contact is re-established, these mechanisms prevent interbreeding between populations. In some cases of secondary contact, isolation may be perfected by selection against inferior hybrids. The parapatric model of speciation assumes that species evolve as contiguous populations. Diverging populations are often peripheral and semi-isolated but always maintain a zone of contact with the parent population. Reproductive isolating mechanisms are postulated to arise at the same time as genetically unique individuals derive the ability to penetrate and exploit a new niche (Bush 1975). Some gene flow may occur initially in the zone of contact but disruptive selection at this border may ultimately perfect the isolating mechanisms. This model assumes the species involved have extremely low vagility and is most often invoked to explain speciation in plants and in animals with low dispersal abilities such as molluscs. It is rarely implicated in hypotheses of coregonine speciation. The sympatric speciation model assumes that species diverge and multiply while in the dispersal range of each other. This model assumes strong disruptive selection for genotypes adapted to different niches in a heterogeneous environment. The empirical test of

sympatric speciation is the recognition of sympatric sister species that share unique, derived characters seen nowhere else and that differ primarily in characters related to resource utilization (Smith and Todd 1984, Bernatchez et al. 1996, Chouinard et al. 1996, Pigeon et al. 1997).

Mechanistically, the allopatric speciation model is the simplest and requires the fewest theoretical assumptions. This process is common in almost all groups of sexually reproducing animals (Grant 1963, Mayr 1963, Dobzhansky 1970, Bush 1975) and has been referred to as the "allopatry paradigm" (Rice and Salt 1990). Thus, it might be considered the null hypothesis for lacustrine speciation (Smith and Todd 1984). The criteria for invoking this model to explain the origin of a sympatric pair is based on the recognition of closely-related sister species (either extant or fossil) found outside of the lake. Bernatchez and Dodson (1990a) found distinct geographic patterns of mtDNA clonal lines in lake whitefish from northern Maine. Where dwarf and normal whitefish phenotypes were found in sympatry, they represented members of these relatively widespread groups. Bernatchez and Dodson (1990a) concluded that allopatric speciation followed by secondary contact best explained the origin of these sympatric forms.

The "Fluctuation Hypothesis" of allopatric speciation (Greenwood 1974), a variation of the classical model, may be useful in explaining the post-glacial biogeography of many northern fishes including coregonines. This hypothesis postulates that fluctuating water levels can cause temporary separation and reunification of lake basins. Following allopatric divergence in disjunct daughter lakes, a rise in water level reunites the two populations that have diverged to the point of reproductive isolation. This process would have occurred repeatedly, on various spatial scales, in the several thousand years during and following Pleistocene glaciation. Mayr (1963) believed that the localization of populations by extrinsic barriers within a lake was an important speciational process

consistent with the theory of allopatric speciation. Expansion and contraction of waterbodies over time provides abundant opportunity for temporary geographical separation and acquisition of reproductive isolating mechanisms. With regard to whitefish evolution, he felt that sympatric sibling species are a result of reinvasion following the lifting of a geographical barrier.

Recent advances in our understanding of genetic systems and speciation processes have cast doubts on the universality of allopatric speciation (Bush 1975). The sympatric, or ecological (Schluter 1996) speciation model is now considered by some as the most plausible explanation for the origin of some sympatric species and incipient species (Lindsey et al. 1970, Smith and Todd 1984, Taylor and Bentzen 1993, Bernatchez et al. 1996, Chouinard et al. 1996, Wood and Foote 1996, Pigeon et al. 1997, Hatfield and Schluter 1999). Sympatric speciation is defined as the multiplication of species while each is physically capable of encountering the other with reasonably high frequency (Bush and Howard 1986). Sympatric speciation models assume opportunities for exploiting distinct food resources exist in the local environment (Schluter and McPhail 1993) and that competition forces populations to diverge to exploit these different resources. Under appropriate conditions, disruptive selection (selection for extreme phenotypes) is believed capable of producing a stable, or balanced, genetic polymorphism that could lead to speciation. Maynard Smith (1966) demonstrated that if sympatric polymorphic subpopulations occupy distinct niches in a heterogeneous environment (i.e., they form two distinct entities with independently regulated population sizes), and if different alleles have greater fitnesses in the different environments, then polymorphisms can be maintained. Recently, Dieckmann and Doebeli (1999) have proposed that a resource base need not be distinctly bimodal for disruptive selection (divergence) to occur. Their model demonstrates how, as an initial monomorphic phenotype reaches the carrying capacity of a unimodal resource, intense competition produces selection for

deviation from the crowded optimal phenotype toward forms that exploit less abundant resources. The negative effect of this shift is more than compensated for by reduced competition. Tregenza and Butlin (1999) pointed out that the intial phase of this model, in which directional selection drives the phenotype to a single intermediate form of maximum fitness, is necessary to explain how subsequent divergent phenotypes can be equally favoured. For disruptive selection to proceed, the initial monomorphic phenotype must be intermediate between the extremes otherwise one divergent form is likely to be favored over the other(s) resulting in selection against all but this one alternative (directional selection).

Disruptive selection alone is incapable of producing speciation. Assortative mating and/or habitat selection by females is usually invoked to explain the restriction of gene flow between diverging populations. The tendency of some individuals to mate in the habitat in which they were raised (philopatry), and are presumably best adapted, has been suggested as an important mechanism in the jump from balanced polymorphisms to reproductive isolation and speciation (Maynard Smith 1966, Rice and Salt 1990, Rice and Hostert 1993, Dieckmann and Doebeli 1999). If genes promoting assortative mating (or some non-random reproduction) evolve in association with alleles conferring a strong selective advantage in a given sub-environment, then, assuming some habitat selection by spawning females, reduced gene flow and sympatric speciation may result (Maynard Smith 1966). A barrier to gene flow arises as offspring consistently return to spawn in the habitat selected by their parents (Rice and Salt 1990).

A number of theories have been proposed to explain this necessary association between a mate preference trait and an ecological preference trait. Rice and Hostert (1993) summarized the experimental support for a "divergence-with-gene-flow" speciation model involving pleiotropic or genetically linked non-random mating effects. The

pleiotropic model assumes a single gene is responsible for both the ecological and mating preference traits. The genetic linkage theory proposes that genes for ecological and mating preference are so close together on a chromosome that recombination rarely separates them. Treganza and Butlin (1999) concede that both of these conditions (pleiotropy and linkage) are possible, but are probably rare events that do not plausibly explain the frequency of occurrence of sympatric forms. However, Dieckmann and Doebeli (1999) have suggested that even transient linkage disequilibrium resulting from stochastic processes (drift) may cause a reduction in gene flow sufficient to initiate ecological divergence. If other isolating mechanisms arise independently during this period of isolation, reproductive cohesion can be maintained even if the linkage disequilibrium breaks down.

Artificial selection studies have demonstrated that both pre- and post-zygotic reproductive isolating mechanisms can develop fortuitously as byproducts of adaptations to different environmental conditions (Rice and Salt 1990). There is some evidence that this can occur under relatively weak divergent selection pressures but selection pressures must exceed the homogenizing forces of gene flow. Rice and Hostert (1993) concluded sympatric speciation is genetically feasible whenever isolation evolves the same way that it evolves allopatrically - through pleiotropy/hitchhiking of genes adapting the populations to different environmental conditions. Recent models (Dieckmann and Doebeli 1999, Kondrashov and Kondrashov 1999, Tregenza and Butlin 1999) propose that selection favors covariation among ecological and mate preference traits and that these associations evolve relatively rapidly under conditions of strong intra-specific competition despite some recombination.

The process of sympatric speciation is assumed to be driven primarily by competition - in large part competition for food resources (Smith and Todd 1984). Rosenzweig (1978),

in fact, used the term "competitive speciation" for sympatric species-level divergence. Phenotypes adapt to variations in "fitness peaks" within an environment and competitive pressure from both peaks on the trough separating them can cause extirpation of forms inhabiting this intermediate zone. The result is a gap between phenotypes and restricted gene flow (Rosenzweig 1978). Therefore, species that have arisen sympatrically are expected to show little, if any, interspecific competition (Bush 1975). This is because divergence is the mechanism for escaping or reducing competition. Conversely, species derived in allopatry that come into secondary contact may be reproductively isolated yet show little ecological divergence (West-Eberhard 1989).

Convincing empirical evidence supporting all of the requisite conditions for sympatric speciation in nature is limited. However, in species where spawning behaviour is well documented and directly observable, such as in *Oncorhychus nerka* (sockeye salmon), it appears the necessary conditions are met. Here, sympatric forms of sockeye salmon and kokanee (anadromous and nonanadromous forms of *O. nerka*) appear genetically distinct (although not at the species level) and reproductively isolated despite broad temporal and spatial overlap in spawning activity. Interbreeding between forms is known to occur to some extent yet they remain distinct (Wood and Foote 1996). In this case, it is obvious that niche differences between the anadromous and nonanadromous forms are substantial. It is, therefore, reasonable to expect that selection pressures and fitness peaks would be equally distinct. Under these conditions, sympatric speciation is plausible.

Sympatric speciation theory is not without its opponents. Explanatory models are based on several assumptions and have often been rejected because of theoretical mechanistic difficulties (Mayr 1963). Svardson (1949) believed that ecological isolation between sympatric populations of the same species probably could never be so complete as

speciation requires. Mayr (1963) believed that in virtually every case where ecological speciation has been proposed, reevaluation has shown that the facts have been misinterpreted. He points out what he perceives as flaws in the sympatric speciation assumptions: 1) Homogamy (assortative mate selection) is rare if it exists at all. Where mild homogamy exists there is still enough gene flow to prevent speciation. 2) Linkage of mate preference and habitat preference, and the assumption that progeny of a founder of a new niche will mate only with descendents of the founder, is a gross oversimplification of natural processes and ignores the effect of dispersal. 3) Preadaptation and niche selection, in which individuals actively search for niches for which they are best preadapted genetically, usually only occurs in a general way and is influenced by non-genetic factors (e.g., conditioning). Mayr (1963:471) concludes "...it would require a veritable systemic mutation to achieve the simultaneous appearance of a genetic preference for a new niche, a special adaptedness for this niche, and a preference for mates with similar niche preference. The known facts do not support these assumptions."

Empirical evidence supporting either sympatric or allopatric speciation can be obtained from population affinity inferences based on shared characters states. Sympatric morphotypes that share unique, apparently derived characters found nowhere else are considered support for an hypothesis of the process of sympatric speciation (Lindsey et al. 1970, Smith and Todd 1984, Bodaly et al. 1992, Pigeon et al. 1997). Sympatrically diverged morphotypes, derived from a single common ancestor (i.e., monophyletic) would be expected to form population clusters that appear more closely related to each other than to any allopatric populations (Smith and Todd 1984, Pigeon et al. 1997). If a member of a sympatric pair shows closer affinity to allopatric populations, a scenario of divergence prior to independent colonization of the waterbody is indicated.

Sympatrically derived forms are also often considered recognizable by differences in

traits related to trophic status (Malmquist et al. 1992, Smith and Todd 1994, Snorrason et al. 1994, Lu and Bernatchez 1999). However, as discussed above, determining which traits, in a functionally integrated phenotype under natural conditions, have little or no relation to any aspect of competition or trophic status is often speculative. Smith and Todd (1984), for example, found strong divergence in ecologically important characters like gillraker and mouth morphology among both allopatric and sympatric ciscoes in the Great Lakes. Therefore, *a priori* character weighting, based on the theoretical or speculated importance of individual traits to some aspect of competition or trophic status seems tenuous. Characters important in feeding optimization are potentially under strong selective and environmental pressures whether derived in allopatry or sympatry. Recognizing whether a trait originated or diverged allopatrically or sympatrically may be difficult in practice.

Speculated Origins of Northeastern Alberta Ciscoes

The ecological evidence in this study, while limited, suggests that several dimensions of a multidimensional niche space overlap between the forms of cisco in Barrow and Ryan lakes. Sympatric forms appear to feed on similar prey items through much of the growing season and spatial overlap is extensive through this time period. The available evidence suggests it is not appropriate to refer to one form of Barrow Lake cisco as "benthic" and the other form as "limnetic" as has been proposed for sympatric *Gasterosteus aculeatus* (threespine stickleback) (McPhail 1983, Hatfield and Schluter 1999, Vamosi and Schluter 1999) and *Salvelinus alpinus* (Arctic charr) (Malmquist et al. 1992, Snorrason et al. 1994). Use of a shallow water niche by the Barrow Lake *C. zenithicus,* is in contrast to the "typical" deepwater habitat of this species in the Great Lakes (Koelz 1929) and George Lake, Manitoba (J. Reist, pers. comm.). This results in broad sympatry with *C. artedi* and, in fact, an apparent reversal in depth distribution with *C. artedi* found at the greatest depths in the lake. No doubt, subtle niche differences do exist between these

forms. The principles of Competitive Exclusion (Gause 1934) and Limiting Similarity predict that no two species can coexist at the same locality if they have identical ecological requirements. However, sympatric speciation models assume large selective differences between niches (Maynard Smith 1966). These models predict that subtle niche shifts are unlikely to drive sympatric divergence to the species level.

Additional work is required to assess the severity of competition between the sympatric plankton-feeding ciscoes in northern Alberta. Mayr (1963) claimed that little evidence for competition or exclusion among plantkton-feeding pelagic fishes exists, at least in the marine environment. This raises the question of how limiting a planktonic food resource is and when do these limitations exert the greatest competitive pressure. Pianka (1976) cautions that niche overlap need not lead to competition unless resources are in short supply. He suggests it may be more realistic to assess competition along a gradient of intensity rather than as an all-or-none phenomenon. Even if the supply of a common resource is significantly less than the demand, organisms can minimize competition by increasing niche separation along other dimensions of the n-dimensional resource utilization spectrum. The number of possible alternative dimensions, or niche breadth, is, by definition, relatively large in generalist species like the coregonines. However, Pianka's (1976) Niche Overlap Theory predicts that maximal tolerable overlap will be lower in intensely competitive situations. Smith and Todd (1984) point out that sympatrically derived populations can overlap occasionally with respect to food and space requirements, providing they are reproductively allopatric or allochronic, but secondary contact of allopatrically derived forms usually results in much greater potential for competition.

Increasingly complex models of competitive speciation require data from many dimensions of an organism's niche space to thoroughly understand the dynamics of competitive

interactions within and between populations. It is possible that the Barrow and Ryan lake sympatric ciscoes have responded morphologically to exploit different resources when food is scarce (e.g., winter). Competition may be much higher at this time than during the growing season. While food is an important controlling factor in competitive situations, many other parameters must also be considered in a thorough assessment of competition. The ecological data in this study are presented only as a suggestion that the ecological distinction between cisco forms in the lakes examined is not obvious.

Based on the available evidence, it seems most plausible that the ciscoes in Barrow Lake represent two species that independently colonized this water body and are secondarily coexisting with much ecological overlap. This overlap seems greater than that expected if the forms had diverged sympatrically. It may be that *C. zenithicus* is a competitively inferior form (as suggested by its low population size) that persists only under temporally changing environmental conditions that periodically alter the relative competitive abilities of component species (Hutchinson 1961).

The multivariate analyses in this study suggest the nominal *C. zenithicus* in Barrow Lake is more similar morphologically to allopatric populations of known *C. zenithicus* than to the sympatric population of *C. artedi*. Additional support for a theory of independent colonization would include the discovery of allopatric conspecifics in the same geographic vicinity. No forms equivalent to *C. zenithicus* were found in any of the six lakes surveyed near Barrow Lake; however, these represent a small proportion of the fish-producing water bodies in the area. Harper and Nichols (1919) reported what some now believe to be *C. zenithicus* (= their *Leucichthys entomophagus*) in the Tazin River approximately 130 km north of Barrow Lake. Dymond and Pritchard (1930) felt there was no doubt that the form they identified as *C. zenithicus* in Lake Athabasca was descended from the same ancestors as the Great Lakes *C. zenithicus*. These are the nearest

known allopatric populations of putative *C. zenithicus* to Barrow Lake and may lend support to the independent colonization hypothesis if their identities can be confirmed.

