AN ANALYSIS OF THE TAXONOMIC STATUS OF THE <u>COREGONUS</u> <u>AUTUMNALIS</u> SPECIES COMPLEX IN NORTH AMERICA, AND AN INVESTIGATION OF THE LIFE HISTORIES OF WHITEFISHES AND CISCOES (PISCES;COREGONINAE) IN NORTH AMERICA AND EURASIA

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By

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ABSTRACT

Aspects of the biology and taxonomy of the *Coregonus autumnalis* species complex were investigated in this study. The taxonomic and zoogeographic relationship of *Coregonus autumnalis* and *C. laurettae* was examined using morphometric, meristic, and distribution data. The morphometric data, a series of head and body measurements, was analyzed using a discriminant function analysis. The percentage of fish misclassified in the analysis was found to be higher than what would be expected for two distinct species, and was more indicative of subspecies, or stocks. The only meristic variable found to be significantly different was gill raker counts for the lower branch of the first gill arch. This character was originally used to separate the two species. An examination of the distribution of gill raker counts between the sample sites along the Beaufort Sea coast revealed a consistent percentage of the fish from the Mackenzie River with gill raker counts representative of the Yukon River species. This percentage was maintained in the hypothesized area of sympatry between the two species. It was concluded, from this analysis, that the original description was incorrect in the establishment of two reproductively isolated species with a single area of sympatry, based on gill raker counts. The actual situation is more likely that of two allopatric subspecies, with no area of sympatry. The distribution data were also analyzed to determine the support for the original zoogeographic hypothesis proposed to explain the separation of the two forms. It was concluded that the Bering Land Bridge was probably not responsible for this, as the present-day distribution of the two populations does not reflect ranges that could have been fragmented by the uplifting of the land bridge. An alternative hypothesis, which better fits the current distribution patterns of each form, involves known stream captures and headwater transfers between the Mackenzie and Yukon Rivers. Insufficient information is presently available to determine the direction of the transfer, or through which river system the transfer was made.

Life histories were investigated at a number of levels. Arctic and Bering cisco populations were investigated using one-way analysis of variance and multiple analysis of covariance. No significant differences were found within the populations for reproductive variables but the two populations differed significantly from each other. It was concluded that, based on the occurrence of alternate spawning and its relatively short life span, Arctic cisco populations appeared unable to compensate reproductively for the rigorous conditions encountered in northern latitudes. Least cisco (C. sardinella) populations were investigated at the same levels. Between latitude comparisons were made using Mackenzie and Yukon River populations. As with Arctic ciscoes, no significant differences were found within populations for reproductive variables, but significant differences were seen in between population comparisons. It was concluded that northern least ciscoes, by virtue of their longer lifespan, are better able to compensate reproductively for the poor conditions encountered in the north than Arctic ciscoes. A second analysis of a number of least cisco populations inhabiting the same latitude found that anadromous populations were larger and more fecund. However, analysis of covariance detected no significant difference in fecundity between populations. An analysis of gonad weight among sympatric coregonines along the Beaufort Sea coast was conducted using an analysis of covariance but again, no significant difference was detected. A principal components analysis was used to determine patterns of life history variation in members of the subfamily Coregoninae using populations from North America and Eurasia. The effects of both phylogeny and latitude were examined. No significant trends in life history traits associated with latitude were found, although the subgenus _Coregonus_ (_coregonus_) did show a non-significant increase in egg size and number of broods with latitude, the subgenus _Coregonus_ (_leucichthys_) showed non-significant inverse relationship for these variables and the genus _Prosopium_ showed a non-significant inverse relationship for age and growth related variables. A number of genera and species appeared to be constrained by phylogeny and were unable to adapt completely to the environmental constraints imposed by northern environments. It was concluded that, despite this apparent inability to adapt, the great deal of variability of life histories demonstrated a large degree of plasticity in the subfamily.

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GENERAL INTRODUCTION

Recent economic development activities in the U.S. and Canadian Beaufort Sea Regions have focused attention on the organisms inhabiting the area. Among those of interest are the populations of the salmonid fish subfamily, Coregoninae.

Aside from their subsistence and commercial importance, the coregonines provide a field case study for such theoretical considerations as the nature of species, the effect of environmental conditions on both morphology and life history, and the role of vicariant events and dispersal mechanisms in determining zoogeographic origin and range. They also present an opportunity to test the role of phylogeny in constraining reproductive plasticity.

The coregonine populations of the Beaufort Sea coast contain at least one species complex consisting of two species of questionable status, and are widely distributed over both latitude and longitude. They also show a great deal of phenotypic plasticity, which could further reflect differing genotypes and life history strategies, and demonstrate behavioral traits, such as anadromy, that have been shown to influence life histories in other fishes (Gross et al, 1988).

Early research in the region concentrated on either taxonomic descriptions (Dymond, 1943; McPhail, 1966) or obtaining baseline life history data (Wohlschlagg, 1954;

Cohen, 1954; Hatfield et al., 1972; Stein et al., 1973; Percy, 1975; Bond, 1982; Lawrence et al., 1984; Bond and Erickson, 1985). While these studies provided a great deal of information concerning life histories, the qualitative nature of these works, in some cases, has precluded the testing of ecological theory.

The present study consists of two major parts. The first is a consideration of the taxonomic relationship between the members of the *Coregonus autumnalis* complex, *C. autumnalis* (Arctic cisco) and *C. laurettae* (Bering cisco). The second deals with a detailed comparison of life history within and between populations of the above fish, and a similar analysis of the sympatric species, *Coregonus sardinella* (least cisco). As well, six populations of *C. sardinella* which exhibit differing phenotypic and behavioral responses to environmental conditions are contrasted and reproductive variables in sympatric coregonine populations along the Beaufort Coast are compared. Finally, a multivariate analysis of life history variables is made among and between coregonine populations from Europe and North America to determine: 1) if populations on both continents are affected similarly by north-south differences in environment; 2) whether any response to latitude is consistent among taxonomic groups between continents; and 3) the roles of environmental variation and phylogeny in the expression of coregonine life histories.

SYSTEMATICS OF THE *Coregonus autumnalis* COMPLEX

INTRODUCTION

The species level taxonomic relationships within the whitefishes and ciscoes (subfamily Coregoninae, family Salmonidae) are not clear. These fishes are known to hybridize readily with one another (Berg, 1948), and introgression is not an uncommon phenomenon (Smith, 1964; Svardson, 1965; Behnke, 1972; Todd et al., 1981). Most of the meristic and morphometric characteristics used in other fish families as identifying features are quite plastic in the coregonines and may undergo a great deal of environmental modification (Behnke, 1972). An exception to this appears to be gill raker numbers. Svardson (1961, 1965) documented the results of a series of transplant experiments on gill raker numbers and found this characteristic to exhibit a great deal of environmental stability making it useful as a taxonomic character. Despite this work, a great deal of controversy still exists as to the plasticity of this characteristic and its use in separating closely related species of whitefishes (Bodaly, 1979; Lindsey, 1981)

The relationships within the *Coregonus autumnalis* complex provide an example of the problems encountered in using gill raker numbers in coregonine taxonomy. The complex presently contains *C. autumnalis* Pallas, the Arctic cisco, and *C. laurettae* Bean, the Bering cisco. The distributions of the two species are as follows: *C. autumnalis* is found from Hazen Point in the Northwest Territories of Canada west to the Mezen River in the U.S.S.R., with disjunct populations occurring in Ireland. *C. laurettae* ranges from the Yukon River/Kuskokwin River delta region of Alaska north to Point Barrow and east to the Oliktok Point Region of Alaska (McPhail, 1966; Alt, 1973; Morrow, 1979). A recent report has been made of two Bering cisco individuals on the Soviet Bering coast (Chereshnev, 1985). Bean (1882) had originally described *C. laurettae* as a new species of cisco closely related to the Arctic cisco, *C. autumnalis*, and the lake cisco, *C. artedi* based on counts and measurements from four specimens from the Alaskan coast.

Dymond (1943) in his "informal" revision of northwestern Canadian whitefishes and ciscoes found that the measurements and counts of *C. laurettae* overlapped with those of *C. autumnalis*, and considered the two species to represent a single species, *Coregonus autumnalis*. Walters (1955) concurred. McPhail (1966) used counts of gill rakers from the lower branch of the first gill arch of approximately 135 specimens which encompassed the entire North American range of this species to split the complex back into two species. McPhail plotted the distributions of these counts and noted the presence of two modes at either end of the range. A bimodal pattern was also detected in a small sample collected from the Colville River-Oliktok Point region of the Alaskan Beaufort Sea coast (McPhail, 1966). It was determined, using these data, that a break between the two species came at the modal discontinuity gill raker count of 25; a count of 25 or less indicated a Bering cisco, while a count of greater than 25 indicated an Arctic cisco. This sample represented the area of sympatry between the two species. The speciation process, as hypothesized by McPhail (1966), was that an originally contiguous population of ciscoes became separated into two allopatric populations by the uplifting of the Bering Land Bridge during the Wisconsin glaciation. The subsequent sinking of the Land Bridge during the retreat of the glaciers enabled the populations, which had undergone evolution in allopatry, to become sympatric. The presence of reproductive isolation, which had evolved during this time spent in allopatry, was demonstrated as maintenance of bimodal gill raker counts in this area of sympatry. The present study examines the relationship of the two species based on new information collected during the course of this study, evaluates the relationship presented by McPhail (1966), and proposes a different view of the species complex and its recent evolutionary history incorporating the role of stream transfers in the separation of the two populations.

1.1. Taxonomic history of the subfamily Coregoninae

The genus Coregonus was first established by Linneaus in 1748 as Salmo. Cope (1872) considered the differences between the Coregoninae and Salmoninae to be sufficient to regard each as a separate family. The family Coregonidae was to contain those fish with united parietals and the Salmonidae would be those with the parietals divided by the supraoccipital.

Gill (1895) considered the parietals in the Coregonidae as not united and re-established the two subfamilies. Regan (1914) thought that gill characters were not appropriate to distinguish the two subfamilies but retained the designations defining the coregonines as being salmonids "with the parietals meeting in the mainline; teeth on the vomer and tongue, when present, in several series; scales numbering 13 or less in a transverse series from the origin of the dorsal fin to the lateral line". Koelz (1929) followed other American writers who in turn followed Cope and kept the family designation of Coregonidae.

Vladykov (1970) concurred with Koeltz. However, Behnke (1972), citing Greenwood et al. (1966), thought that the great diversity within the order Salmoniformes and the essential uniform nature of the family Salmonidae in regards to such fundamental characteristics as skull, caudal skeleton, pectoral girdle, and DNA content of chromosomes made for the arrangement of three subfamilies (Coregoninae, Salmoninae, and Thymallinae) within the Salmonidae. The literature is very fragmented on just how to refer to the subfamily in question. The term coregonid (which refers to the family Coregonidae) appears perhaps more frequently, despite the fact that it suggests a now discredited taxonomy. This paper chooses to follow Nelson (1984) and refer to members of the subfamily as coregonines.

The taxonomic distinctions within the subfamily Coregoninae have undergone a great deal of transition, based upon changes in the validity of characteristics used. What follows is a description of the genera and their phylogenetic position. The differences between the genera, as may be seen below, are with one major exception, fairly clear cut.

Norden (1961) described the subfamily Coregoninae and the three recognized genera as follows:

> "Subfamily Coreqoninae - salmonid fishes with an orbitosphenoid, dermospenotic and hyperethmoid; no epipleurals or suprapreopercle; not more than fifteen dorsal fin rays; large rounded scales; no maxillary teeth; small ova and a post-larval stage; young with or without parr marks; and parietals meet at the mid-line.
>
> Genus <u>Prosopium</u> - Light boned coregonine fishes with an open orbital ring, short first supraorbital, small mouth, a basisphenoid and a basibranchial plate, no or weak teeth, long third post cleithrum, post orbitals in contact with preopercle, elongate supraethmoid, a single nasal flap, and parr marks in known juveniles."

The genus <u>Prosopium</u> is readily distinguishable by the single nose flap and juvenile parr marks, which are characteristics shared by the subfamily Salmoninae. Despite these rather obvious distinguishing characteristics Berg (1948) classified Prosopium as a subgenus of Coregonus.

> "Genus Stenodus - Heavy boned coregonine fishes with closed orbital ring, long first supraorbital and dermospenotic, a basisphenoid, no basibranchial plate, persistent jaw teeth, numerous teeth on vomer and palatine, rounded third postcleithrum, post orbitals not in contact with preopercle, short supraethmoid, and two nasal flaps." (Norden, 1961).

The major distinguishing feature in the genus Stenodus is the retention of their dentition throughout the adult form.

> "Genus Coregonus - Light boned coregonine fishes with an open orbital ring, intermediate sized first supraorbital, small mouth, no basibranchial plate, usually a basisphenoid, no or weak teeth, long third post cleithrum, post orbitals in contact with preopercle, short supraethmoid, no parr marks, and two nasal flaps." (Norden, 1961).

The taxonomic difficulties in this subfamily have come in distinguishing the members of the genus Coregonus, whitefishes and the ciscoes, two extremely diverse groups, from one another. Berg (1948) recognized the ciscoes as a distinct genus and therefore split Coregonus into two genera: Coregonus, the whitefishes and Leucichthys, the ciscoes. Norden (1961) in his osteological analysis of the Salmonidae found no support for the genus Leucichthys and recommended its submergence back into Coregonus. Behnke (1972) also suggested that the distinction was best made at the subgeneric level, as Coregonus (Coregonus), the whitefishes and Coregonus (Leucichthys), the ciscoes. This split is due to the recognized frequency of hybridization between the ciscoes and the whitefishes in nature, the high hybrid fertility, and the presence of a form that appears to be intermediate between the two, Coregonus ussuriensis, from the Ainur River, in the U.S.S.R.. Ferguson et al. (1978) questions the validity of the two subgenera, as some members of the Leucichthys subgenus appear more closely related to some members of the Coregonus subgenus than to each other. Nelson (1984) recognizes three genera in the subfamily: Coregonus, Prosopium, and Stenodus.