Despite important similarities, several characters were notably different between the Barrow Lake putative *C. zenithicus* and known populations of this species across North America. The largest Barrow Lake specimen (467 mm fork length), reported by Paterson (1969), was much larger than any other *C. zenithicus* specimen examined. Clarke (1973) found the Barrow Lake low gillraker form was the largest of his "low group" (which he called *C. prognathus*) in Canada. The largest *C. zenithicus* measured by Koelz (1929) from the Great Lakes was 332 mm in length. The Barrow Lake *C. zenithicus* also had an exceptionally long dorsal fin base; the range of variation overlapping little with *C. zenithicus* specimens examined (Fig. 11). Dymond and Pritchard (1930) reported that *C. zenithicus* typically has a very short dorsal fin base. In addition, the Barrow Lake low gillraker form had shorter gillrakers than most other *C. zenithicus* populations examined; however, short gillrakers are apparently also known from several populations not examined in this study (T. Todd pers. comm. 1998).

Most of the populations examined in this study, representing both *C. zenithicus* and *C. artedi*, exhibit some unique quantitative traits. Given the extent of phenotypic plasticity known in coregonines, it does not seem reasonable to suggest that these are all distinct species. The challenge is to disentangle the phenotypic "noise" from the evolutionary "signal" useful for delimiting species and elucidating their historical relationships. A more accurate assessment of the distinctiveness of the Barrow Lake population will require examination of additional *C. zenithicus* populations. For now, it seems most plausible that the morphological differences between the Barrow Lake low gillraker cisco and other *C. zenithicus* populations represent local modifications of a common form. In addition to a greater understanding of the morphological variation in *C. zenithicus*

from throughout its range, further investigation is needed to establish the genetic basis (validity) of these divergent characters before proceeding to an assessment of whether they may represent species level differences (i.e., a new species in Barrow Lake). The consistency with which traits such as gillraker number, upper jaw length, and head length and depth have been used to identify *C. zenithicus* may justify ascribing extra weight to their taxonomic significance. Clarke (1973) felt these morphological similarities, particularly gillraker number, should be interpreted as evidence of monophyly. The genetic data presented in this study, while inconclusive, is consistent with that of Bodaly et al. (1998), Reist et al. (1998), and Reed et al. (1998) in demonstrating no meaningful differences between *C. artedi* and *C. zenithicus* in the portion of the mitochondrial genome sequenced. These data, therefore, do not conflict with the morphological conclusion that the most reasonable taxonomic placement of the Barrow Lake low gillraker cisco appears to be *C. zenithicus*.

Morphologically, both ciscoes in Ryan Lake appear to represent *C. artedi*. Based on the available evidence, it is not possible to make an objective choice between a scenario of post-glacial intralacustrine divergence and one of independent colonization of distinct morphs of *C. artedi* that differentiated prior to, or during, post-glacial dispersal. A high degree of niche overlap between sympatric forms and the similarity of the high gillraker form with the widespread *C. nipigon* (synonymized with *C. artedi* by Scott and Crossman in 1973) perhaps favours the latter explanation. Undoubtedly, many morphologically distinct and at least partially reproductively isolated forms of *C. artedi* existed prior to post-Pleistocene dispersal. Reports of the distinctive, large bodied and high gillrakered *C. nipigon* from inland waters across north-central Canada raises the possibility that this form may have arisen prior to post-glacial colonization. However, microsatellite DNA variation does not support the hypothesis that *C. nipigon* differentiated from *C. artedi* any earlier than other morphotypes of the *C. artedi* complex (Turgeon et al. 1999).

The two cisco forms in Unnamed Lake appear less differentiated morphologically than the other sympatric populations examined. As in Ryan Lake, it is not possible to suggest, based on the available evidence, whether these forms of *C. artedi* diverged prior to or following colonization of the lake. Minimal differentiation may favour a scenario of recent intralacustrine divergence.

One member of the sympatric cisco pair in Bocquene Lake seems to be *C. sardinella*. This species has never been reported from Alberta but it is known from Great Slave Lake, Northwest Territories (K. Howland pers. comm. 1997). There should be little impediment to its access into northern Alberta via the Slave River. The Bocquene River, connecting Bocquene Lake with the Slave River, is one of few major watercourses in the Precambrian Shield of Alberta. Although not studied in detail, it appears to provide better habitat and a far more likely dispersal avenue for ciscoes than, for example, Ryan Creek which connects Barrow and Ryan lakes to the Slave River (see study area section in Methods). It is quite plausible that *C. sardinella* may have gained access to Bocquene Lake in relatively recent times. An assessment of the ecological overlap between this putative *C. sardinella* and the symptric *C. artedi* awaits further investigation.

Proposed Origins of Other Sympatric Coregonines

Reports of sympatric coregonines are relatively common (Kennedy 1943, Fenderson 1964, Lindsey 1963, Schweitzer 1968, Clarke 1969, Lindsey et al. 1970, Bodaly 1979, Kirkpatrick and Selander 1979, Mann and McCart 1981, Smith and Todd 1984, Bernatchez and Dodson 1990, Bodaly et al. 1992, Shields et al. 1992, Vuorinen et al. 1993, Bernatchez et al. 1996, Pigeon et al. 1997) but conclusions regarding their origins and evolutionary relationships differ among localities. Evidence for allopatric divergence with secondary contact and for sympatric divergence has been presented. Lindsey (1963) felt members of the sympatric pair of *C. clupeaformis* in Squanga Lake, Yukon

likely arose in separate glacial refugia. Bernatchez and Dodson (1990a) and Vuorinen et al. (1993) also believed, based on mtDNA evidence, that sympatric dwarf and normal forms of whitefish in the Allegash Basin of Maine and in Como Lake, Ontario were representatives of different glacial races. However, Bodaly et al. (1992) reported that sympatric whitefish pairs in Yukon, Ontario, and Labrador were derived from a single glacial race, either originating in the Bering or Mississippi-Missouri glacial refugia, and that there was no evidence of secondary contact between races. They suggested that the process of divergence in lake whitefish of the Allegash Basin (allopatric with secondary contact) was different from that producing sympatric populations in Yukon, Ontario, and Labrador (sympatric divergence). Pigeon et al. (1997) also found that mtDNA variation patterns in whitefish from Quebec and northern Maine supported an hypothesis of sympatric divergence and polyphyly of dwarf and normal forms.

It appears the origin of sympatric coregonines varies depending on a variety of factors including geographic influences (including patterns of Pleistocene glaciation and deglaciation), habitat heterogeneity, and probably stochastic events. The complex interaction of a multitude of factors producing a variety of outcomes would be expected in the tumultuous and dynamic environmental conditions during and following the Pleistocene. Each sympatric situation must be analysed individually before any large-scale trends can be assessed.

Genetics of Barrow Lake Ciscoes

Variable levels of genetic divergence have been reported in coregonine populations across North America. Mitochondrial DNA has been considered particularly useful in elucidating relationships among closely related organisms due to its rapid rate of evolution. Brown et al. (1979) estimated nucleotide substitution rates in mammalian mtDNA were 5-10 times faster than in nuclear DNA and the d-loop in the control region of the

mtDNA molecule has been shown in humans to evolve as much as five times faster than protein coding regions (Brown 1985). Despite this resolving power, closely related coregonine species typically demonstrate low levels of genetic variation. Snyder et al. (1992) found minimal mtDNA nucleotide sequence divergence between populations of *Coregonus artedi* and *C. hoyi* in the Great Lakes (maximum divergence between any pair of haplotypes = 0.6%). Bernatchez and Dodson (1990b) found little mtDNA sequence divergence (maximum 1%) in anadromous *C. artedi* in rivers of James and Hudson Bay. These values are approximately 10-fold lower than those frequently found in other closely related fishes (Berg and Ferris 1984, Avise and Saunders 1984, Avise et al. 1986). Similarly, Bernatchez and Dodson (1990a) found little difference in restriction fragment length polymorphisms (RFLP) of mtDNA in lake whitefish from the Allegash basin of northern Maine. They concluded that speciation of lake whitefish in eastern North America has occurred with little alteration of the ancestral gene pool. Reist et al. (1998) found a relatively high degree of mtDNA sequence variation among 16 coregonine taxa examined but no differences among allopatric *C. artedi* populations in northern Manitoba. Bodaly et al. (1998) found significant differences in mtDNA sequences between populations of *C. artedi* and *C. clupeaformis* in the area of Playgreen Lake, northern Manitoba but little difference among *C. clupeaformis* populations. They suggest a severe post-glacial population bottleneck, particularly among female lake whitefish, may be responsible for the low mtDNA diversity. Shields et al. (1990) found high intrapopulation mtDNA diversity in 3 populations of *C. artedi* in Minnesota but no congruence between mtDNA patterns and morphology among populations. Shields et al. (1992) also reported no detectable variation in mtDNA RFLP profiles in four populations of lake whitefish from north-central Minnesota but found diagnostic differences between ciscoes and whitefishes at these localities. Sajdak and Phillips (1997) found the sequences of the first internal transcribed spacer (ITS1) in North American ciscoes (*C. artedi, C. zenithicus, C. hoyi, C. kiyi*, and *C. nigripinnis*) to be identical. However,

Chouinard et al. (1996) found highly significant differences in the frequency of mtDNA RFLP haplotypes and alleles at one of two polymorphic enzyme loci in dwarf and normal lake whitefishes in Lac de l'Est, Quebec despite an almost complete lack of morphological differentiation.

Minimal and inconsistent differences between mtDNA sequences examined from Barrow Lake *C. artedi* and *C. zenithicus* are consistent with the findings of Sajdak (1995) and Reed et al. (1998). In the former study, only a single nucleotide difference was found in mitochondrial ATPase 6 sequences of *C. artedi* and *C. zenithicus* from Lake Nipigon. Reed et al. (1998) examined sequence divergence in the entire mtDNA d-loop (approximately 1200 bp) for *C. artedi* and *C. zenithicus* specimens from George Lake, Manitoba, Lake of the Woods, Ontario, Lake Nipigon, and Lake Superior as well as comparative samples of *C. kiyi, C. hoyi* (Lake Superior), and *C. clupeaformis* (Lake of the Woods). Ciscoes differed from whitefish by an average of 50.86 substitutions but individual cisco sequences differed by only 2 to 9 substitutions. This represented an average percent sequence divergence of 0.49. A phylogenetic tree based on pairwise evolutionary distances did not cluster sequences based on species or locality. Reed et al. (1998) concluded that morphological differentiation in ciscoes has occurred with very little genetic differentiation and suggested that lineage sorting is still occurring for mitochondrial markers in this group. Therefore, the mtDNA similarity between *C. artedi* and *C. zenithicus* is likely due to insufficient time for divergence in this evolutionarily recent group, and need not be interpreted as evidence for conspecificity.

Typically, closely related populations share many of the same alleles but these may occur in different frequencies. Hypervariable nuclear loci (e.g., microsatellites) may be more sensitive to low levels of DNA variation than mtDNA and therefore more suitable for discriminating among recently diverged taxa (but see Ferguson and Danzmann 1998).

Turgeon et al. (1999) found that only one of four morphotypes of cisco in Lake Nipigon was genetically distinct based on microsatellite variation. It was suggested that this form may represent *C. zenithicus*. Preliminary results of microsatellite analyses of Barrow and Ryan lake ciscoes suggest the presence of two distinct gene pools in each of these lakes (J. Turgeon pers. comm. 1998). Additional samples are needed to demonstrate allele frequency differences with a high degree of statistical confidence but the technique holds promise for corroborating the taxonomic decisions made in this study.

Postglacial Dispersal and Zoogeography of *Coregonus zenithicus* and *C. artedi*

C. zenithicus and *C. artedi* were probably original post-glacial colonizers of many northern North American lakes east of the continental divide (Bailey and Smith 1981, Smith and Todd 1984). It is believed both of these species survived Pleistocene glaciation in a Mississippi refugium and only one stock of each invaded inland Canada (Clarke 1973, Bailey and Smith 1981). Bailey and Smith (1981) felt major differentiation of ciscoes probably occurred prior to 9000 years ago. This assumption is based largely on the similarity of ciscoes in Lake Nipigon and Lake Superior, water bodies that are now isolated by barrier falls on the Nipigon River but were connected by proglacial lakes about 9000 years ago. Bailey and Smith (1981) concluded that differentiation of *C. artedi* and *C. zenithicus* probably occurred during the 70,000 years of the Wisconsinan glaciation or earlier, although the possibility of rapid post-glacial evolution could not be ruled out. Turgeon et al. (1999) found corroborating microsatellite DNA evidence that putative *C. zenithicus* and *C. artedi* diverged earlier than did morphotypes of *C. artedi* in Lake Nipigon. It seems most likely that these species were distinct prior to their post-glacial dispersal from the Great Lakes basin, or the Mississippi/Missouri headwaters region, into northwestern Canada. However, much of the morphological variation now exhibited by these species probably arose post-glacially via allopatric and sympatric intralacustrine genetic differentiation and phenotypic plasticity. The capacity for this rapid diversification may have been aided by genetic heterogeneity acquired through introgression of original stocks in glacial refugia and proglacial waterbodies.

Both *C. zenithicus* and *C. artedi* are suitably adapted for survival in the cold-water environment of proglacial lakes and rivers that connected the upper Mississippi/Missouri refugium with much of northwestern North America in late-Wisconsinan times (McPhail and Lindsey 1970, Teller 1987, Dyke and Prest 1987). Although cold, turbid, unproductive,

and generally unstable conditions probably existed in most proglacial aquatic environments, it is believed that microhabitats capable of supporting fish faunas did exist, at least in some of the larger lakes like Lake Agassiz (Stewart and Lindsey 1983, Beierle 1996). Extensive water connections, including at various times glacial lakes Agassiz, Saskatchewan, Edmonton, Peace, and McConnell as well as a host of smaller lakes and drainage channels, provided ample opportunity for cold-tolerant fishes to move from the headwaters of the Mississippi River as far north as the lower Mackenzie River. In fact, 28-30 fish species now inhabiting the upper Mackenzie and Hudson Bay basins are believed to have originated in the Mississippi/Missouri refugium (Lindsey and McPhail 1986, Rempel and Smith 1998). Of particular importance to northern Alberta populations is recent geological evidence suggesting a major drainage of Lake Agassiz into the Mackenzie basin in the area of the Clearwater River 9900 years ago (Smith and Fisher 1993, Fisher and Smith 1994, Rempel and Smith 1998). These authors believe Lake Agassiz overtopped a drainage divide near the Alberta-Saskatchewan border creating a catastrophic "paleoflood" from the northwestern tip of the lake into east-central Alberta through the Clearwater River valley. This "Clearwater spillway" turned north in the Athabasca River valley and extended another 75 km to the southern tip of Lake McConnell that drained to the Arctic Ocean via the Mackenzie River. While this paleoflood is estimated to have lasted only 78 days (Smith and Fisher 1993), post-flood annual flow is believed to have continued for about 400 years (Clayton 1983). This undoubtedly facilitated the northward migration of many species into the Mackenzie system although it would be but one of several spatially and temporally distinct potential dispersal routes. The Agassiz-Clearwater dispersal hypothesis has been suggested as the best explanation of the current pattern of morphological and genetic differentiation in *C. clupeaformis* as determined by Lindsey et al. (1970), Franzin and Clayton (1977), Bernatchez and Dodson (1991), and Foote et al. (1992). Since whitefish and ciscoes tend to be widely sympatric, it would be surprising if ciscoes did not follow the same route into northern Alberta and beyond.

The sporadic distribution of *C. zenithicus* populations across northern North America is intriguing. It appears the distribution of *C. zenithicus* is much patchier than that of *C. artedi* although the overall range of *zenithicus* appears to be extensive. There is verifiable evidence of its occurrence as far north and west as Great Slave Lake (Royal Ontario Museum cat. nos. 16878-17138). It must be assumed that the localized distribution of this species outside the Great Lakes basin is not based simply on inadequate sampling. Given the number of fish-supporting waterbodies in remote regions of northern Canada and the overall morphological similarity among cisco species (leading to the possiblity of incorrect identifications), this assumption is almost certainly violated to some extent. However, it is likely that our present understanding of the range of *C. zenithicus* is basically correct.

It may be that in sympatric situations, *C. artedi* was, and continues to be, the more successful competitor in the relatively small and shallow lakes that remained after the proglacial lakes receded. In many cases, *C. zenithicus* may have been excluded or eliminated from these sub-optimal habitats. Presumably this species prefers deeper water than *C. artedi* and its ability to exploit planktonic prey as an alternative food resource may be constrained by fewer and widely spaced gillrakers. Occasionally, however, conditions were suitable for the establishment and persistence of inferior phenotypes. Such conditions may include a slightly higher proportion of suitable habitat for the less fit species, local environmental perturbations that temporarily increased the fitness of the inferior species, site-specific dynamics of competitor and predator interactions limiting the population size of competing species, or other factors. Genetic change in some of these isolated populations may have also provided suitable intrinsic conditions for a sufficient increase in fitness of inferior forms to permit their continued existence. Under these marginal conditions it might be predicted that populations would persist in relatively low numbers and that their existence is tenuous.

Such an hypothesis may explain the rarity of *C. zenithicus* in Barrow Lake. There is weak evidence to suggest that this population may have declined in the past 30 years. Of the 78 ciscoes Paterson (1969) collected in 1966, 16 were *C. zenithicus* (20.5%). In the present study, 351 ciscoes were collected and only 19 were *C. zenithicus* (5.4%). Granted, assessing population trends from only two samples is entirely inadequate – yet the numbers are intriguing and warrant additional investigation. Regular monitoring of this population would be beneficial as would a continued search for additional inland populations of this species.

Taxonomic Summary of Sympatric Northeastern Alberta Ciscoes

Identity of Barrow Lake Ciscoes

The morphological and ecological evidence in this study suggests that the low gillraker form of cisco in Barrow Lake is *Coregonus zenithicus* as first reported by Paterson (1969). Morphologically, this form exhibits characters used traditionally to recognize *C. zenithicus* and it overlaps completely with known *C. zenithicus* populations in multivariate ordination plots. Based on the characters examined, there is no evidence to suggest that the sympatric forms in Barrow Lake are each other's closest relatives. Therefore, there is little evidence to support sympatric speciation and an independent origin of this population. Some expected morphological differences, due most likely to postglacial genetic divergence or phenotypic plasticity, were found between the Barrow Lake *C. zenithicus* and other conspecific populations, but these are believed insufficient to consider the Barrow Lake population a distinct species.

Mitochondrial DNA results were inconclusive but provide no evidence to suggest that the ciscoes in Barrow Lake are anything other than *C. zenithicus* or *C. artedi*. Further ecological data are needed to adequately define the niches and the level of competition between the sympatric species in Barrow Lake. However, the available evidence suggests more niche overlap and potential competition than would be expected if these forms had diverged sympatrically within Barrow Lake. A scenario of secondary contact between two independently invading species appears to conform best to the morphological and ecological data.

Identity of Bocquene Lake Ciscoes

The "superior" form of cisco in Bocquene Lake conforms morphologically to *C. sardinella*; the "terminal" form to *C. artedi*. Additional morphological and genetic data is needed to confirm the presence of *C. sardinella* in this lake.

Identity of Ryan Lake and Unnamed Lake Ciscoes

The cisco morphotypes in Ryan Lake and Unnamed Lake probably represent variants of *C. artedi*. Morphologically, they are congruent with characters used traditionally to identify *C. artedi* (especially gillraker number) and do not form distinct clusters in multivariate ordination plots of *C. artedi* from the same geographic region. Further ecological and biogeographic data are needed to assess whether they arose by intralacustrine sympatric divergence or whether their co-occurrence represents independent invasions of forms that had diverged prior to, or during, the last glacial retreat. Based on microsatellite and mitochondrial DNA data, J. Turgeon (pers. comm. 1999) believes most sympatric morphotypes of *C. artedi* are products of sympatric divergence. Undoubtedly, the current distribution of forms across North America represents a complex combination of both sympatric and allopatric divergence confounded by recent and historical intermixing of variously differentiated populations and phenotypic plasticity.

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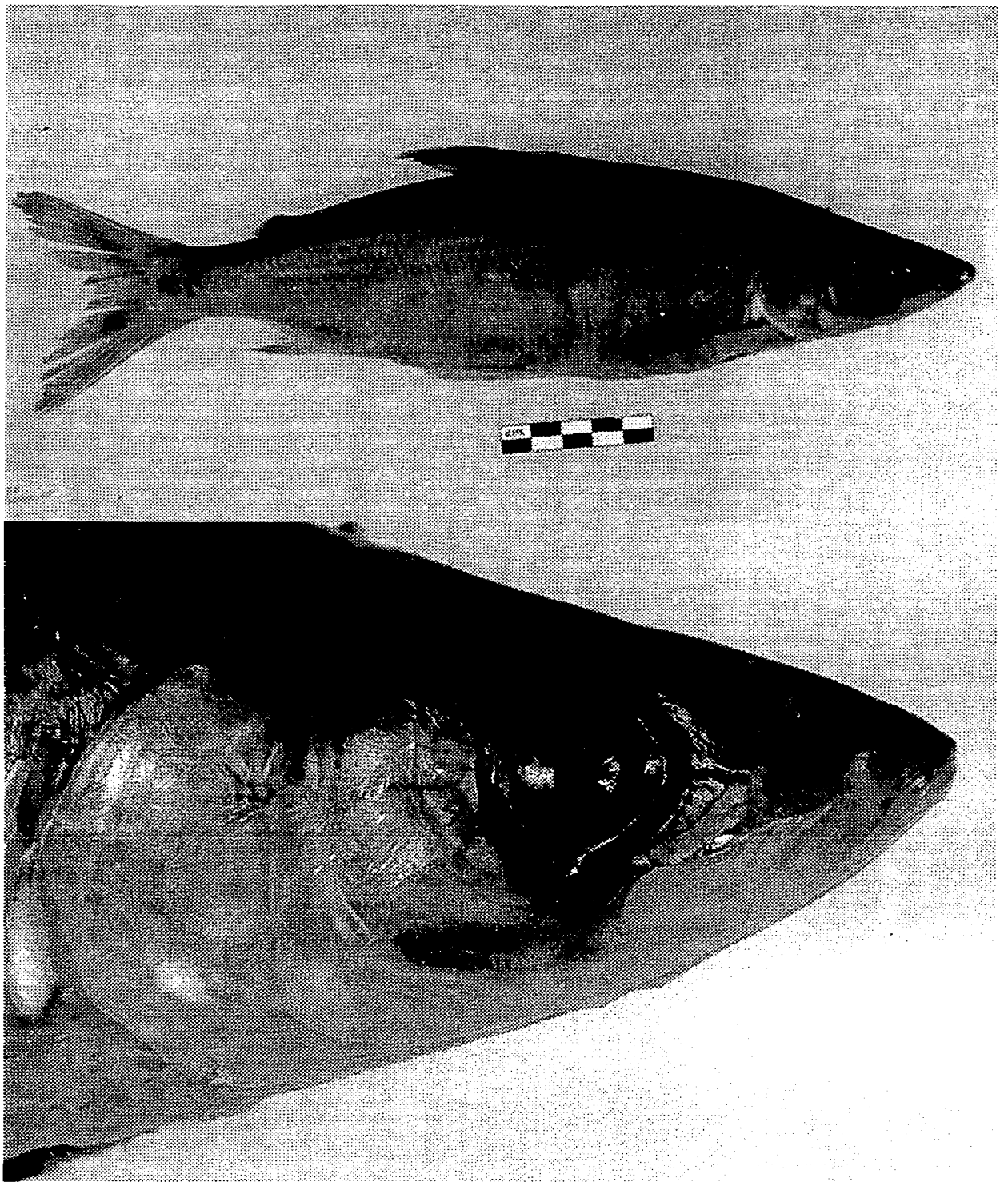

Plate 1. Barrow Lake low gillraker cisco (putative *C. zenithicus*). This specimen is a four year old female, 242 mm standard length with 43 gillrakers on the first, left branchial arch.

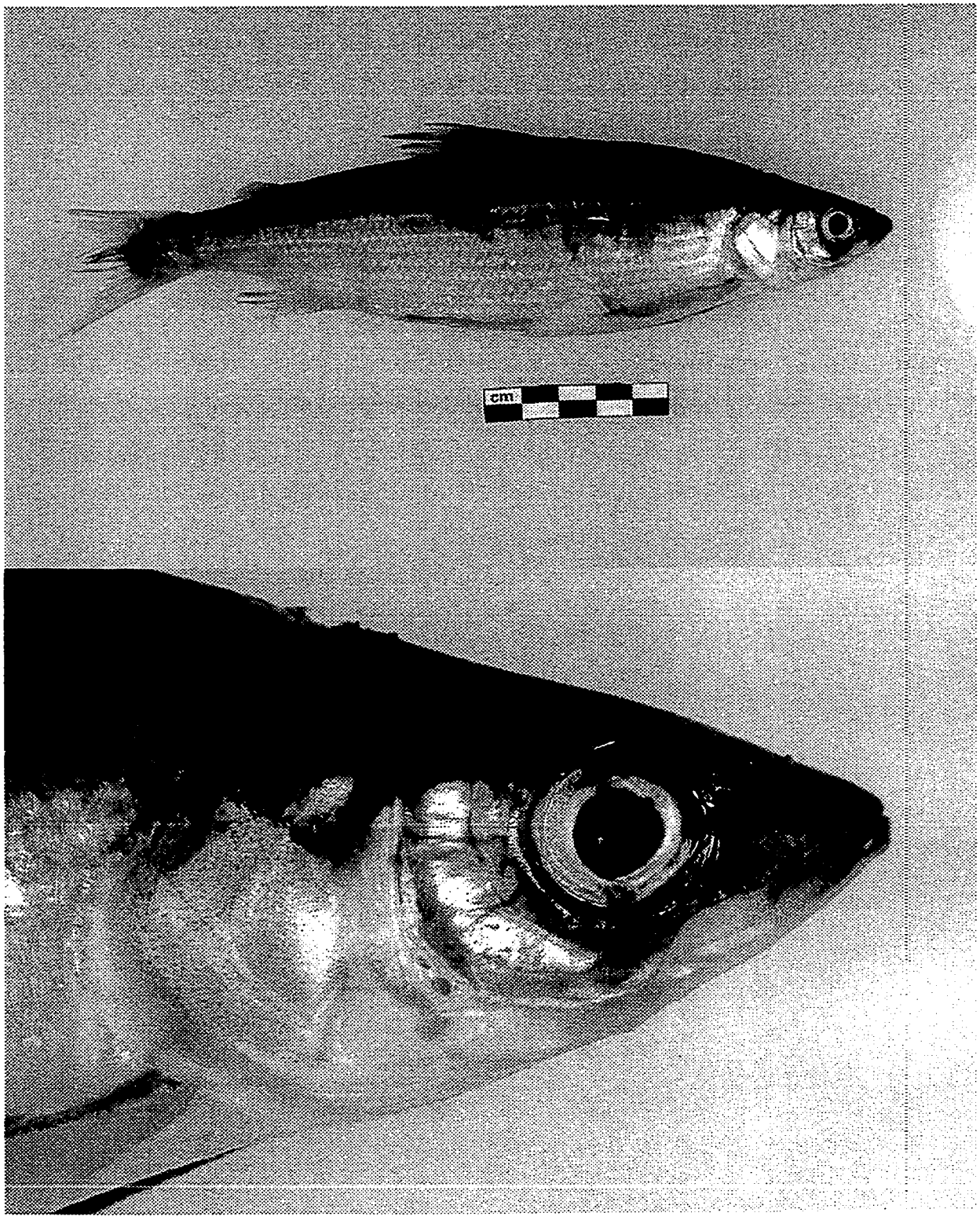

Plate 2. Barrow Lake high gillraker cisco (*C. artedi*). This specimen is a four year old female, 190 mm standard length with 50 gillrakers on the first, left branchial arch.

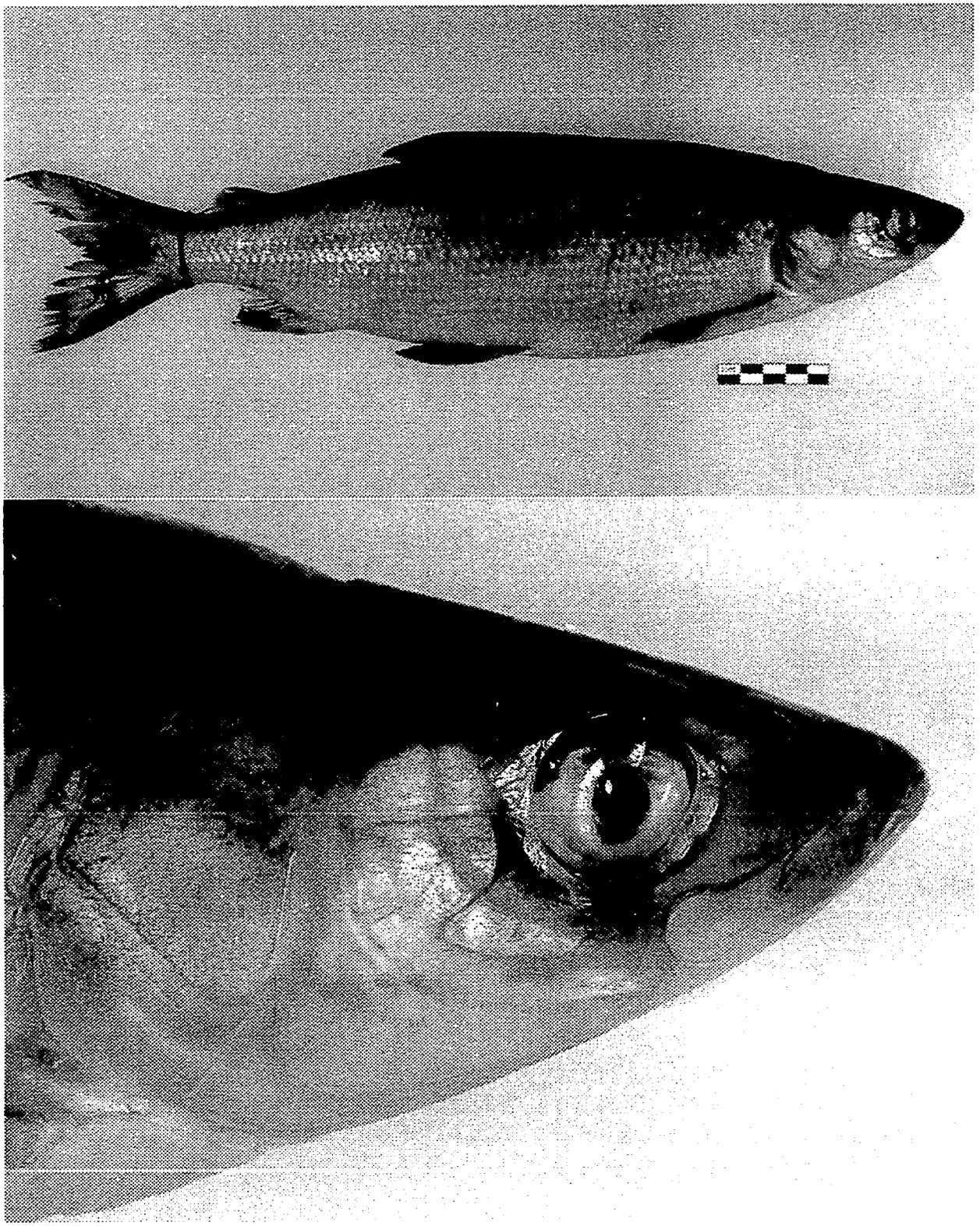

Plate 3. Ryan Lake high gillraker cisco (*C. artedi*). This specimen is a five year old female, 335 mm standard length with 55 gillrakers on the first, left branchial arch.