1.2. Phylogenetic relationships within the subfamily

The phylogeny of the subfamily Coregoninae is known and generally agreed upon to the level of genus. Smith (1957) considered Stenodus, with its resemblance to the subfamily Salmoninae, its less reduced teeth, and tendency to undertake extensive migrations as probably closest to the ancestral coregonine. Norden (1961) in his study of the osteology of the Salmonidae cites the single nasal flap, retention of parr marks and the presence of a basibranchial plate as evidence for the more primitive nature of Prosopium. Both Coregonus and Stenodus are marked by the loss of this plate. Behnke (1972), considered to be the latest authority on this topic, agreed and pointed out that the retention of primitive salmonine characters by Prosopium and the lack of maxillary teeth in Stenodus argued for the former as the most primitive genus.

1.3. An evaluation of taxonomic relationships within Eurasian *Coregonus* (*Leucichthys*) *autumnalis*

A great deal of intra-specific variability in morphology and meristics may be seen in *Coregonus autumnalis* and a number of its subspecies in Europe and Siberia. Berg (1948) described the omul (*C. autumnalis*) overall, as having 35-51 gill rakers. A range of 39-50 and a mean of 44.7 was found in the Yenisei River population and a range of 38-51 and mean of 46 in the Lena River population.

Berg also recognized a subspecies from Lake Baikal, *Coregonus autumnalis migratorius* with a gill raker count of 47-51 (mean of 48.5) which differed from the Yenisei form in the following characteristics: a larger eye, narrower forehead and somewhat greater number of gill rakers. The Baikal form was further subdivided into three races with differing life history characteristics and mean gill raker counts (43.1, 48.4 and 39.3). He further lists a separate species, *Coregonus subautumnalis*, which had a gill raker count of 45. This species had been described on the basis of a single specimen, taken from the Penzhina River, on the basis of a maxilary longer than the width of the suborbital, but it is now considered to be *Coregonus autumnalis* (Nikolsky and Reshetnikoff, 1970; Behnke, 1972).

Shaposhnikova (1970) analyzed Berg's *Coregonus autumnalis migratorius* and, on the basis of skeletal characteristics elevated this form to the species level, *C.*

migratorius. Behnke (1972) concurred and suggested full subspecific status for the three races of Baikal *C. migratorius*. However, Nikolsky and Reshetnikov (1970) disagreed, based on an extension of the range of gill raker counts to 32-54 to overlap the distribution of *C. autumnalis*. Current literature retains *C. autumnalis migratorius* (Smirnov et al., 1987).

Another subspecies of *Coregonus autumnalis* inhabits four lakes in northern Ireland: Lough Neagh, Lough Erne, Lough Ree and Lough Derg. This fish was described at different times as belonging to four other species (Maitland, 1970) and was also considered to be a separate species, *Coregonus pollan* (Gasowska, 1964). Behnke (1972) found the specimens of *C. pollan* to be indistinguishable from *C. autumnalis* and therefore considered it to be a subspecies of *C. autumnalis*. Behnke (1972) also concluded that, on the basis of this lack of differentiation, the separation of these forms occurred rather recently, perhaps since the last glaciation. Genetic analysis by Ferguson et al. (1978) confirmed this hypothesis; no difference between Alaskan *C. autumnalis* and Irish *C. autumnalis pollan* was found in any of the twenty four electrophoretic loci examined.

Based on the above, it can be seen that the picture presented by the species *Coregonus autumnalis* is one of considerable taxonomic uncertainty. The tremendous variability presented by the forms, subspecies and species suggest that a classification of *C. autumnalis* based on gill raker counts may be unwise, or at least somewhat premature. The differing gill raker counts, and the life history strategies of the Lake Baikal forms of *C. autumnalis* would, under these gill raker count criteria, confer species status to each because their mean gill raker numbers are (based on the sample size obtained) significantly different. The elevation of the Baikal form into a separate species may indeed be justified based on time of separation and the distinctiveness of skull osteology, however, this requires further analysis to determine if these characteristics have a clear genetic basis. Shaposhnikova (1970) had a limited amount of data with which to evaluate the validity of skull morphology criteria. If the criteria of Shaposhnikova (1970) and Behnke (1972) were applied to the Irish form, *C. autumnalis pollan*, it could be divided into a number of species. Regan (1914) distinguished it as three separate subspecies, as well as being different from the other British whitefishes based on its mouth characteristics. Ferguson et al. (1978) showed that such a species distinction would have been highly unwarranted based on genetic information.

1.4. A review of the taxonomic relationships of other coregonine fishes

As mentioned previously, the coregonine fishes show a great deal of morphological plasticity and similarity, as well as a propensity for hybridization and introgression (Smith, 1964; Todd et al., 1981). A great deal of research has been undertaken to determine the events and mechanisms responsible for the taxonomic relationships seen in the various groups of coregonines.

The major study dealing with taxonomic relationships in the North American members of the *Coregonus* (*Leucichthys*) is that of Koelz (1929). Working on the Great Lakes ciscoes, which at that time were considered part of the genus *Leucichthys*, he analyzed a number of morphological features with regard to their utility in taxonomic distinction. Measurements included length, snout to dorsal ray, snout to anal ray, dorsal fin to adipose fin, adipose fin to caudal fin, head length, head depth, occiput snout, maxillary, mandible, eye, fin length, depth, width, and a number of ratios from the above measurements. Counts included gill rakers, lateral line scales, longitudinal scale rows, fin rays, vertebrae, pyloric caecae and branchiostegal rays.

Koelz was able to use these morphological characters to separate the three genera (*Coregonus*, *Leucichthys* and *Prosopium*). Further examination of the genus *Leucichthys* in this region, revealed that only gill raker counts were reliable taxonomic characters. The other characters mentioned, which included length of the lower jaw, length of the maxillary and the pigmentation of the maxillary had their utility confined to the peculiar species "flock" of the Great Lakes. Koelz was able, however, through his analysis of variability, to determine that a number of morphologically different, species could be united as a single species, *Coregonus artedii*.

Svardson's (1950) research on whitefish populations in Sweden noted that the number of scales increased with body size and the number of gill rakers decreased. Conversely, Svardson (1952), commenting upon differing growth characteristics of whitefishes, found that body part growth differed when the fish were raised in different environments, but that gill raker counts appeared stable for the first year of transplant.

Svardson (1953) determined that two groups of coregonine sibling species existed: *C. albula* in eastern Asia and North America, and *C. lavaretus* in Europe and Western Russia. The great morphological similarity within these two sibling species was considered to be the result of environmental plasticity, but gill raker counts were the strongest genetic character for distinguishing the different species.

Svardson (1965) considered the diversity of forms seen in European whitefishes to be the result of: 1) the formation of sibling species in allopatry during successive glaciations; and 2) introgressions in sympatry. He thought the number of gill rakers was the only morphological character not considerably modified by environment, and proved this by transplants, artificial selection experiments and the presence of intermediate numbers in hybrids. He suggested that this characteristic was the only one stable enough to be used in taxonomic studies. These studies served to establish gill rakers as an appropriate taxonomic character for distinguishing species of coregonines.