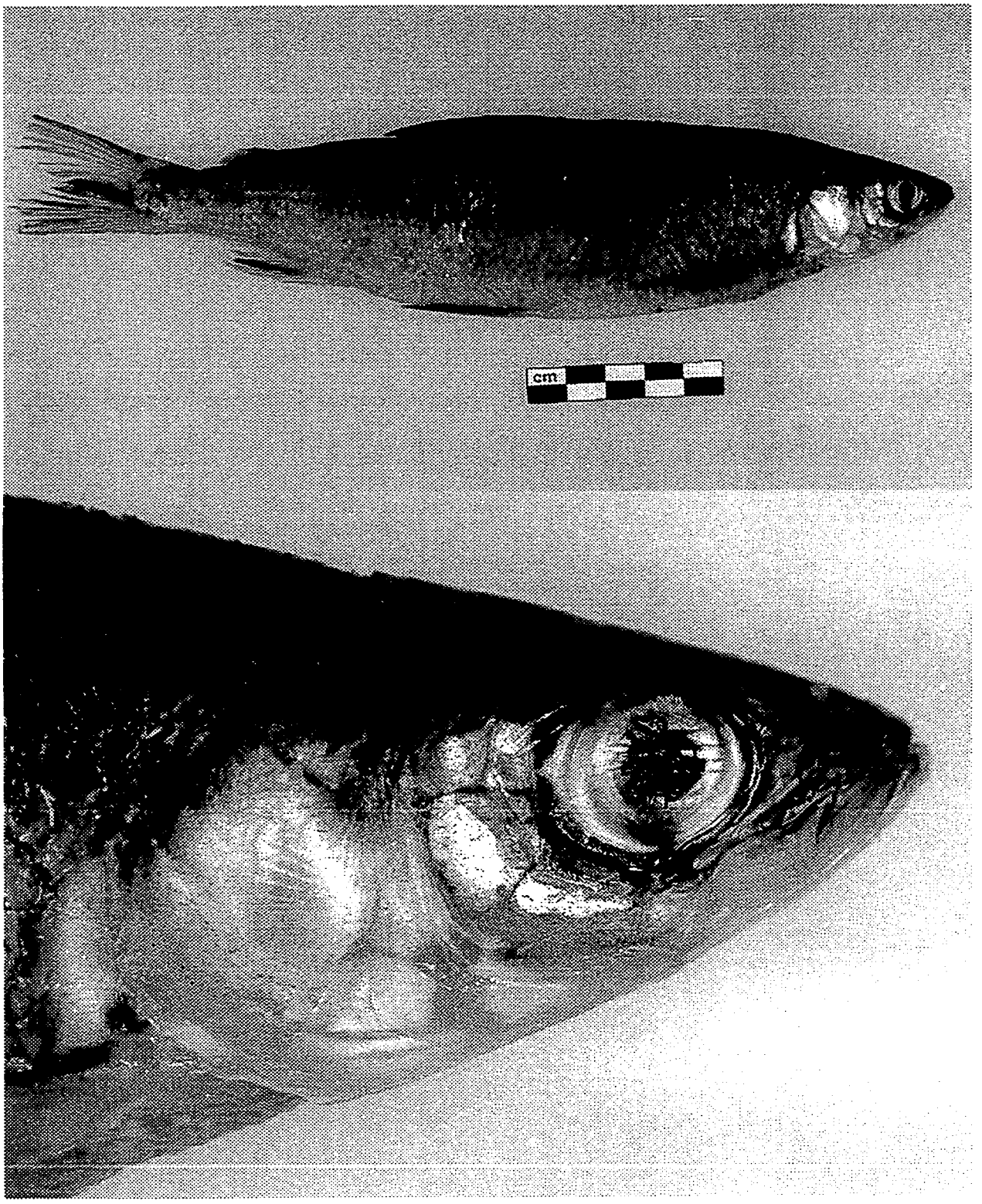

Plate 4. Ryan Lake low gillraker cisco (*C. artedi*). This specimen is a five year old female, 200 mm standard length with 46 gillrakers on the first, left branchial arch.

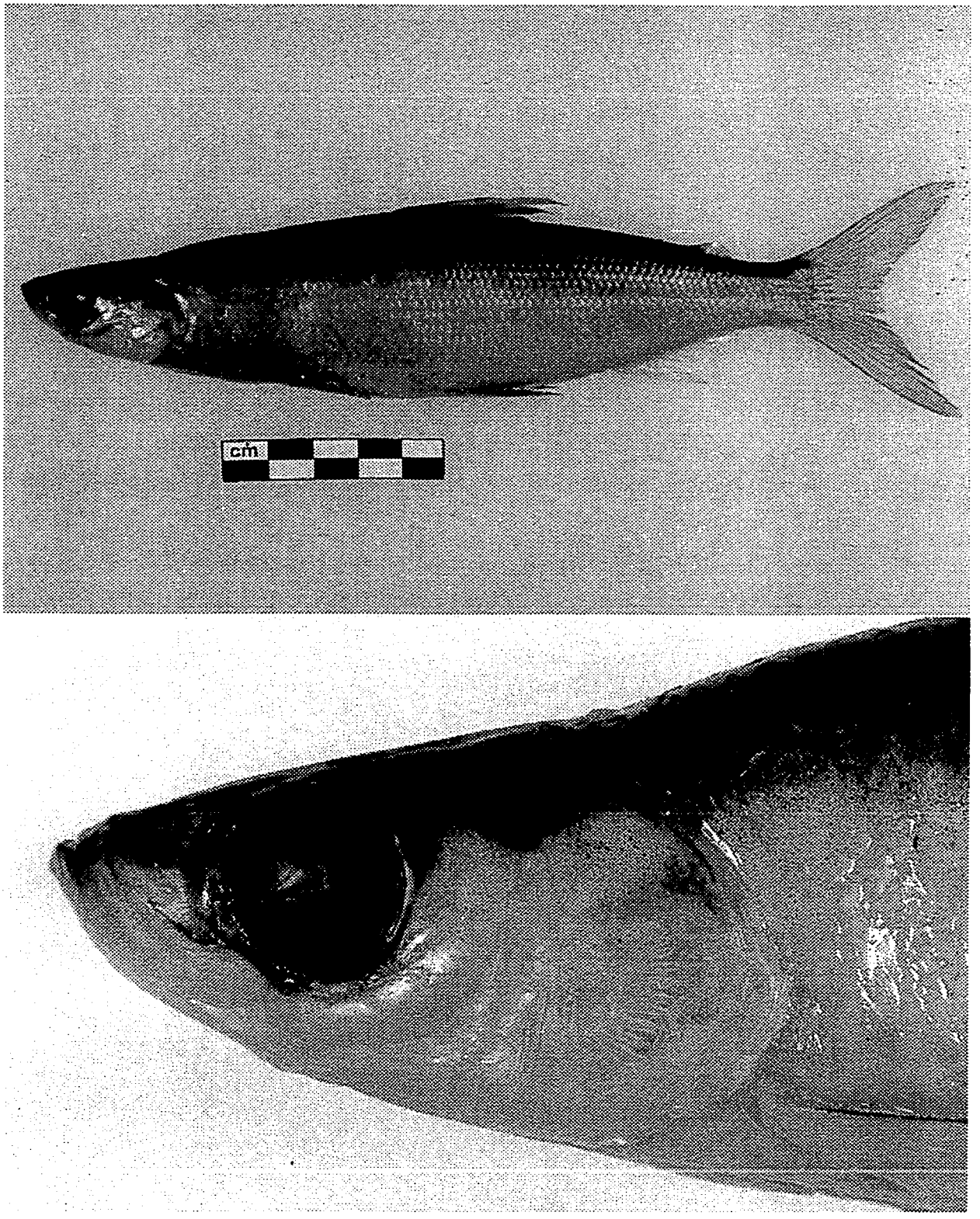

Plate 5. Bocquene Lake "superior" form of cisco (putative *C. sardinella*). This specimen is a four year old female, 173mm standard length with 47 gillrakers on the first, left branchial arch.

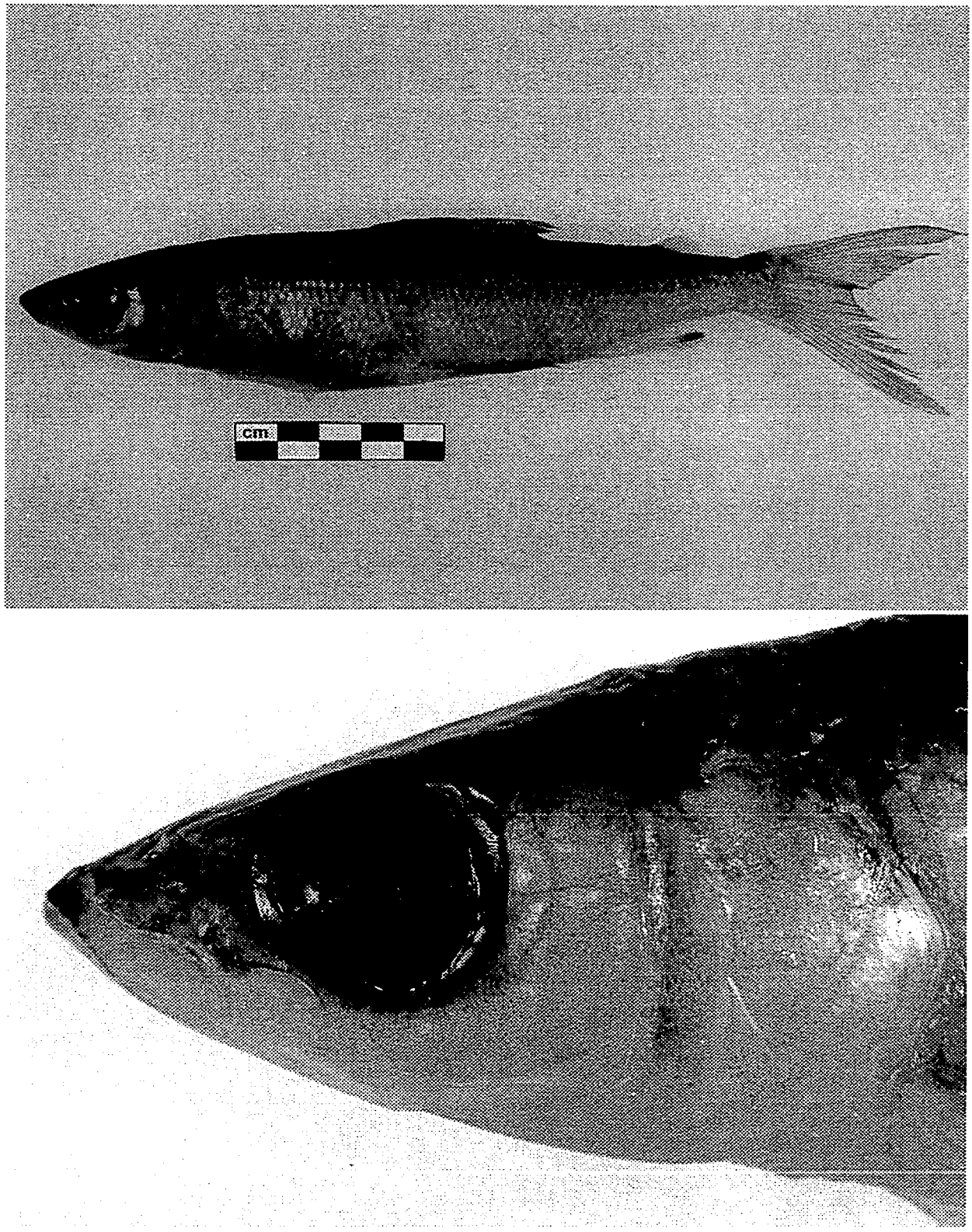

Plate 6. Bocquene Lake "terminal" cisco (*C. artedi*). This specimen is a four year old female, 175 mm standard length with 48 gillrakers on the first, left branchial arch.

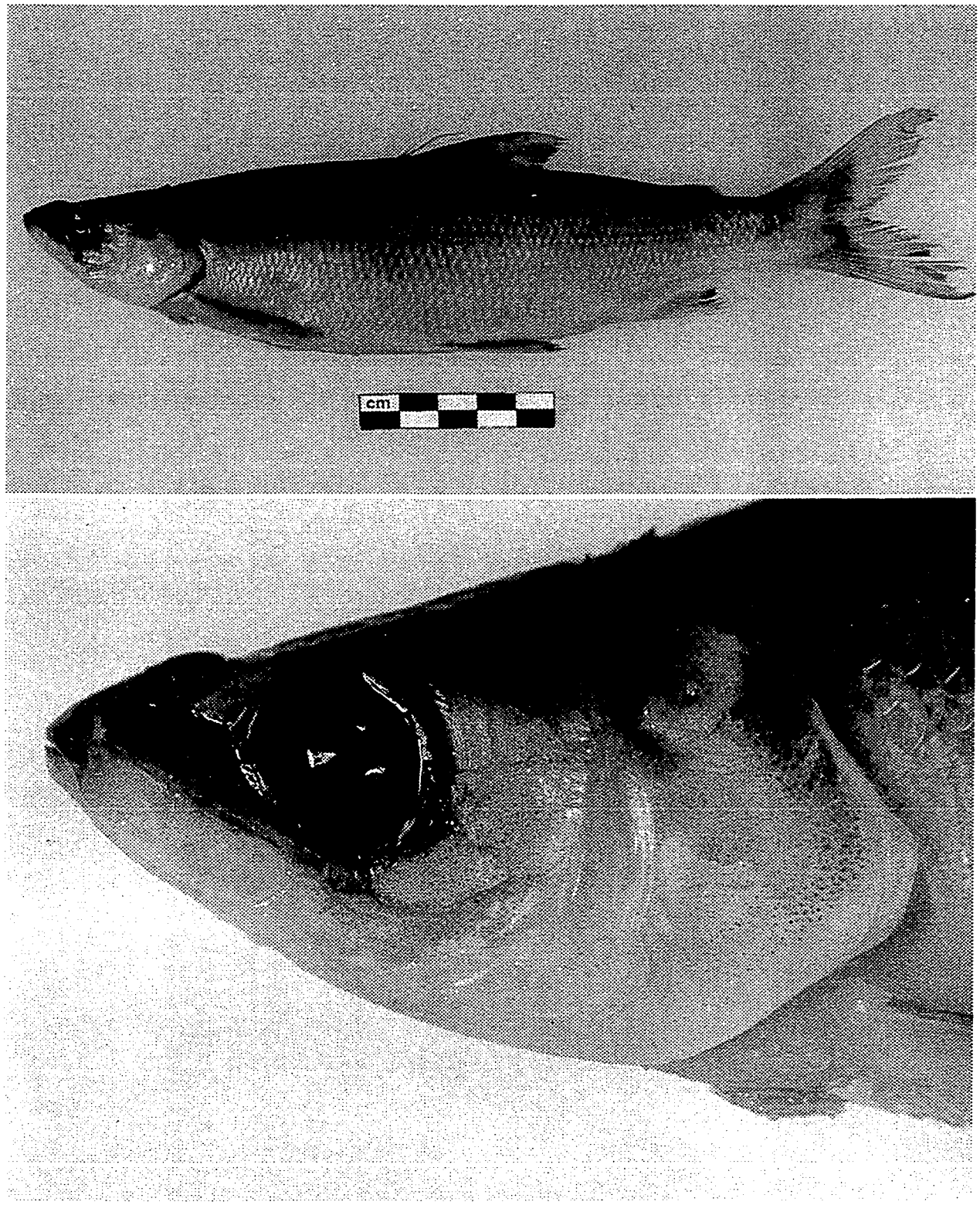

Plate 7. Unnamed Lake "normal" cisco (*C. artedi*). This specimen is a three year old female, 191 mm standard length with 51 gillrakers on the first, left branchial arch. This individual is slightly damaged on the dorsal surface of the snout.