Lindsey (1963b) stated that two groups of fish which were sympatric without interbreeding, in which every individual could be assigned to one or the other groups by morphology, should be two distinct species. This position was taken in reference to two sympatric forms of lake whitefish found in Yukon Territory lakes which had different numbers of gill raker counts and morphologies.

Lindsey (1981) summarized the information available and concluded that, while the number of gill rakers is relatively stable genetically, there is still some degree of plasticity in the character. This was based on the occurrence of a number of sympatric forms of whitefish with widely differing gill raker counts. These included the sympatric _Coregonus_ _clupeaformis_ populations in the Yukon (Bodaly, 1979) and Maine (Fenderson, 1964; Kirkpatrick and Selander, 1979), as well as the Baikal cisco (_Coregonus_ autumnalis migratorius), which has demonstrated shifts in gill raker number based on age and feeding mode (Smirnov et al., 1987). A number of other species show discontinuities of mean numbers of gill rakers throughout their ranges. These include Prosopium cylindraceum (McPhail and Lindsey, 1970), P. coulteri (McCart, 1966, 1970), and Coregonus clupeaformis (Lindsey et al., 1970; Franzin and Clayton, 1977). Lindsey suggested that the majority of these examples resulted from evolution in allopatry during the Wisconsin glaciation, and subsequent introgression of the forms from the two major refugia during the post-glacial period. This appears to be confirmed in the coregonine fishes as Franzin and Clayton (1977), Bodaly and Lindsey (1977), Bodaly (1977), and Foote (1980) have all found genetic evidence for the existence of refugial forms of Coregonus clupeaformis.

Bodaly (1977,1979) looked at sympatric whitefish in a lake in the Yukon Territory. A high degree of correlation was found between feeding types and modal gill raker counts, similar to that found by Lindsay (1963b). It was concluded by Bodaly that the high raker form probably evolved from the low raker form during and following isolation by the Wisconsin glaciation. More importantly, Bodaly considered it was possible to produce a high gill rakered population through selection. As a result, despite the heritability of gill raker numbers, this weakens their utility as a genetic marker.

McCart (1970), as the result of his study of "sibling" species of the pygmy whitefish Prosopium coulteri in Alaskan lakes, suggested that morphological traits could not be used to separate the forms, and that meristic characters were more conservative. Meristic characters for this species included gill rakers, caudal peduncle scale counts, dorsal finray counts, and pyloric caeca. He further hypothesized that two distinct refugia gave rise to the different forms determined by the meristic analysis, a conclusion similar to that of Svardson (1961). Svardson (1950) had noticed that in more slowly growing whitefish populations head size was larger, bodies were shallower, eyes larger and maxillaries larger. The dwarf form of P. coulteri seen by McCart (1966) had these characters, however, McCart did not invoke this work of Svardson's as evidence for his theory of the non-utility of morphological traits for separating sympatric forms.

Lindsey and Franzin (1972), also studying the same species as McCart (1970) (Prosopium coulteri), found the distribution of fish was highly disjunct, with two readily apparent forms. The morphologies of new specimens from the Peel River and Waterton Lakes did not match populations close to them and complicated the situation as first seen by McCart. Lindsey and Franzin suggested that a mixture of fish from six possible refugia may have been responsible for the observed character mosaic, with the Peel River form originating in a small local refugium. The character traits were the result of local environmental conditions, as had been suggested by other authors studying other fishes (Smirnov, 1969; Ustyugov, 1976).

In the U.S.S.R., Ustyugov (1976), studying variation in *C. albula sardinella* (he had united *C. albula* and *C. sardinella*), looked at a total of 30 body characters, of which 15 were meristic counts (including lateral line scales, number of vertebrae, length of base of dorsal fin, and height of dorsal fin). He determined that a single monotypic species had separated into local forms through a series of hydrological events. The most important was considered to be the regression and transgression of the sea, but this did not suggest a genetic basis for separating these local forms into species.

Gasowska (1964), in a taxonomic analysis of the British whitefishes, found that three fish, the Powan, the Gwyniad and the Schelly were simply different morphological forms of a single polytypic species. The minimal overlap in gill raker counts suggested a subspecific classification for these forms.

Dymond (1943), after observing *C. autumnalis* and *C. laurettae* in Alaska and the Mackenzie River, suggested that *C. laurettae* merely represented eastward extensions of *C. autumnalis*, based on overlaps in body measurements and meristics. At the same time, and using the same criteria, he lumped Schoefield's genus Argyrosomus (containing two species) into C. autumnalis. Walters (1955) concurred with this view as have several Russian authors (Andriayshev, 1964; Reshetnikoff, 1974).

Franzin and Clayton (1977), studying the genetic relationships of lake whitefish in western Canada, were able to detect the presence of two genetically differentiated forms. Two alternative hypotheses were erected to account for this: 1) post-glacial selection and mutation; and 2) a mixture of slightly different genetic stocks as the result of isolation in different refugia during the Pleistocene glaciation. The second hypothesis was considered to be correct on the basis of allele frequencies and determination of marker loci.

Foote (1980), using genetic characters, analyzed the whitefish populations in the Great Plains region and the Nahanni area of Canada and determined that the fish seen on the plains were derived solely from populations isolated in the Mississippian Refugium and that a possible "corridor" component to the genetic diversity of the lake whitefish in the region could be identified.

It is clear from this survey of coregonine taxonomic studies that: 1) a great deal of intra-specific variability in morphological and meristic characteristics is present. Even in cases where significant differences between mean values exist, the ranges may overlap completely; and 2) analysis of coregonine taxonomic relationships requires not only data on morphometrics and meristics but a knowledge of the distribution of characteristics over the range of the taxa in question, the distribution of the taxa (spatial and temporal) and aspects of their life history.

As well, the use of meristic and morpohometric characteristics in determining inter- and intra-specific relationships in non-coregonine fishes has met with mixed success (Crossman, 1966; Morrow, 1979; Gold, 1977). Species-level relationships have shown the least degree of responsiveness to the use of meristic and morphometric characters (McPhail, 1961; Morrow, 1979; McCart, 1980) with the most success coming in cases where geographic distance and/or the number of characters used in the analysis is greatest (Carscadden and Leggett, 1975; Sharpe et al., 1978). The most successful use of the technique is in distinguishing stocks and races, probably due to the lesser need for clear-cut distinctions (MacCrimmon and Claytor, 1985). Clearly those fish which represent the greatest latitudinal or geographic separation between populations, and the least amount of hybridization, are most likely to be successfully distinguished using these techniques.