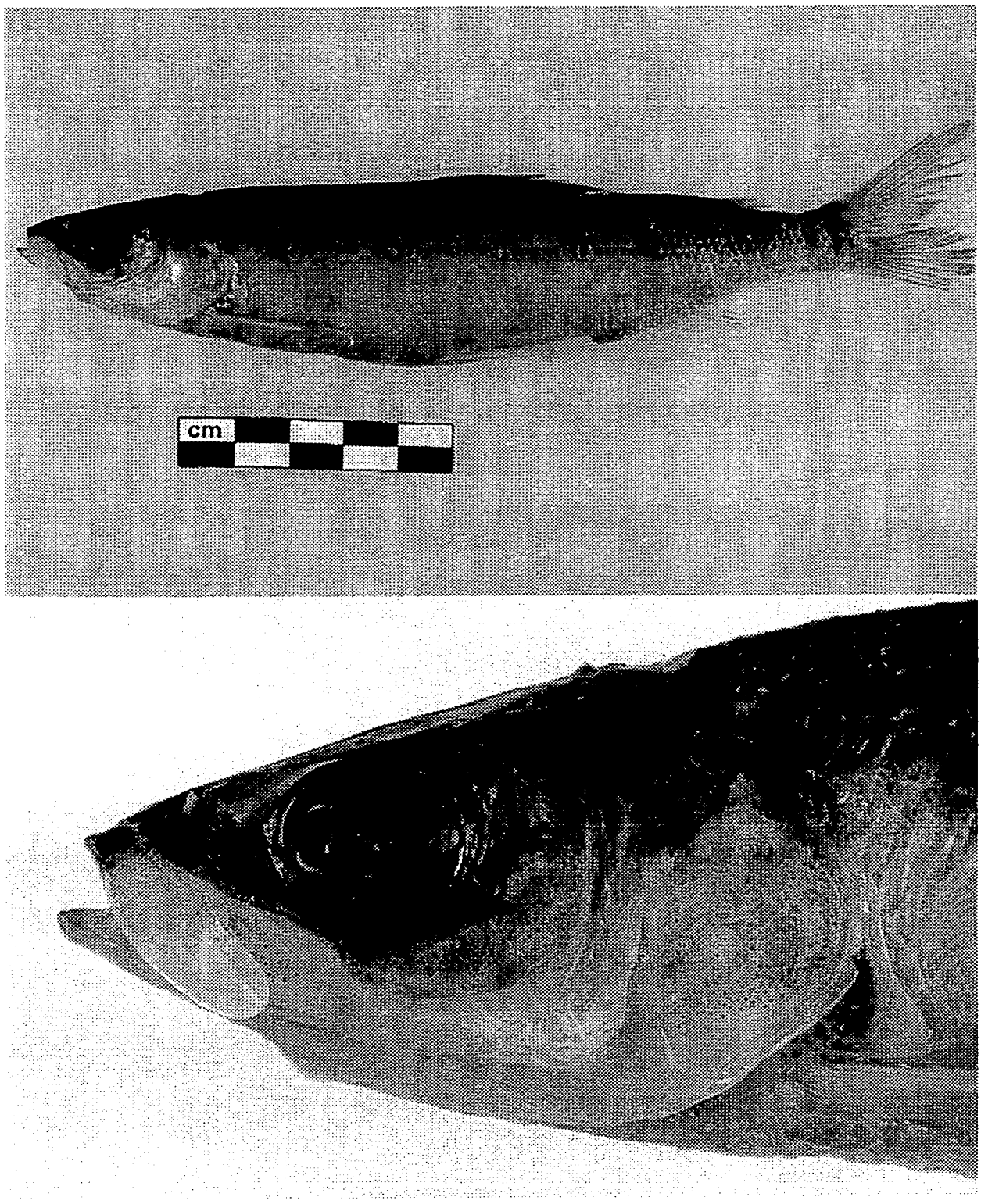

Plate 8. Unnamed Lake "dwarf" cisco (*C. artedi*). This specimen is a three year old male, 143 mm standard length with 46 gillrakers on the first, left branchial arch.

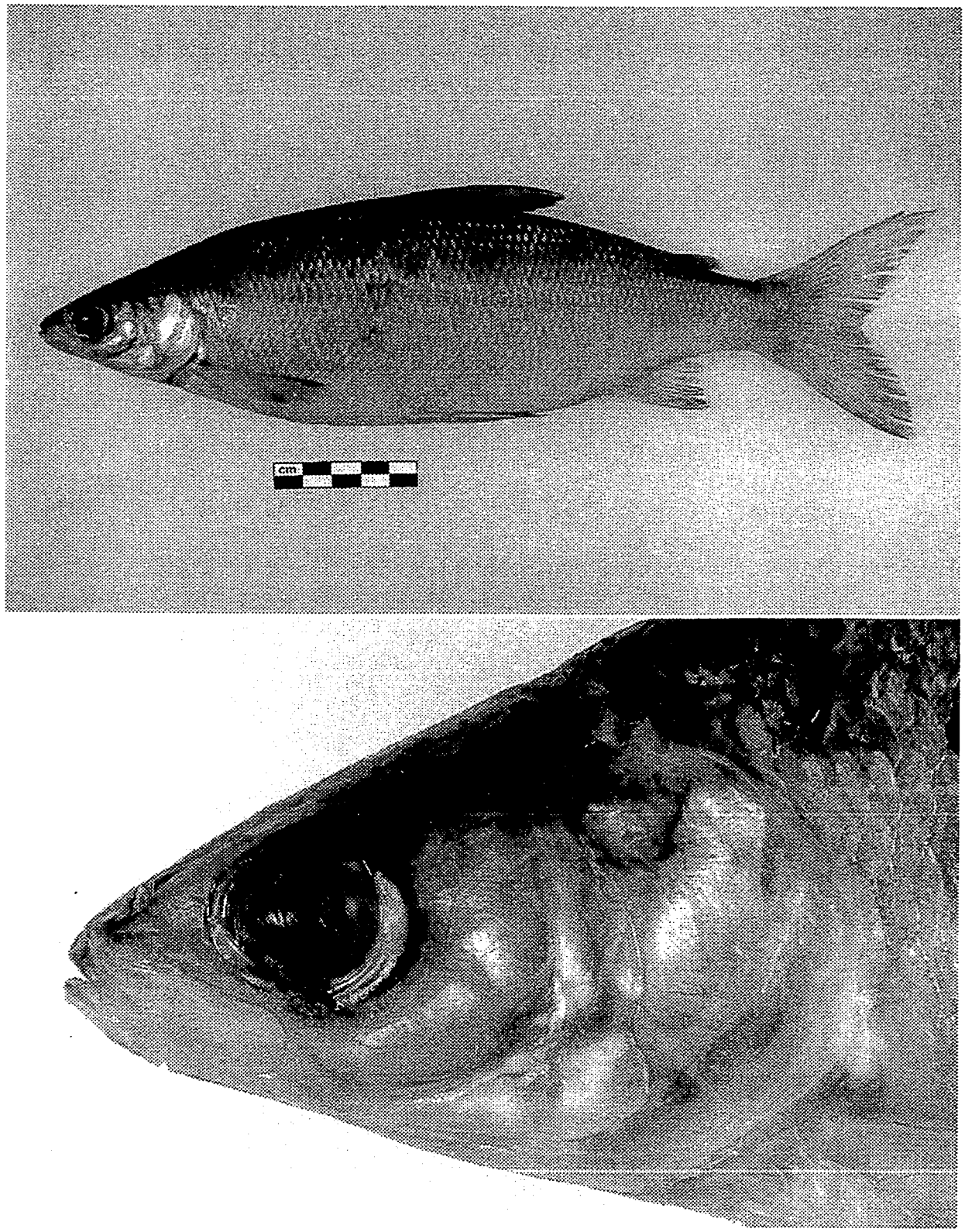

Plate 9. Myers Lake cisco (*C. artedi*). This specimen is an five year old female, 250 mm standard length with 50 gillrakers on the first, left branchial arch.

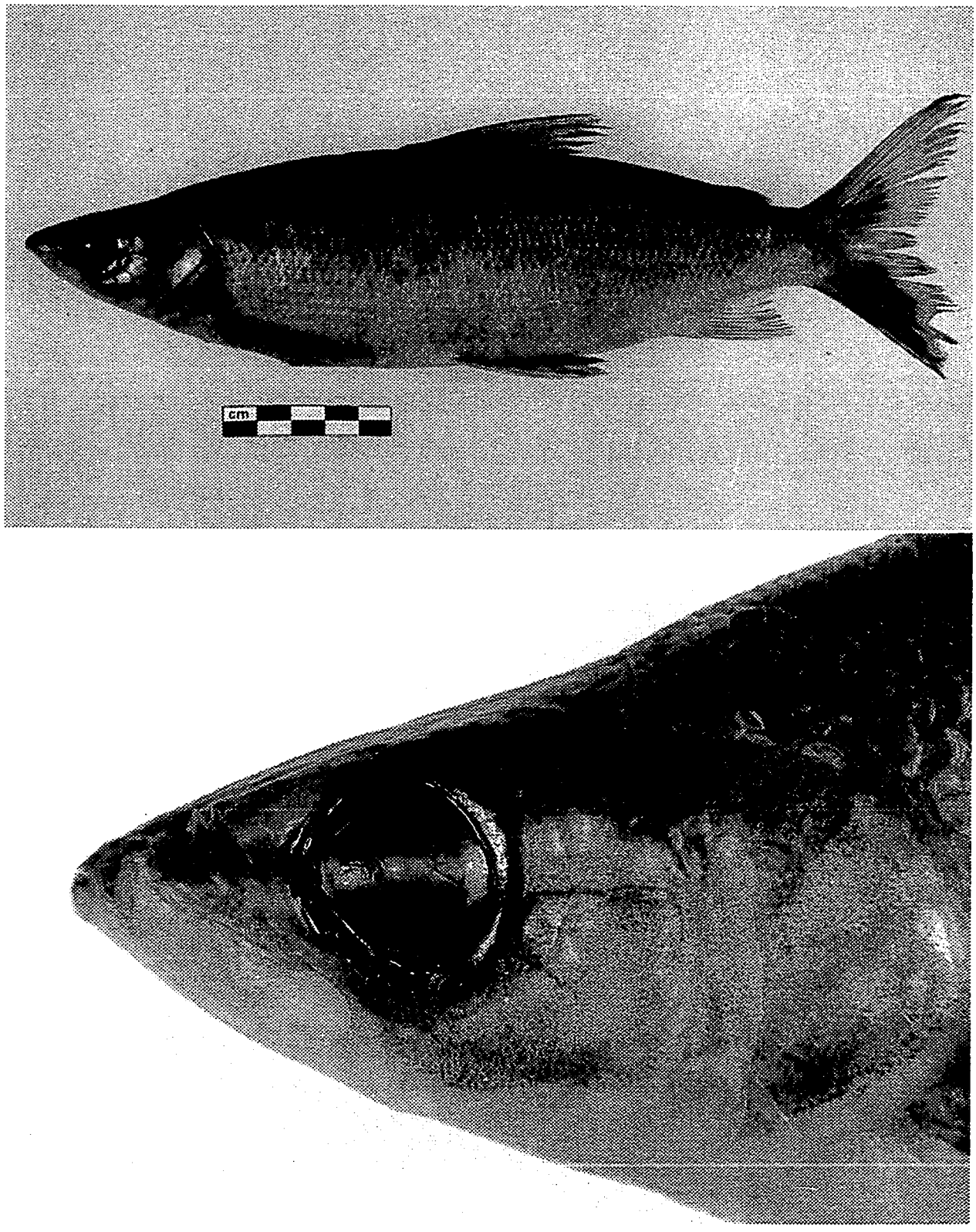

Plate 10. Daly Lake cisco (*C. artedi*). This specimen is a seven year old female, 227 mm standard length with 48 gillrakers on the first, left branchial arch.

Appendix 1. Pairwise comparison of mean differences between selected characters from nine Alberta cisco populations. Values in bold are significantly different ($P<.05$). The Tamhane correction factor was used to adjust the significance level for the multiple pairwise tests. All values are based on adjusted regression residuals. See text for population abbreviations.

		Mean Difference between Forms								
Character		Gillraker length	Orbit diameter	Snout length	Upper jaw length	Truss 1	Truss 3	Truss 5	Truss 9	Truss 12
Population 1	*Population 2*									
Barrow lgr	Barrow hgr	**-3.2487**	**-1.0511**	**1.1308**	**2.2247**	**1.8170**	**2.8019**	**2.3451**	.2059	**-1.9820**
	Bocquene "s"	**-1.9387**	**-1.3351**	**1.8049**	**3.3981**	**5.6941**	**4.3209**	**2.1980**	-.2511	**2.6131**
	Bocquene "t"	**-3.0458**	**-.9191**	**1.3640**	**2.9121**	**2.5471**	**2.9040**	**3.2100**	-8.0526E-03	.1020
	Daly	**-2.5987**	**-1.1702**	**1.7569**	**2.5911**	**2.6121**	**2.4218**	**4.5531**	1.9229	-.8530
	Myers	**-2.2577**	**-.6711**	**2.4810**	**4.3522**	**3.0871**	-1.5642	**2.3650**	**-4.6962**	**-1.9339**
	Ryan lgr	**-3.5546**	**-1.4411**	**2.1129**	**2.5420**	1.6071	1.9319	**2.5660**	.2309	-.9561
	Ryan hgr	**-3.5336**	**-1.4405**	-.6103	**1.5527**	-.2309	1.8539	.9610	.3459	**-4.2760**
	Unnamed	**-3.0990**	**-.4883**	**1.3405**	**2.9923**	**3.2990**	**4.6659**	**3.0880**	.2289	-.1480
Barrow hgr	Barrow lgr	**3.2487**	**1.0511**	**-1.1308**	**-2.2247**	**-1.8170**	**-2.8019**	**-2.3451**	-.2059	**1.9820**
	Bocquene "s"	**1.3100**	-.2840	**.6740**	**1.1734**	**3.8771**	**1.5191**	-.1471	-.4570	**4.5951**
	Bocquene "t"	.2029	.1321	.2331	**.6874**	**.7300**	.1021	**.8650**	-.2140	**2.0840**
	Daly	.6500	-.1190	.6261	.3664	.7950	-.3800	**2.2080**	1.7170	1.1290
	Myers	**.9909**	.3800	**1.3502**	**2.1275**	**1.2701**	**-4.3660**	1.999E-02	**-4.9021**	4.810E-02
	Ryan lgr	-.3060	-.3900	.9821	.3173	-.2100	-.8700	.2209	2.500E-02	1.0259
	Ryan hgr	-.2849	-.3894	**-1.7411**	-.6720	**-2.0480**	-.9480	**-1.3840**	.1400	**-2.2940**
	Unnamed	.1497	**.5629**	.2097	**.7676**	**1.4820**	**1.8640**	.7429	2.298E-02	**1.8340**
Bocquene "s"	Barrow lgr	**1.9387**	**1.3351**	**-1.8049**	**-3.3981**	**-5.6941**	**-4.3209**	**-2.1980**	.2511	**-2.6131**
	Barrow hgr	**-1.3100**	.2840	**-.6740**	**-1.1734**	**-3.8771**	**-1.5191**	.1471	.4570	**-4.5951**
	Bocquene "t"	**-1.1071**	**.4161**	-.4409	-.4860	**-3.1470**	**-1.4170**	**1.0120**	.2430	**-2.5110**
	Daly	-.6600	.1650	-4.7963E-02	-.8071	**-3.0820**	**-1.8991**	**2.3551**	2.1740	**-3.4661**
	Myers	-.3191	**.6640**	.6761	**.9541**	**-2.6070**	**-5.8851**	.1670	**-4.4451**	**-4.5470**
	Ryan lgr	**-1.6160**	-.1060	.3080	**-.8562**	**-4.0870**	**-2.3890**	.3680	.4820	**-3.5692**
	Ryan hgr	**-1.5950**	-.1054	**-2.4152**	**-1.8454**	**-5.9250**	**-2.4670**	**-1.2370**	.5970	**-6.8890**
	Unnamed	**-1.1604**	**.8469**	-.4644	-.4058	**-2.3951**	.3449	.8900	.4800	**-2.7611**
Bocquene "t"	Barrow lgr	**3.0458**	**.9191**	**-1.3640**	**-2.9121**	**-2.5471**	**-2.9040**	**-3.2100**	8.053E-03	-.1020

Appendix 1
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Character		Gillraker length	Orbit diameter	Snout	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 9	Truss 12
Population 1	*Population 2*									
Bocquene "t"	Barrow hgr	-.2029	-.1321	-.2331	**-.6874**	**-.7300**	-.1021	**-.8650**	.2140	**-2.0840**
	Bocquene "s"	**1.1071**	**-.4161**	.4409	.4860	**3.1470**	**1.4170**	**-1.0120**	-.2430	**2.5110**
	Daly	.4471	-.2511	.3929	-.3210	6.500E-02	-.4821	**1.3431**	1.9310	-.9551
	Myers	**.7880**	.2480	**1.1170**	**1.4402**	.5400	**-4.4681**	-.8450	**-4.6881**	**-2.0359**
	Ryan lgr	-.5089	-.5220	.7489	-.3701	-.9400	-.9721	-.6440	.2390	-1.0581
	Ryan hgr	-.4879	-.5214	**-1.9743**	**-1.3594**	**-2.7780**	-1.0501	**-2.2490**	.3540	-4.3780
	Unnamed	-5.3256E-02	**.4308**	-2.3467E-02	8.023E-02	.7520	**1.7619**	-.1221	.2370	-.2501
Daly	Barrow lgr	**2.5987**	**1.1702**	**-1.7569**	**-2.5911**	**-2.6121**	**-2.4218**	**-4.5531**	-1.9229	.8530
	Barrow hgr	-.6500	.1190	-.6261	-.3664	-.7950	.3800	**-2.2080**	-1.7170	-1.1290
	Bocquene "s"	.6600	-.1650	4.796E-02	.8071	**3.0820**	**1.8991**	**-2.3551**	-2.1740	**3.4661**
	Bocquene "t"	-.4471	.2511	-.3929	.3210	-6.5000E-02	.4821	**-1.3431**	-1.9310	.9551
	Myers	.3410	.4990	.7241	**1.7612**	.4750	**-3.9860**	**-2.1880**	**-6.6191**	-1.0809
	Ryan lgr	-.9560	-.2710	.3560	-4.9083E-02	-1.0050	-.4900	**-1.9871**	-1.6920	-.1030
	Ryan hgr	**-.9349**	-.2704	**-2.3672**	**-1.0383**	**-2.8430**	-.5680	**-3.5921**	-1.5770	**-3.4229**
	Unnamed	-.5003	**.6819**	-.4164	.4013	.6870	**2.2440**	**-1.4651**	-1.6940	.7050
Myers	Barrow lgr	**2.2577**	**.6711**	**-2.4810**	**-4.3522**	**-3.0871**	1.5642	**-2.3650**	**4.6962**	**1.9339**
	Barrow hgr	**-.9909**	-.3800	**-1.3502**	**-2.1275**	**-1.2701**	**4.3660**	-1.9991E-02	**4.9021**	-4.8095E-02
	Bocquene "s"	.3191	**-.6640**	-.6761	**-.9541**	**2.6070**	**5.8851**	-.1670	**4.4451**	**4.5470**
	Bocquene "t"	**-.7880**	-.2480	**-1.1170**	**-1.4402**	-.5400	**4.4681**	.8450	**4.6881**	**2.0359**
	Daly	-.3410	-.4990	-.7241	**-1.7612**	-.4750	**3.9860**	**2.1880**	**6.6191**	1.0809
	Ryan lgr	**-1.2969**	-.7700	-.3681	**-1.8103**	-1.4800	**3.4960**	.2010	**4.9271**	.9778
	Ryan hgr	**-1.2759**	**-.7694**	**-3.0913**	**-2.7995**	**-3.3180**	**3.4180**	-1.4040	**5.0421**	**-2.3421**
	Unnamed	**-.8413**	.1828	**-1.1405**	**-1.3599**	.2119	**6.2300**	.7229	**4.9251**	**1.7859**
Ryan lgr	Barrow lgr	**3.5546**	**1.4411**	**-2.1129**	**-2.5420**	-1.6071	**-1.9319**	**-2.5660**	-.2309	.9561
	Barrow hgr	.3060	.3900	-.9821	-.3173	.2100	.8700	-.2209	-2.5000E-02	-1.0259
	Bocquene "s"	**1.6160**	.1060	-.3080	**.8562**	**4.0870**	**2.3890**	-.3680	-.4820	**3.5692**
	Bocquene "t"	.5089	.5220	-.7489	.3701	.9400	.9721	.6440	-.2390	1.0581
	Daly	.9560	.2710	-.3560	4.908E-02	1.0050	.4900	**1.9871**	1.6920	.1030
	Myers	**1.2969**	.7700	.3681	**1.8103**	1.4800	**-3.4960**	-.2010	**-4.9271**	-.9778

Appendix 1
con't.

Character		Gillraker length	Orbit diameter	Snout	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 9	Truss 12
Population 1	*Population 2*									
Ryan lgr	Ryan hgr	2.102E-02	5.946E-04	**-2.7232**	**-.9893**	**-1.8380**	-7.8000E-02	-1.6050	.1150	**-3.3199**
	Unnamed	.4556	**.9528**	-.7724	.4504	**1.6920**	**2.7340**	.5220	-2.0222E-03	.8080
Ryan hgr	Barrow lgr	**3.5336**	**1.4405**	.6103	**-1.5527**	.2309	-1.8539	-.9610	-.3459	**4.2760**
	Barrow hgr	.2849	.3894	**1.7411**	.6720	**2.0480**	.9480	**1.3840**	-.1400	**2.2940**
	Bocquene "s"	**1.5950**	.1054	**2.4152**	**1.8454**	**5.9250**	**2.4670**	**1.2370**	-.5970	**6.8890**
	Bocquene "t"	.4879	.5214	**1.9743**	**1.3594**	**2.7780**	1.0501	**2.2490**	-.3540	**4.3780**
	Daly	**.9349**	.2704	**2.3672**	**1.0383**	**2.8430**	.5680	**3.5921**	1.5770	**3.4229**
	Myers	**1.2759**	**.7694**	**3.0913**	**2.7995**	**3.3180**	**-3.4180**	1.4040	**-5.0421**	**2.3421**
	Ryan lgr	-2.1022E-02	-5.9459E-04	**2.7232**	**.9893**	**1.8380**	7.800E-02	1.6050	-.1150	**3.3199**
	Unnamed	.4346	**.9522**	**1.9508**	**1.4396**	**3.5300**	**2.8120**	**2.1270**	-.1170	**4.1279**
Unnamed	Barrow lgr	**3.0990**	**.4883**	**-1.3405**	**-2.9923**	**-3.2990**	**-4.6659**	**-3.0880**	-.2289	.1480
	Barrow hgr	-.1497	**-.5629**	-.2097	**-.7676**	**-1.4820**	**-1.8640**	-.7429	-2.2978E-02	**-1.8340**
	Bocquene "s"	**1.1604**	**-.8469**	.4644	.4058	**2.3951**	-.3449	-.8900	-.4800	**2.7611**
	Bocquene "t"	5.326E-02	**-.4308**	2.347E-02	-8.0233E-02	-.7520	**-1.7619**	.1221	-.2370	.2501
	Daly	.5003	**-.6819**	.4164	-.4013	-.6870	**-2.2440**	**1.4651**	1.6940	-.7050
	Myers	**.8413**	-.1828	**1.1405**	**1.3599**	-.2119	**-6.2300**	-.7229	**-4.9251**	**-1.7859**
	Ryan lgr	-.4556	**-.9528**	.7724	-.4504	**-1.6920**	**-2.7340**	-.5220	2.022E-03	-.8080
	Ryan hgr	-.4346	**-.9522**	**-1.9508**	**-1.4396**	**-3.5300**	**-2.8120**	**-2.1270**	.1170	**-4.1279**

Appendix 2. Pairwise comparison of mean differences between selected characters from nine Alberta cisco populations and eight *C. zenithicus* populations from across North America. Values in bold are significantly different ($P<.05$). The Tamhane correction factor was used to adjust the significance level for the multiple pairwise tests. All values are based on adjusted regression residuals. See text for population name abbreviations (for now, the Bocquene Lake "superior" form is labelled *C. artedi*).

		Mean Difference between Populations					
Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Lake Superior *C. zenithicus*	Lake Winnipeg *C. zenithicus*	-.1320	**2.6482**	3.2243	**-4.2970**	3.4390	-.3651
	Reindeer Lake *C. zenithicus*	-8.2000E-02	1.8141	1.8821	**-4.0750**	3.9860	-.1471
	Basswood Lake *C. zenithicus*	1.300E-02	.7392	-.2867	-2.8819	3.3212	-.1700
	Little Athapap. *C. zenithicus*	-.5001	3.608E-02	-1.8959	**-4.2680**	3.7383	-.4309
	Great Slave Lake *C. zenithicus*	-.4469	**4.4142**	4.4322	**-5.2390**	1.9931	2.4781
	Sandy Lake *C. zenithicus*	-1.2590	.2321	.8531	-3.2668	4.1611	-.2080
	Lake Nipigon *C. zenithicus*	-.9549	1.2201	.5102	-2.2729	2.5660	.6190
	Barrow Lake *C. zenithicus*	1.1849	.9560	.2021	**-10.1650**	1.7941	3.400E-02
	Barrow Lake *C. artedi*	**-2.0651**	**3.1401**	2.0620	**-7.2538**	4.0461	-1.9020
	Bocquene Lake "s" *C. artedi*	-.7300	**4.3101**	**5.9661**	**-5.6690**	3.8441	2.7190
	Bocquene Lake "t" *C. artedi*	**-1.8330**	**3.7004**	2.8279	**-7.0580**	**4.8300**	.2170
	Daly Lake *C. artedi*	-1.4050	**3.5311**	2.8402	**-7.6790**	**6.4670**	-.7921
	Myers Lake *C. artedi*	-1.0750	**5.3102**	3.2851	**-11.7359**	4.1640	-1.9030
	Ryan Lake lgr *C. artedi*	**-2.3442**	**3.4521**	1.8831	**-8.0459**	4.2011	-.8449
	Ryan Lake hgr *C. artedi*	**-2.3791**	**2.5610**	-.1140	**-8.5240**	2.9350	**-4.3280**
	Unnamed Lake *C. artedi*	**-1.8981**	**3.9180**	**3.5501**	**-5.3759**	**4.7781**	-6.3022E-02
Lake Winnipeg *C. zenithicus*	Lake Superior *C. zenithicus*	.1320	**-2.6482**	-3.2243	**4.2970**	-3.4390	.3651
	Reindeer Lake *C. zenithicus*	5.000E-02	-.8341	-1.3422	.2220	.5470	.2180
	Basswood Lake *C. zenithicus*	.1450	**-1.9090**	-3.5110	1.4151	-.1178	.1951
	Little Athapap. *C. zenithicus*	-.3681	-2.6121	**-5.1202**	2.898E-02	.2993	-6.5784E-02
	Great Slave Lake *C. zenithicus*	-.3149	1.7660	1.2079	-.9420	-1.4459	**2.8432**
	Sandy Lake *C. zenithicus*	-1.1270	**-2.4161**	-2.3712	1.0302	.7221	.1571
	Lake Nipigon *C. zenithicus*	-.8229	-1.4281	-2.7140	2.0242	-.8730	.9841
	Barrow Lake *C. zenithicus*	1.3169	-1.6921	-3.0222	**-5.8680**	-1.6449	.3991
	Barrow Lake *C. artedi*	**-1.9331**	.4919	-1.1623	-2.9568	.6071	-1.5370
	Bocquene Lake "s" *C. artedi*	-.5980	1.6619	2.7418	-1.3720	.4051	**3.0841**
	Bocquene Lake "t" *C. artedi*	**-1.7010**	1.0522	-.3963	-2.7610	1.3910	.5821
	Daly Lake *C. artedi*	-1.2730	.8829	-.3841	**-3.3820**	3.0280	-.4270
	Myers Lake *C. artedi*	-.9430	**2.6620**	6.087E-02	**-7.4389**	.7250	-1.5380
	Ryan Lake lgr *C. artedi*	**-2.2122**	.8039	-1.3412	**-3.7489**	.7621	-.4798