1.5. A review of morphometric and meristic methodology

The utility of morphometric comparisons in vertebrate taxonomic studies has long been recognized. Measurements have been used to distinguish geographically isolated populations as well as to determine intra- and interspecific differences in a wide variety of fish species (Gilbert, 1969; Cowan, 1970; Reed and McCann, 1973; Lavin and McPhail, 1985; MacCrimmon and Claytor, 1985; Power and Ni, 1985; Strauss, 1985; Winans, 1985; Francis et al., 1986; Kenchington, 1986 and others). Within this broad framework there exists a number of differing analytical procedures. Univariate comparisons (eg. analysis of variance) of mean measurements are useful when sample sizes are sufficiently large or when comparisons are restricted to specific size ranges (Chernoff and Miller, 1986). Problems develop when a wide range of specimens is used in the analysis and the effect of differences in size must be removed (Mais, 1972; Sharp et al., 1978) or when a "shape component", which incorporates a variety of body and body part measurements, is suspected (Humphries et al., 1981; Rohlf and Bookstein, 1987; Bookstein et al., 1985; Willig et al., 1986). A long-accepted technique, recently fallen into some statistical disfavour, is that of establishing a proportion (or ratio) between the body measurement and some indication of size, usually a body length measurement such as standard length (Gilbert, 1969; Oxnard, 1978; Daniels and Moyle, 1984; Chernoff and Miller, 1986; Minckley and Minckley, 1986). This had been regarded as an effective means of standardizing different size classes of fish for statistical comparison and was the most common technique until the late 1970's. At that time, Atcheley et al. (1976) pointed out a number of statistical problems associated with ratios. These included: 1) compounding of error terms that occurs when the ratio is established; 2) alteration of the distributional properties of the data; 3) alteration of the correlation between variables used as the numerator, or the creation of spurious correlations; and 4) the inability of this technique to completely remove the influence of size (Atcheley et al., 1976; Atcheley, 1978; Atcheley and Anderson, 1978; Reist, 1985). These objections have led to suggestions that ratios not be used as a standardization technique in morphometric studies (Albrecht, 1978; Reist, 1985). Despite this, the use of such data recently by a number of authors illustrates the on-going nature of the controversy (Daniels and Moyle, 1984; Chernoff and Miller, 1986; Minckley and Minckley, 1986). Lemen (1983) suggested that a log of the ratio or a ratio of log transformed data could be used instead of the simple ratio comparison, but this was found to still be unacceptable in comparison with other techniques, as the effect of size was still not removed (Reist, 1985).

Statistically appropriate methodologies used to compensate for the effect of size in morphological studies include analysis of covariance and multivariate techniques such as principal components analysis (Reist, 1985). A number of investigators have determined that the first component in an analyis of morphometric data usually describes a size function (Thorpe, 1976; Lemen, 1983). Humphries et al. (1981) proposed removal of the size effect through "shearing", a process whereby population principal component scores were regressed against size and the residuals used to approximate a shape factor that could be compared among populations. The disadvantage of this method is its unreliability; frequently size is not totally explained by the first factor (Reist, 1985). Claytor and MacCrimmon (1986) in an analysis of five statistical techniques used to partition size from morphometric data, found the shearing technique useful only if there was some size overlap present in the populations examined. A number of authors have used the shearing technique in association with proportional standardization but have not addressed the problems associated with either methodology (Chernoff and Miller, 1986; Minckley and Minckley, 1986). A "hybrid" method using principle components analysis and ranking procedures was used by Chapleau and Pageau (1985) who ran a principal components analysis to select five characters, which were coded and used to assign fish to groups according to an index of these characters. This technique seems to be useful when applied to discrete data (such as meristics) rather than continuous (morphometric) data. Other investigators have determined that regressing the covariate (usually standard length) upon the variable of interest and then using the residuals in the analysis is an effective way of removing size while retaining the desired shape variables (Atcheley et al., 1976; Thorpe, 1976; Reist, 1985; Claytor and MacCrimmon, 1986). A somewhat similar technique involving standardizing all variables by adjusting them to a certain predetermined length, using the linear regression of the log value of each variable on the log of the standard length (McPhail, 1984; Lavin and McPhail, 1985), is problematical as differences in growth rates between two sample populations may serve to exaggerate any morphological differences (Reist, 1985).

A large number of meristic characters have been utilized in the past to classify populations and species of fish. These include just about anything that may be counted on a fish, such as gill raker counts (McPhail, 1966), branchiostegal counts (Crossman, 1966), lateral line scale counts (McCart and Pepper, 1971; Pivnicka and Hensel, 1978), vertebrae counts (Bodaly and Lindsey, 1977), head scale counts, and dorsal and anal fin ray counts (McPhail and Lindsey, 1970). These data are usually analyzed using means and/or distributions of counts and ranges. Statistical methodology, while not as complex in the analysis of these types of data, still involves some knowledge of the characters being studied. A significant difference in means may have little biological significance when the range or distribution of the character are analyzed. As well, major difficulties with this technique were discovered in the analysis of fish having a wide latitudinal or environmental range when it was found that these traits could be modified by environmental factors (McAllister et al., 1981; Beacham, 1985; Moodie, 1985). Prominent among these was the influence of temperature (Barlow, 1961; Lindsey, 1966). As a result, taxonomists now generally avoid dependence upon meristics as the sole factor in fish taxonomy. An exception to this in coregonines has been the use of gill raker counts. Increasingly, taxonomists are turning to the use of biochemical techniques as a means of avoiding this problem.

MATERIALS AND METHODS

2.1. Study areas

Samples of arctic cisco were taken from the following locations: Colville River, Alaska (41); Simpson Lagoon, Alaska (87); Prudhoe Bay, Alaska (47); Bollen Point, Alaska (15); Barter Island, Alaska (30); Spring River and Phillips Bay, Yukon Territories (330); Aklavik, Northwest Territories (12); Peel River Yukon Territories (45); and Point Lay, Alaska (1). Bering cisco were collected from Point Lay, Alaska (9) and the Yukon River near Ruby, Alaska (182) (Figure 1).

Collections were made during the following summer field seasons: Yukon River (1985), Pt. Lay (1983, 1984), Simpson Lagoon (1977, 1978, 1979), Prudhoe Bay (1983, 1984, 1988), Barter Island (1983), Phillips Bay (1985), Peel River (1986, 1988). Samples were collected from Bollen Pt, Spring River, and Aklavik in 1975. Samples from the Coville River were collected in the winters of 1983 and 1984.

Collection techniques included gillnets, beach seines, and fish wheels. Gill nets were both 2 1/2" stretched standard mesh and experimental mesh nets consisting of 1", 2", 3" and 4" stretched mesh panels. Beach seines consisted of a 30 ft-1/4" mesh bag seine and a 300 ft-1 1/2" mesh beach seine. The fish wheels had three 8 ft baskets covered with 2 1/2" mesh fencing.