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Lake Winnipeg *C. zenithicus*	Ryan Lake hgr *C. artedi*	**-2.2471**	-8.7144E-02	**-3.3382**	**-4.2270**	-.5040	**-3.9629**
	Unnamed Lake *C. artedi*	**-1.7661**	1.2698	.3259	-1.0789	1.3391	.3021
Reindeer Lake *C. zenithicus*	Lake Superior *C. zenithicus*	8.200E-02	-1.8141	-1.8821	**4.0750**	-3.9860	.1471
	Lake Winnipeg *C. zenithicus*	-5.0000E-02	.8341	1.3422	-.2220	-.5470	-.2180
	Basswood Lake *C. zenithicus*	9.500E-02	-1.0749	-2.1688	1.1931	-.6648	-2.2889E-02
	Little Athapap. *C. zenithicus*	-.4181	-1.7780	-3.7780	-.1930	-.2477	-.2838
	Great Slave Lake *C. zenithicus*	-.3649	2.6001	2.5501	-1.1640	-1.9929	2.6252
	Sandy Lake *C. zenithicus*	**-1.1770**	-1.5820	-1.0290	.8082	.1751	-6.0889E-02
	Lake Nipigon *C. zenithicus*	-.8729	-.5940	-1.3719	1.8022	-1.4200	.7661
	Barrow Lake *C. zenithicus*	**1.2669**	-.8581	-1.6800	**-6.0899**	-2.1918	.1811
	Barrow Lake *C. artedi*	**-1.9831**	1.3260	.1799	**-3.1788**	6.011E-02	-1.7549
	Bocquene Lake "s" *C. artedi*	-.6480	**2.4960**	**4.0840**	-1.5940	-.1419	2.8661
	Bocquene Lake "t" *C. artedi*	**-1.7510**	1.8863	.9459	**-2.9830**	.8440	.3641
	Daly Lake *C. artedi*	**-1.3230**	1.7170	.9581	**-3.6039**	2.4811	-.6450
	Myers Lake *C. artedi*	-.9930	**3.4961**	1.4030	**-7.6609**	.1781	-1.7559
	Ryan Lake lgr *C. artedi*	**-2.2622**	1.6380	1.000E-03	**-3.9709**	.2151	-.6978
	Ryan Lake hgr *C. artedi*	**-2.2971**	.7469	-1.9961	**-4.4490**	-1.0509	**-4.1809**
	Unnamed Lake *C. artedi*	**-1.8161**	2.1039	1.6681	-1.3009	.7921	8.409E-02
Basswood Lake *C. zenithicus*	Lake Superior *C. zenithicus*	-1.3000E-02	-.7392	.2867	2.8819	-3.3212	.1700
	Lake Winnipeg *C. zenithicus*	-.1450	1.9090	3.5110	-1.4151	.1178	-.1951
	Reindeer Lake *C. zenithicus*	-9.5000E-02	1.0749	2.1688	-1.1931	.6648	2.289E-02
	Little Athapap. *C. zenithicus*	-.5131	-.7031	-1.6092	-1.3861	.4171	-.2609
	Great Slave Lake *C. zenithicus*	-.4599	**3.6750**	**4.7189**	-2.3571	-1.3281	2.6481
	Sandy Lake *C. zenithicus*	-1.2720	-.5071	1.1398	-.3849	.8399	-3.8000E-02
	Lake Nipigon *C. zenithicus*	-.9679	.4809	.7969	.6091	-.7552	.7890
	Barrow Lake *C. zenithicus*	1.1719	.2168	.4888	**-7.2831**	-1.5270	.2040
	Barrow Lake *C. artedi*	**-2.0781**	**2.4009**	2.3487	**-4.3719**	.7249	-1.7320
	Bocquene Lake "s" *C. artedi*	-.7430	**3.5709**	**6.2528**	**-2.7871**	.5229	**2.8890**
	Bocquene Lake "t" *C. artedi*	**-1.8460**	**2.9612**	**3.1147**	**-4.1761**	1.5088	.3870
	Daly Lake *C. artedi*	-1.4180	**2.7919**	**3.1269**	**-4.7970**	3.1459	-.6221
	Myers Lake *C. artedi*	-1.0880	**4.5710**	**3.5718**	**-8.8540**	.8429	-1.7330
	Ryan Lake lgr *C. artedi*	**-2.3572**	**2.7129**	2.1698	**-5.1640**	.8799	-.6749
	Ryan Lake hgr *C. artedi*	**-2.3921**	**1.8218**	.1727	**-5.6421**	-.3862	**-4.1580**
	Unnamed Lake *C. artedi*	**-1.9111**	**3.1788**	**3.8369**	**-2.4940**	1.4569	.1070
Little Athapapuskow *C. zenithicus*	Lake Superior *C. zenithicus*	.5001	-3.6077E-02	1.8959	**4.2680**	-3.7383	.4309
	Lake Winnipeg *C. zenithicus*	.3681	2.6121	**5.1202**	-2.8980E-02	-.2993	6.578E-02

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Little Athapapuskow *C. zenithicus*	Reindeer Lake *C. zenithicus*	.4181	1.7780	3.7780	.1930	.2477	.2838
	Basswood Lake *C. zenithicus*	.5131	.7031	1.6092	1.3861	-.4171	.2609
	Great Slave Lake *C. zenithicus*	5.324E-02	**4.3781**	**6.3281**	-.9710	-1.7452	2.9090
	Sandy Lake *C. zenithicus*	-.7589	.1960	2.7490	1.0012	.4228	.2229
	Lake Nipigon *C. zenithicus*	-.4548	1.1840	2.4061	1.9952	-1.1723	1.0499
	Barrow Lake *C. zenithicus*	**1.6851**	.9199	2.0980	**-5.8969**	-1.9442	.4649
	Barrow Lake *C. artedi*	-1.5649	3.1040	3.9579	**-2.9858**	.3078	-1.4712
	Bocquene Lake "s" *C. artedi*	-.2299	**4.2740**	**7.8620**	-1.4010	.1058	3.1499
	Bocquene Lake "t" *C. artedi*	-1.3329	**3.6643**	**4.7239**	**-2.7900**	1.0917	.6479
	Daly Lake *C. artedi*	-.9049	**3.4950**	**4.7361**	**-3.4109**	2.7287	-.3612
	Myers Lake *C. artedi*	-.5748	**5.2741**	**5.1810**	**-7.4679**	.4257	-1.4722
	Ryan Lake lgr *C. artedi*	**-1.8441**	**3.4160**	3.7790	**-3.7779**	.4628	-.4140
	Ryan Lake hgr *C. artedi*	**-1.8789**	2.5249	1.7819	**-4.2560**	-.8033	**-3.8971**
	Unnamed Lake *C. artedi*	-1.3980	**3.8819**	**5.4461**	-1.1079	1.0398	.3679
Great Slave Lake *C. zenithicus*	Lake Superior *C. zenithicus*	.4469	**-4.4142**	-4.4322	**5.2390**	-1.9931	-2.4781
	Lake Winnipeg *C. zenithicus*	.3149	-1.7660	-1.2079	.9420	1.4459	**-2.8432**
	Reindeer Lake *C. zenithicus*	.3649	-2.6001	-2.5501	1.1640	1.9929	-2.6252
	Basswood Lake *C. zenithicus*	.4599	**-3.6750**	**-4.7189**	2.3571	1.3281	-2.6481
	Little Athapap. *C. zenithicus*	-5.3236E-02	**-4.3781**	**-6.3281**	.9710	1.7452	-2.9090
	Sandy Lake *C. zenithicus*	-.8121	**-4.1821**	-3.5791	1.9722	2.1680	**-2.6861**
	Lake Nipigon *C. zenithicus*	-.5081	-3.1941	-3.9220	2.9662	.5729	-1.8591
	Barrow Lake *C. zenithicus*	1.6318	**-3.4582**	**-4.2301**	**-4.9259**	-.1989	**-2.4441**
	Barrow Lake *C. artedi*	-1.6182	-1.2741	-2.3702	-2.0148	2.0530	**-4.3802**
	Bocquene Lake "s" *C. artedi*	-.2832	-.1041	1.5339	-.4300	1.8510	.2409
	Bocquene Lake "t" *C. artedi*	-1.3861	-.7138	-1.6043	-1.8190	2.8369	**-2.2611**
	Daly Lake *C. artedi*	-.9582	-.8831	-1.5920	-2.4399	4.4740	**-3.2702**
	Myers Lake *C. artedi*	-.6281	.8960	-1.1471	**-6.4969**	2.1710	**-4.3812**
	Ryan Lake lgr *C. artedi*	-1.8973	-.9621	-2.5491	-2.8069	2.2080	**-3.3230**
	Ryan Lake hgr *C. artedi*	-1.9322	-1.8532	**-4.5462**	-3.2850	.9419	**-6.8061**
	Unnamed Lake *C. artedi*	-1.4512	-.4962	-.8821	-.1369	2.7850	**-2.5411**
Sandy Lake *C. zenithicus*	Lake Superior *C. zenithicus*	1.2590	-.2321	-.8531	3.2668	-4.1611	.2080
	Lake Winnipeg *C. zenithicus*	1.1270	**2.4161**	2.3712	-1.0302	-.7221	-.1571
	Reindeer Lake *C. zenithicus*	**1.1770**	1.5820	1.0290	-.8082	-.1751	6.089E-02
	Basswood Lake *C. zenithicus*	1.2720	.5071	-1.1398	.3849	-.8399	3.800E-02
	Little Athapap. *C. zenithicus*	.7589	-.1960	-2.7490	-1.0012	-.4228	-.2229
	Great Slave Lake *C. zenithicus*	.8121	**4.1821**	3.5791	-1.9722	-2.1680	**2.6861**
	Lake Nipigon *C. zenithicus*	.3041	.9880	-.3429	.9940	-1.5951	.8270

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Sandy Lake *C. zenithicus*	Barrow Lake *C. zenithicus*	**2.4439**	.7239	-.6510	**-6.8981**	-2.3669	.2420
	Barrow Lake *C. artedi*	**-.8061**	**2.9080**	1.2089	**-3.9870**	-.1150	-1.6940
	Bocquene Lake "s" *C. artedi*	.5290	**4.0780**	**5.1130**	**-2.4022**	-.3170	**2.9270**
	Bocquene Lake "t" *C. artedi*	**-.5740**	**3.4683**	1.9749	**-3.7912**	.6689	.4250
	Daly Lake *C. artedi*	-.1460	**3.2990**	1.9871	**-4.4121**	**2.3060**	-.5841
	Myers Lake *C. artedi*	.1840	**5.0781**	**2.4320**	**-8.4691**	2.952E-03	-1.6950
	Ryan Lake lgr *C. artedi*	-1.0852	**3.2200**	1.0300	**-4.7791**	4.000E-02	-.6369
	Ryan Lake hgr *C. artedi*	**-1.1201**	**2.3289**	-.9671	**-5.2572**	-1.2261	**-4.1200**
	Unnamed Lake *C. artedi*	**-.6391**	**3.6859**	**2.6971**	-2.1091	.6170	.1450
Lake Nipigon *C. zenithicus*	Lake Superior *C. zenithicus*	.9549	-1.2201	-.5102	2.2729	-2.5660	-.6190
	Lake Winnipeg *C. zenithicus*	.8229	1.4281	2.7140	-2.0242	.8730	-.9841
	Reindeer Lake *C. zenithicus*	.8729	.5940	1.3719	-1.8022	1.4200	-.7661
	Basswood Lake *C. zenithicus*	.9679	-.4809	-.7969	-.6091	.7552	-.7890
	Little Athapap. *C. zenithicus*	.4548	-1.1840	-2.4061	-1.9952	1.1723	-1.0499
	Great Slave Lake *C. zenithicus*	.5081	3.1941	3.9220	-2.9662	-.5729	1.8591
	Sandy Lake *C. zenithicus*	-.3041	-.9880	.3429	-.9940	1.5951	-.8270
	Barrow Lake *C. zenithicus*	**2.1399**	-.2641	-.3081	**-7.8921**	-.7719	-.5850
	Barrow Lake *C. artedi*	-1.1101	1.9200	1.5518	**-4.9809**	1.4801	**-2.5210**
	Bocquene Lake "s" *C. artedi*	.2249	**3.0900**	**5.4559**	**-3.3962**	1.2781	2.1000
	Bocquene Lake "t" *C. artedi*	-.8781	**2.4803**	2.3177	**-4.7852**	2.2640	-.4020
	Daly Lake *C. artedi*	-.4501	**2.3110**	2.3300	**-5.4061**	**3.9010**	-1.4111
	Myers Lake *C. artedi*	-.1200	**4.0901**	2.7749	**-9.4631**	1.5980	**-2.5220**
	Ryan Lake lgr *C. artedi*	-1.3892	**2.2320**	1.3729	**-5.7731**	1.6351	-1.4639
	Ryan Lake hgr *C. artedi*	**-1.4241**	1.3409	-.6242	**-6.2511**	.3690	**-4.9470**
	Unnamed Lake *C. artedi*	-.9431	**2.6979**	3.0399	**-3.1030**	2.2121	-.6820
Barrow Lake *C. zenithicus*	Lake Superior *C. zenithicus*	-1.1849	-.9560	-.2021	**10.1650**	-1.7941	-3.4000E-02
	Lake Winnipeg *C. zenithicus*	-1.3169	1.6921	3.0222	**5.8680**	1.6449	-.3991
	Reindeer Lake *C. zenithicus*	**-1.2669**	.8581	1.6800	**6.0899**	2.1918	-.1811
	Basswood Lake *C. zenithicus*	-1.1719	-.2168	-.4888	**7.2831**	1.5270	-.2040
	Little Athapap. *C. zenithicus*	**-1.6851**	-.9199	-2.0980	**5.8969**	1.9442	-.4649
	Great Slave Lake *C. zenithicus*	-1.6318	**3.4582**	**4.2301**	**4.9259**	.1989	**2.4441**
	Sandy Lake *C. zenithicus*	**-2.4439**	-.7239	.6510	**6.8981**	**2.3669**	-.2420
	Lake Nipigon *C. zenithicus*	**-2.1399**	.2641	.3081	**7.8921**	.7719	.5850
	Barrow Lake *C. artedi*	**-3.2500**	**2.1840**	1.8599	**2.9112**	**2.2519**	**-1.9360**
	Bocquene Lake "s" *C. artedi*	**-1.9150**	**3.3541**	**5.7640**	**4.4959**	**2.0499**	**2.6850**
	Bocquene Lake "t" *C. artedi*	**-3.0179**	**2.7444**	**2.6259**	**3.1070**	**3.0358**	.1830
	Daly Lake *C. artedi*	**-2.5900**	**2.5751**	**2.6381**	**2.4860**	**4.6729**	-.8261

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Barrow Lake *C. zenithicus*	Myers Lake *C. artedi*	**-2.2599**	**4.3541**	**3.0830**	-1.5709	**2.3699**	**-1.9370**
	Ryan Lake lgr *C. artedi*	**-3.5291**	**2.4961**	1.6810	2.1191	**2.4069**	-.8789
	Ryan Lake hgr *C. artedi*	**-3.5640**	**1.6050**	-.3161	1.6410	1.1409	**-4.3620**
	Unnamed Lake *C. artedi*	**-3.0830**	**2.9620**	**3.3481**	**4.7891**	**2.9840**	-9.7022E-02
Barrow Lake *C. artedi*	Lake Superior *C. zenithicus*	**2.0651**	**-3.1401**	-2.0620	**7.2538**	-4.0461	1.9020
	Lake Winnipeg *C. zenithicus*	**1.9331**	-.4919	1.1623	2.9568	-.6071	1.5370
	Reindeer Lake *C. zenithicus*	**1.9831**	-1.3260	-.1799	**3.1788**	-6.0111E-02	1.7549
	Basswood Lake *C. zenithicus*	**2.0781**	**-2.4009**	-2.3487	**4.3719**	-.7249	1.7320
	Little Athapap. *C. zenithicus*	1.5649	-3.1040	-3.9579	**2.9858**	-.3078	1.4712
	Great Slave Lake *C. zenithicus*	1.6182	1.2741	2.3702	2.0148	-2.0530	**4.3802**
	Sandy Lake *C. zenithicus*	**.8061**	**-2.9080**	-1.2089	**3.9870**	.1150	1.6940
	Lake Nipigon *C. zenithicus*	1.1101	-1.9200	-1.5518	**4.9809**	-1.4801	**2.5210**
	Barrow Lake *C. zenithicus*	**3.2500**	**-2.1840**	-1.8599	**-2.9112**	**-2.2519**	**1.9360**
	Bocquene Lake "s" *C. artedi*	**1.3350**	**1.1700**	**3.9041**	**1.5848**	-.2020	**4.6210**
	Bocquene Lake "t" *C. artedi*	.2321	**.5603**	**.7659**	.1958	.7839	**2.1190**
	Daly Lake *C. artedi*	.6600	.3910	.7782	-.4252	**2.4210**	1.1099
	Myers Lake *C. artedi*	**.9901**	**2.1701**	1.2231	**-4.4821**	.1180	-1.0054E-03
	Ryan Lake lgr *C. artedi*	-.2791	.3120	-.1789	-.7921	.1550	1.0571
	Ryan Lake hgr *C. artedi*	-.3140	-.5790	**-2.1760**	-1.2702	-1.1111	**-2.4260**
	Unnamed Lake *C. artedi*	.1670	**.7779**	**1.4881**	**1.8779**	.7320	**1.8390**
Bocquene Lake "s" *C. artedi*	Lake Superior *C. zenithicus*	.7300	**-4.3101**	**-5.9661**	**5.6690**	-3.8441	-2.7190
	Lake Winnipeg *C. zenithicus*	.5980	-1.6619	-2.7418	1.3720	-.4051	**-3.0841**
	Reindeer Lake *C. zenithicus*	.6480	**-2.4960**	**-4.0840**	1.5940	.1419	-2.8661
	Basswood Lake *C. zenithicus*	.7430	**-3.5709**	**-6.2528**	**2.7871**	-.5229	**-2.8890**
	Little Athapap. *C. zenithicus*	.2299	**-4.2740**	**-7.8620**	1.4010	-.1058	-3.1499
	Great Slave Lake *C. zenithicus*	.2832	.1041	-1.5339	.4300	-1.8510	-.2409
	Sandy Lake *C. zenithicus*	-.5290	**-4.0780**	**-5.1130**	**2.4022**	.3170	**-2.9270**
	Lake Nipigon *C. zenithicus*	-.2249	**-3.0900**	**-5.4559**	**3.3962**	-1.2781	-2.1000
	Barrow Lake *C. zenithicus*	**1.9150**	**-3.3541**	**-5.7640**	**-4.4959**	**-2.0499**	**-2.6850**
	Barrow Lake *C. artedi*	**-1.3350**	**-1.1700**	**-3.9041**	**-1.5848**	.2020	**-4.6210**
	Bocquene Lake "t" *C. artedi*	**-1.1030**	-.6097	**-3.1381**	**-1.3890**	.9859	**-2.5020**
	Daly Lake *C. artedi*	-.6750	**-.7790**	**-3.1259**	**-2.0099**	**2.6230**	**-3.5111**
	Myers Lake *C. artedi*	-.3449	1.0001	**-2.6810**	**-6.0669**	.3200	**-4.6220**
	Ryan Lake lgr *C. artedi*	**-1.6141**	-.8580	**-4.0830**	**-2.3769**	.3570	**-3.5639**
	Ryan Lake hgr *C. artedi*	**-1.6490**	**-1.7491**	**-6.0801**	**-2.8550**	-.9091	**-7.0470**
	Unnamed Lake *C. artedi*	**-1.1680**	-.3921	**-2.4159**	.2931	.9340	**-2.7820**

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Bocquene Lake "t" *C. artedi*	Lake Superior *C. zenithicus*	**1.8330**	**-3.7004**	-2.8279	**7.0580**	**-4.8300**	-.2170
	Lake Winnipeg *C. zenithicus*	**1.7010**	-1.0522	.3963	2.7610	-1.3910	-.5821
	Reindeer Lake *C. zenithicus*	**1.7510**	-1.8863	-.9459	**2.9830**	-.8440	-.3641
	Basswood Lake *C. zenithicus*	**1.8460**	**-2.9612**	**-3.1147**	**4.1761**	-1.5088	-.3870
	Little Athapap. *C. zenithicus*	1.3329	**-3.6643**	**-4.7239**	**2.7900**	-1.0917	-.6479
	Great Slave Lake *C. zenithicus*	1.3861	.7138	1.6043	1.8190	-2.8369	**2.2611**
	Sandy Lake *C. zenithicus*	**.5740**	**-3.4683**	-1.9749	**3.7912**	-.6689	-.4250
	Lake Nipigon *C. zenithicus*	.8781	**-2.4803**	-2.3177	**4.7852**	-2.2640	.4020
	Barrow Lake *C. zenithicus*	**3.0179**	**-2.7444**	**-2.6259**	**-3.1070**	**-3.0358**	-.1830
	Barrow Lake *C. artedi*	-.2321	**-.5603**	**-.7659**	-.1958	-.7839	**-2.1190**
	Bocquene Lake "s" *C. artedi*	**1.1030**	.6097	**3.1381**	**1.3890**	-.9859	**2.5020**
	Daly Lake *C. artedi*	.4280	-.1693	1.223E-02	-.6209	1.6371	-1.0091
	Myers Lake *C. artedi*	.7580	**1.6098**	.4572	**-4.6779**	-.6659	**-2.1200**
	Ryan Lake lgr *C. artedi*	-.5112	-.2483	-.9449	-.9879	-.6289	-1.0619
	Ryan Lake hgr *C. artedi*	-.5461	**-1.1394**	**-2.9419**	-1.4660	**-1.8950**	**-4.5450**
	Unnamed Lake *C. artedi*	-6.5067E-02	.2176	.7222	**1.6821**	-5.1878E-02	-.2800
Daly Lake *C. artedi*	Lake Superior *C. zenithicus*	1.4050	**-3.5311**	-2.8402	**7.6790**	**-6.4670**	.7921
	Lake Winnipeg *C. zenithicus*	1.2730	-.8829	.3841	**3.3820**	**-3.0280**	.4270
	Reindeer Lake *C. zenithicus*	**1.3230**	-1.7170	-.9581	**3.6039**	-2.4811	.6450
	Basswood Lake *C. zenithicus*	1.4180	**-2.7919**	**-3.1269**	**4.7970**	-3.1459	.6221
	Little Athapap. *C. zenithicus*	.9049	**-3.4950**	**-4.7361**	**3.4109**	-2.7287	.3612
	Great Slave Lake *C. zenithicus*	.9582	.8831	1.5920	2.4399	-4.4740	**3.2702**
	Sandy Lake *C. zenithicus*	.1460	**-3.2990**	-1.9871	**4.4121**	**-2.3060**	.5841
	Lake Nipigon *C. zenithicus*	.4501	**-2.3110**	-2.3300	**5.4061**	**-3.9010**	1.4111
	Barrow Lake *C. zenithicus*	**2.5900**	**-2.5751**	**-2.6381**	**-2.4860**	**-4.6729**	.8261
	Barrow Lake *C. artedi*	-.6600	-.3910	-.7782	.4252	**-2.4210**	-1.1099
	Bocquene Lake "s" *C. artedi*	.6750	.7790	**3.1259**	**2.0099**	**-2.6230**	**3.5111**
	Bocquene Lake "t" *C. artedi*	-.4280	.1693	-1.2229E-02	.6209	-1.6371	1.0091
	Myers Lake *C. artedi*	.3301	**1.7791**	.4450	**-4.0570**	**-2.3030**	-1.1110
	Ryan Lake lgr *C. artedi*	-.9391	-7.9000E-02	-.9571	-.3670	**-2.2660**	-5.2821E-02
	Ryan Lake hgr *C. artedi*	-.9740	-.9701	**-2.9541**	-.8450	**-3.5320**	**-3.5359**
	Unnamed Lake *C. artedi*	-.4930	.3869	.7100	**2.3031**	-1.6889	.7291
Myers Lake *C. artedi*	Lake Superior *C. zenithicus*	1.0750	**-5.3102**	-3.2851	**11.7359**	-4.1640	1.9030
	Lake Winnipeg *C. zenithicus*	.9430	**-2.6620**	-6.0866E-02	**7.4389**	-.7250	1.5380
	Reindeer Lake *C. zenithicus*	.9930	**-3.4961**	-1.4030	**7.6609**	-.1781	1.7559
	Basswood Lake *C. zenithicus*	1.0880	**-4.5710**	**-3.5718**	**8.8540**	-.8429	1.7330
	Little Athapap. *C. zenithicus*	.5748	**-5.2741**	**-5.1810**	**7.4679**	-.4257	1.4722

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Myers Lake	Great Slave Lake *C. zenithicus*	.6281	-.8960	1.1471	**6.4969**	-2.1710	**4.3812**
C. artedi	Sandy Lake *C. zenithicus*	-.1840	**-5.0781**	**-2.4320**	**8.4691**	-2.9524E-03	1.6950
	Lake Nipigon *C. zenithicus*	.1200	**-4.0901**	-2.7749	**9.4631**	-1.5980	**2.5220**
	Barrow Lake *C. zenithicus*	**2.2599**	**-4.3541**	**-3.0830**	1.5709	-2.3699	**1.9370**
	Barrow Lake *C. artedi*	**-.9901**	**-2.1701**	-1.2231	**4.4821**	-.1180	1.005E-03
	Bocquene Lake "s" *C. artedi*	.3449	**-1.0001**	**2.6810**	**6.0669**	-.3200	**4.6220**
	Bocquene Lake "t" *C. artedi*	-.7580	**-1.6098**	-.4572	**4.6779**	.6659	**2.1200**
	Daly Lake *C. artedi*	-.3301	**-1.7791**	-.4450	**4.0570**	**2.3030**	1.1110
	Ryan Lake lgr *C. artedi*	-1.2692	**-1.8581**	-1.4020	**3.6900**	3.705E-02	1.0581
	Ryan Lake hgr *C. artedi*	**-1.3041**	**-2.7491**	**-3.3991**	**3.2119**	-1.2290	**-2.4250**
	Unnamed Lake *C. artedi*	**-.8231**	**-1.3922**	.2650	**6.3600**	.6141	**1.8400**
Ryan Lake lgr	Lake Superior *C. zenithicus*	**2.3442**	**-3.4521**	-1.8831	**8.0459**	-4.2011	.8449
C. artedi	Lake Winnipeg *C. zenithicus*	**2.2122**	-.8039	1.3412	**3.7489**	-.7621	.4798
	Reindeer Lake *C. zenithicus*	**2.2622**	-1.6380	-1.0000E-03	**3.9709**	-.2151	.6978
	Basswood Lake *C. zenithicus*	**2.3572**	**-2.7129**	-2.1698	**5.1640**	-.8799	.6749
	Little Athapap. *C. zenithicus*	**1.8441**	**-3.4160**	-3.7790	**3.7779**	-.4628	.4140
	Great Slave Lake *C. zenithicus*	1.8973	.9621	2.5491	2.8069	-2.2080	**3.3230**
	Sandy Lake *C. zenithicus*	1.0852	**-3.2200**	-1.0300	**4.7791**	-4.0000E-02	.6369
	Lake Nipigon *C. zenithicus*	1.3892	**-2.2320**	-1.3729	**5.7731**	-1.6351	1.4639
	Barrow Lake *C. zenithicus*	**3.5291**	**-2.4961**	-1.6810	-2.1191	**-2.4069**	.8789
	Barrow Lake *C. artedi*	.2791	-.3120	.1789	.7921	-.1550	-1.0571
	Bocquene Lake "s" *C. artedi*	**1.6141**	.8580	**4.0830**	**2.3769**	-.3570	**3.5639**
	Bocquene Lake "t" *C. artedi*	.5112	.2483	.9449	.9879	.6289	1.0619
	Daly Lake *C. artedi*	.9391	7.900E-02	.9571	.3670	**2.2660**	5.282E-02
	Myers Lake *C. artedi*	1.2692	**1.8581**	1.4020	**-3.6900**	-3.7048E-02	-1.0581
	Ryan Lake hgr *C. artedi*	-3.4886E-02	-.8911	**-1.9971**	-.4781	-1.2661	**-3.4831**
	Unnamed Lake *C. artedi*	.4461	.4659	1.6671	**2.6700**	.5770	.7819
Ryan Lake hgr	Lake Superior *C. zenithicus*	**2.3791**	**-2.5610**	.1140	**8.5240**	-2.9350	**4.3280**
C. artedi	Lake Winnipeg *C. zenithicus*	**2.2471**	8.714E-02	**3.3382**	**4.2270**	.5040	**3.9629**
	Reindeer Lake *C. zenithicus*	**2.2971**	-.7469	1.9961	**4.4490**	1.0509	**4.1809**
	Basswood Lake *C. zenithicus*	**2.3921**	**-1.8218**	-.1727	**5.6421**	.3862	**4.1580**
	Little Athapap. *C. zenithicus*	**1.8789**	-2.5249	-1.7819	**4.2560**	.8033	**3.8971**
	Great Slave Lake *C. zenithicus*	1.9322	1.8532	**4.5462**	3.2850	-.9419	**6.8061**
	Sandy Lake *C. zenithicus*	**1.1201**	**-2.3289**	.9671	**5.2572**	1.2261	**4.1200**
	Lake Nipigon *C. zenithicus*	**1.4241**	-1.3409	.6242	**6.2511**	-.3690	**4.9470**
	Barrow Lake *C. zenithicus*	**3.5640**	**-1.6050**	.3161	-1.6410	-1.1409	**4.3620**
	Barrow Lake *C. artedi*	.3140	.5790	**2.1760**	1.2702	1.1111	**2.4260**

Appendix 2 con't.

Character		Gillraker length	Upper jaw	Truss 1	Truss 3	Truss 5	Truss 12
Population 1	*Population 2*						
Ryan Lake hgr *C. artedi*	Bocquene Lake "s" *C. artedi*	**1.6490**	**1.7491**	**6.0801**	**2.8550**	.9091	**7.0470**
	Bocquene Lake "t" *C. artedi*	.5461	**1.1394**	**2.9419**	1.4660	**1.8950**	**4.5450**
	Daly Lake *C. artedi*	.9740	.9701	**2.9541**	.8450	**3.5320**	**3.5359**
	Myers Lake *C. artedi*	**1.3041**	**2.7491**	**3.3991**	**-3.2119**	1.2290	**2.4250**
	Ryan Lake lgr *C. artedi*	3.489E-02	.8911	**1.9971**	.4781	1.2661	**3.4831**
	Unnamed Lake *C. artedi*	.4810	**1.3570**	**3.6641**	**3.1481**	**1.8431**	**4.2650**
Unnamed Lake *C. artedi*	Lake Superior *C. zenithicus*	**1.8981**	**-3.9180**	**-3.5501**	**5.3759**	**-4.7781**	6.302E-02
	Lake Winnipeg *C. zenithicus*	**1.7661**	-1.2698	-.3259	1.0789	-1.3391	-.3021
	Reindeer Lake *C. zenithicus*	**1.8161**	-2.1039	-1.6681	1.3009	-.7921	-8.4089E-02
	Basswood Lake *C. zenithicus*	**1.9111**	**-3.1788**	**-3.8369**	**2.4940**	-1.4569	-.1070
	Little Athapap. *C. zenithicus*	1.3980	**-3.8819**	**-5.4461**	1.1079	-1.0398	-.3679
	Great Slave Lake *C. zenithicus*	1.4512	.4962	.8821	.1369	-2.7850	**2.5411**
	Sandy Lake *C. zenithicus*	**.6391**	**-3.6859**	**-2.6971**	2.1091	-.6170	-.1450
	Lake Nipigon *C. zenithicus*	.9431	**-2.6979**	-3.0399	**3.1030**	-2.2121	.6820
	Barrow Lake *C. zenithicus*	**3.0830**	**-2.9620**	**-3.3481**	**-4.7891**	**-2.9840**	9.702E-02
	Barrow Lake *C. artedi*	-.1670	**-.7779**	**-1.4881**	**-1.8779**	-.7320	**-1.8390**
	Bocquene Lake "s" *C. artedi*	**1.1680**	.3921	**2.4159**	-.2931	-.9340	**2.7820**
	Bocquene Lake "t" *C. artedi*	6.507E-02	-.2176	-.7222	**-1.6821**	5.188E-02	.2800
	Daly Lake *C. artedi*	.4930	-.3869	-.7100	**-2.3031**	1.6889	-.7291
	Myers Lake *C. artedi*	**.8231**	**1.3922**	-.2650	**-6.3600**	-.6141	**-1.8400**
	Ryan Lake lgr *C. artedi*	-.4461	-.4659	-1.6671	**-2.6700**	-.5770	-.7819
	Ryan Lake hgr *C. artedi*	-.4810	**-1.3570**	**-3.6641**	**-3.1481**	**-1.8431**	**-4.2650**