Figure 1. Study areas

Legend

1 - Ruby, Alaska

2 - Point Lay, Alaska

3 - Colville River, Alaska

4 - Simpson Lagoon, Alaska

5 - Prudhoe Bay, Alaska

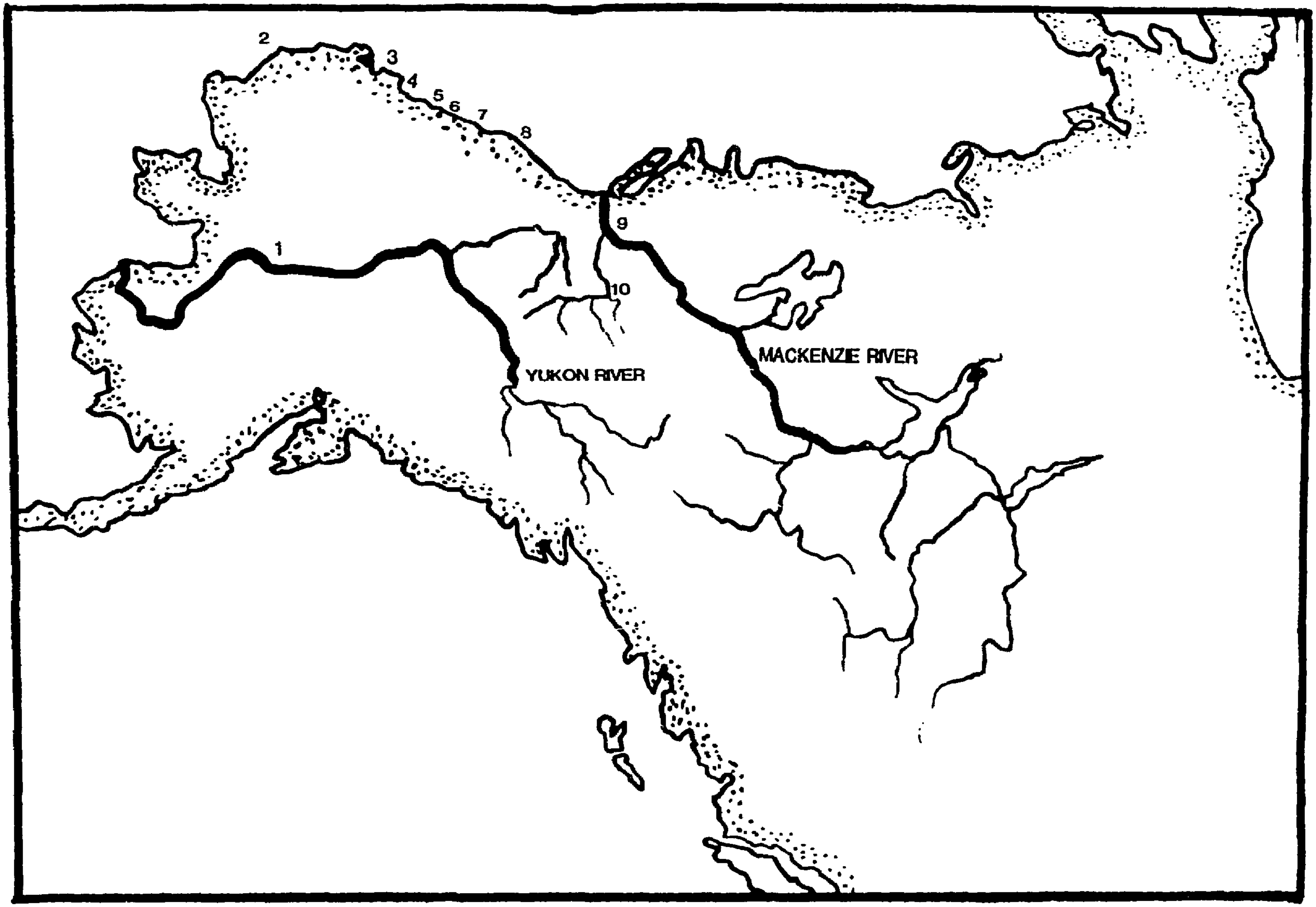
6 - Bollen Point, Alaska

7 - Barter Island, Alaska

8 - Phillips Bay, Yukon

9 - Aklavik, Northwest Territories

10 - Peel River, Yukon


2
3
4
5
6
7
8
1
9
10
YUKON RIVER
MACKENZIE RIVER

The following meristic counts were recorded: upper and lower gill rakers from the first gill arch, lateral line scales, and dorsal and anal fin rays. Morphometric measurements included: fork length, total weight, standard length, head length, body depth, eye diameter, caudal peduncle depth, opercule cover length and snout length.

2.2. Morphometric comparisons

Methods for Arctic cisco morphometrics:

Fork length : Distance from tip of snout to fork of caudal fin.

Standard length : Distance from tip of snout to the caudal base.

Head length : Distance from tip of snout to rear of opercular cover on the left side.

Body depth : Caliper distance from dorsal surface of body directly in front of dorsal fin to ventral surface at right angle to lateral line.

Width of eye orbit : Inside caliper measure of distance from front of eye orbit to rear on left side of fish. Calipers actual inserted partially into eye socket and spread firmly.

Width of caudal peduncle : Caliper distance from top to bottom of caudal peduncle including caudal fin rays pressed parallel to lateral line.

Width of opercular cover : Distance from preopercular to posterior edge of left operculum.

Snout length : Distance from front of eye orbit to tip of snout, same as pre-orbital length.

Counts and measurements were done from the left side of the fish where possible and followed Hubbs and Lagler (1958). Measurements were made using dial calipers accurate to 0.01 mm.

The measurements and counts were selected for the following reasons:

1. Previous studies in the region exist with the aforementioned measurements.
2. The characteristics of head length and associated measurements of head structure have long been utilized in coregonine taxonomic distinctions (Koelz, 1929).
3. Body depth was observed, in the field, as being potentially different in the two species in question (J. Helmericks, pers. comm.).
4. The counts were made, in the case of gill rakers, as taxonomically distinguishing features or with the potential to be so.

Statistical analyses were performed using the Statistical Program for the Social Sciences (SPSS^x version 3.0) on the VMS-VAX system at Memorial University of Newfoundland.

The morphometric data were subjected to discriminant function analysis in an effort to determine the taxonomic relationship between *Coregonus autumnalis* and *C. laurettae*. Discriminant function analysis can be used to group unknown samples by the use of two or more predetermined categorizations typified by two or more dependent measures (variables). The analysis derives one or more functions that best discriminate between the known groups. The maximum number of functions which can be derived is either one less than the number of groups or equal to the number of discriminating variables, if there are more groups than variables.

The assumptions are a multivariate normal distribution and equal variance-covariance matrices within each group. The test is considered to be quite robust. The objective was to discriminate between groups of fishes and to predict which category or group a fish falls, based on the values of the variables. Discriminant analysis is considered to be very parsimonious in that comparisons of a number of groups using a number of variables can be reduced to as few as one dimension which is the discriminant function. As well, if the clarity of the descriptions is good, the separation of the groups along one discriminant function is not related to any of the other functions (Stevens, 1986).

To classify a sample in which group membership is unknown, known groups can be used to generate the discriminant function, which is then used to classify the unknowns. The data in this study were first $\log_{10}$ transformed to conform to normality. Standard length was then regressed on the other variables and discriminant analysis was performed on the residuals, in the manner suggested by Reist (1985). Two known groups, of 75 fish each, were randomly selected and established as discriminators. The fish from the Yukon River were regarded as a pure stock of Bering cisco (based on gill raker counts), while the Mackenzie River fish (Peel River and Yukon Coast), with gill raker counts of greater than 26, were regarded as a pure stock of Arctic cisco. The presence of lower gill raker count fish in this population made this selective process necessary. These two groups were then analyzed to determine: 1) classification success; and 2) their ability to discriminate ungrouped specimens. A total of 602 fish were used in the analysis. The breakdown of sample sites and numbers were as follows: Yukon River (183), Point Lay (9), Colville River (30), Prudhoe Bay (24), Barter Island (30), Spring River and Phillips Bay (295) and Peel River (31).

RESULTS

3.1. Morphometric analysis

Two levels of discriminant analysis were performed. A step-wise analysis was done to determine which of the variables contributed the most to distinguishing the two groups, classified on the basis of gill raker counts. A direct analysis was done to determine the ability of all of the variables to distinguish species differences. Head length was the most useful variable in discriminating the groups, followed by depth of the caudal peduncle, eye orbit diameter, and snout length (Table 1). The depth of the caudal peduncle was the characteristic which accounted for the second largest amount of variation with the head characteristics of eye orbit and snout length completing the analysis. Body depth, which had been hypothesized as the chief distinguishing feature between the two species in the Colville River system did not enter the stepwise analysis at the selection level of 0.05 (Table 1).

Table 1. Stepwise discriminant analysis.

Variable	Step Entered	F-value	Wilk's Lambda	D. F.
log Head length	1	20.96	0.87665	1,149
log Caudal peduncle depth	2	46.88	0.61219	2,148
log Eye orbit diameter	3	34.60	0.58580	3,147
log Snout length	4	26.90	0.57570	4,146

Fork length and standard length were not used in this analysis. When body depth was forced into the analysis, no difference was seen in the effectiveness of the classification.

Using the above variables, the following misclassification rates were obtained: 15 percent of the Bering cisco from the original grouping sample were misclassified as Arctic cisco, and 20 percent of the Arctic cisco were classified as Bering cisco. When the ungrouped sample, containing the remaining Bering cisco from the Yukon River, the Arctic ciscos from the Mackenzie River, and the remaining fish from the other sample areas were classified using the grouped samples, the following misclassification rates were obtained: a 10 percent rate for Bering cisco from the Yukon River, a 15 percent rate for Point Lay Bering cisco and a 40 percent rate for Beufort Sea coast Bering cisco. For Arctic cisco the rates were: 30 percent for the Beaufort Sea coast in general, and 45 percent from the Colville River sample. None of the three Arctic ciscoes from Point Lay or the Yukon River were classified as such (Table 2). Ungrouped samples were identified as to species (group membership) by using gill raker counts.

To further break the samples down, the Prudhoe Bay misclassifications rates were 20 percent for Bering ciscoes and 66 percent for Arctic ciscoes. Rates for Barter Island were 100 percent for Bering ciscoes and 83 percent for

Arctic ciscoes. Peel River rates were 50 percent and 74 percent, respectively (Table 2).

Table 2. Misclassification rates

Site	Total	# misclassified	% incorrect
Yukon River	181 Bering	21	12
	2 Arctic	2	100
Point Lay	8 Bering	1	8
	1 Arctic	1	100
Colville R.	17 Bering	6	35
	13 Arctic	6	46
Prudhoe Bay	15 Bering	3	20
	9 Arctic	6	66
Barter Is.	2 Bering	2	100
	28 Arctic	23	83
Mackenzie R.	27 Bering	17	63
	268 Arctic	41	15
Peel R.	4 Bering	2	50
	27 Arctic	20	74

A second discriminant analysis was done using the same numbers of fish in each group, but chosen on a random basis without regard to gill raker number. These analyses did not increase the classification success.

In the hypothesized zone of sympatry between C. autumnalis and C. laurettae, the morphometric variables are successful in determining C. laurettae only about 65 percent of the time. A similar situation, only more pronounced, occurs when the "known" Bering cisco contained within the

Mackenzie River populations are analyzed. About 63 percent of these fish are classified as Arctic cisco (Table 2). When coupled with the nearly 15 percent misclassification rate of known Bering cisco, this certainly precludes the establishment of specific differences on the basis of morphometric characteristics but suggests that the two populations are recently separated. If the populations in question represented two good species, the discriminant analysis should not produce the picture seen in this study (Fig. 2)

3.2. Meristic analysis

Gill raker counts were done from all fish in the samples. An analysis of the distribution of the key character of gill raker counts reveals a different picture than that presented by McPhail (1966). As mentioned above, McPhail (1966) plotted the distribution of gill raker counts from approximately 120 specimens taken from the North American range of the *Coregonus autumnalis* complex. Two modes of gill raker were detected, one from the Yukon River and the other around the Mackenzie River. These modes were maintained in the Oliktok Point/Colville River area of Alaska. McPhail considered this to be the zone of sympatry between these populations and used it to determine the existence of *Coregonus autumnalis* and *C. laurettae*.

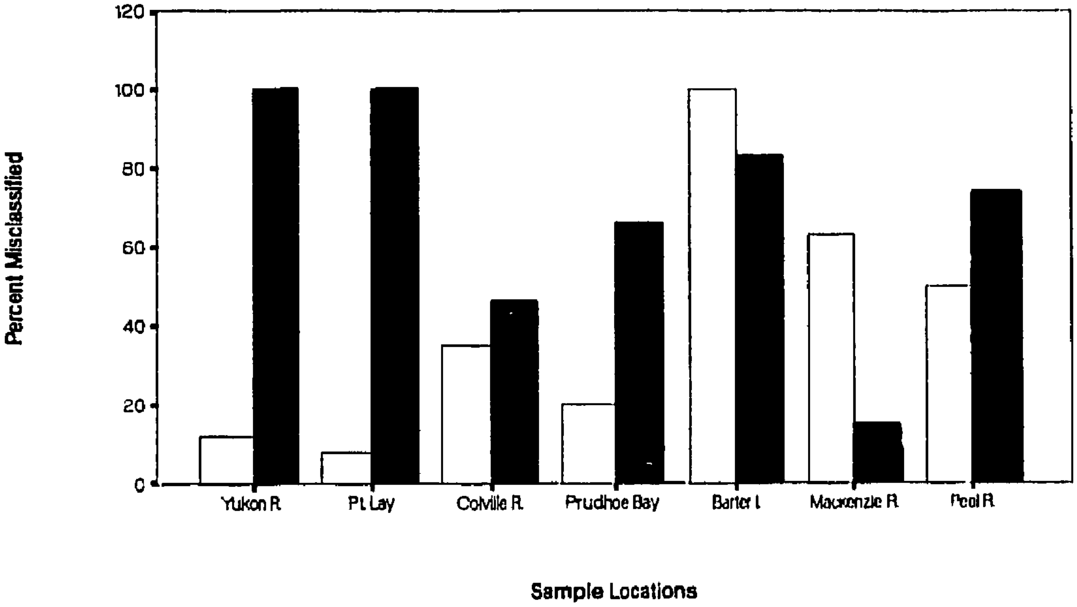


Figure 2. Percent misclassification rates

Arctic and Bering cisco

McPhail's chief difficulty lay in the small number of samples obtained from the areas outside the two major river systems. My sampling, concentrated in and between the river systems, has produced a different picture. Approximately six to ten percent of the fish taken along the Yukon Territory coast and in the Mackenzie River system in 1985 and 1986 had gill raker counts from the lower limb of the first gill arch that were diagnostic of C. laurettae (Figs. 3-9). The percentage is similar in samples from various regions of the Alaskan Beaufort coast. The ranges of total gill raker counts for the two species in North America (35-42 and 41-48) are, when combined, equivalent to the gill raker count range for C. autumnalis in Europe and Asia (Berg, 1948).

The presence of low gill raker count fish on the Beaufort Sea coast, throughout a major portion of the range of Coregonus autumnalis, is not restricted to this study. Stein et al. (1973) had noted the occurrence of immature Bering cisco in the main stream of the Mackenzie River between Arctic Red River and Norman Wells.

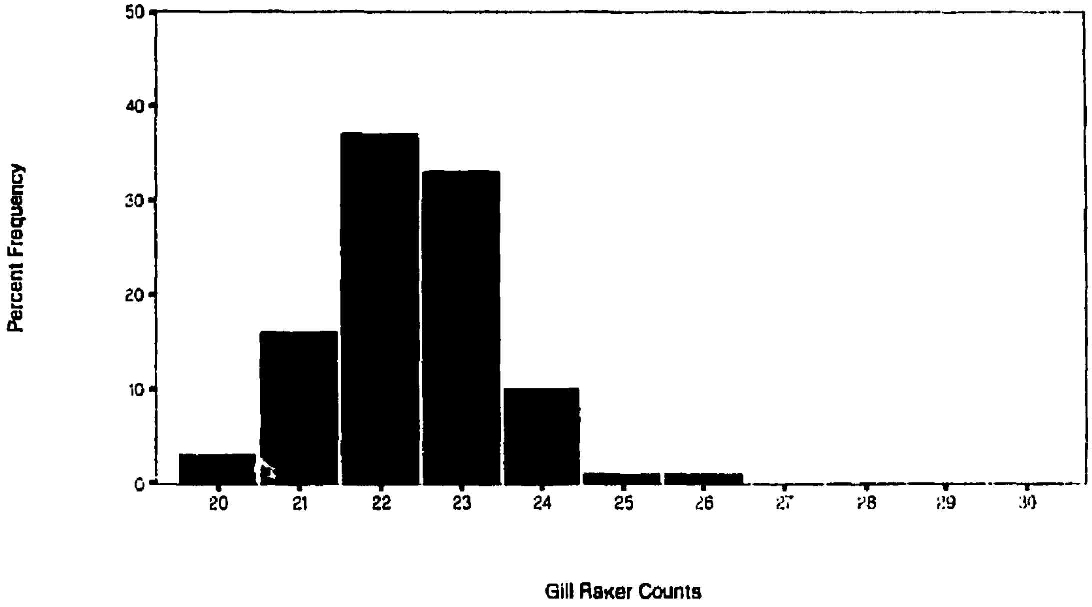


Figure 3. Gill raker count distributions

Yukon River

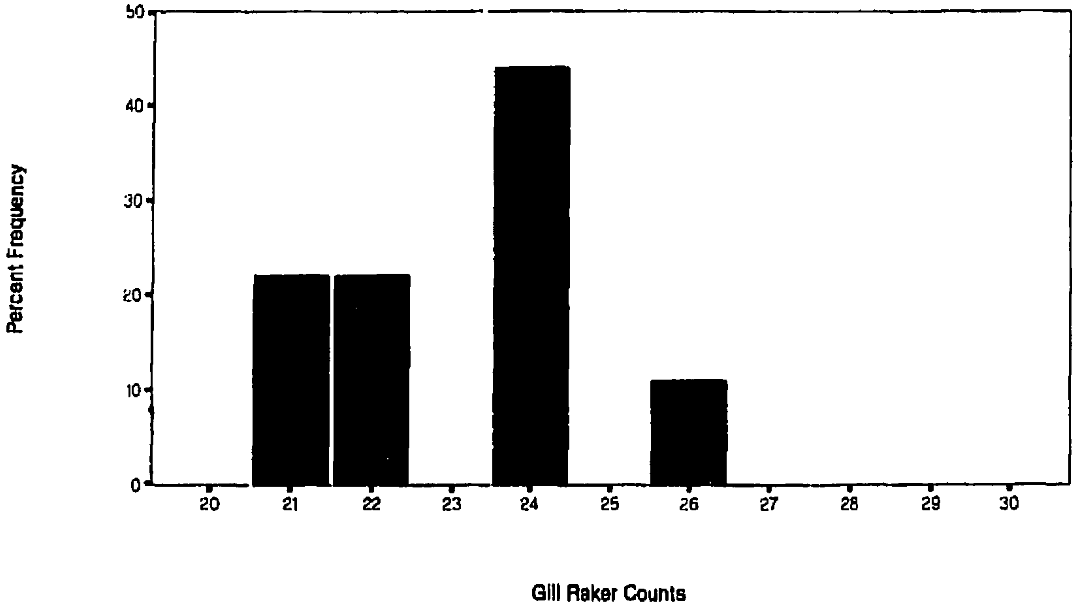


Figure 4. Gill raker count distributions

Point Lay

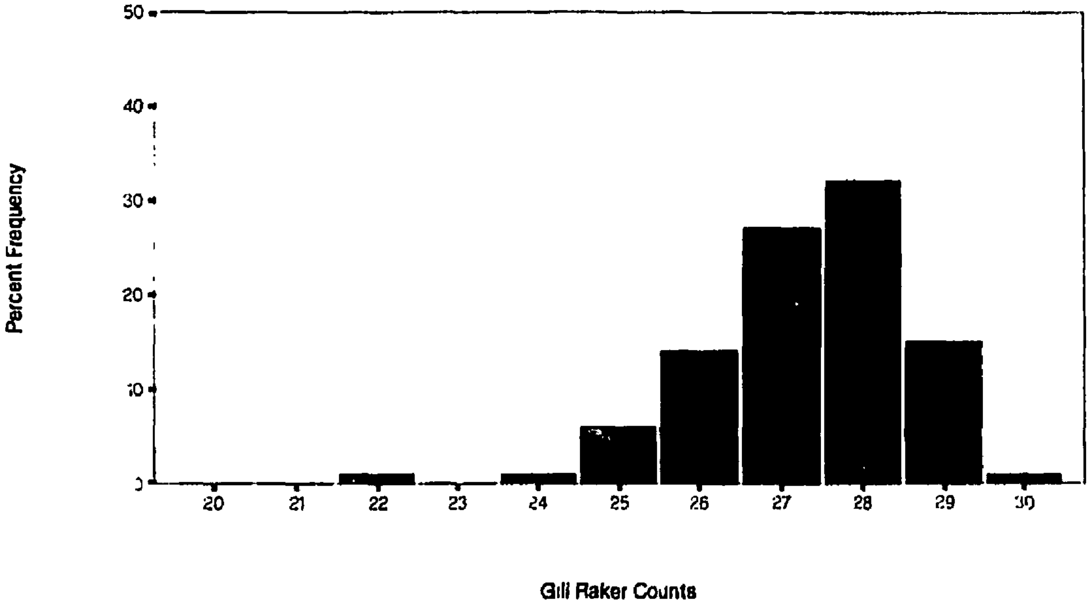


Figure 5. Gill raker count distributions

Colville River

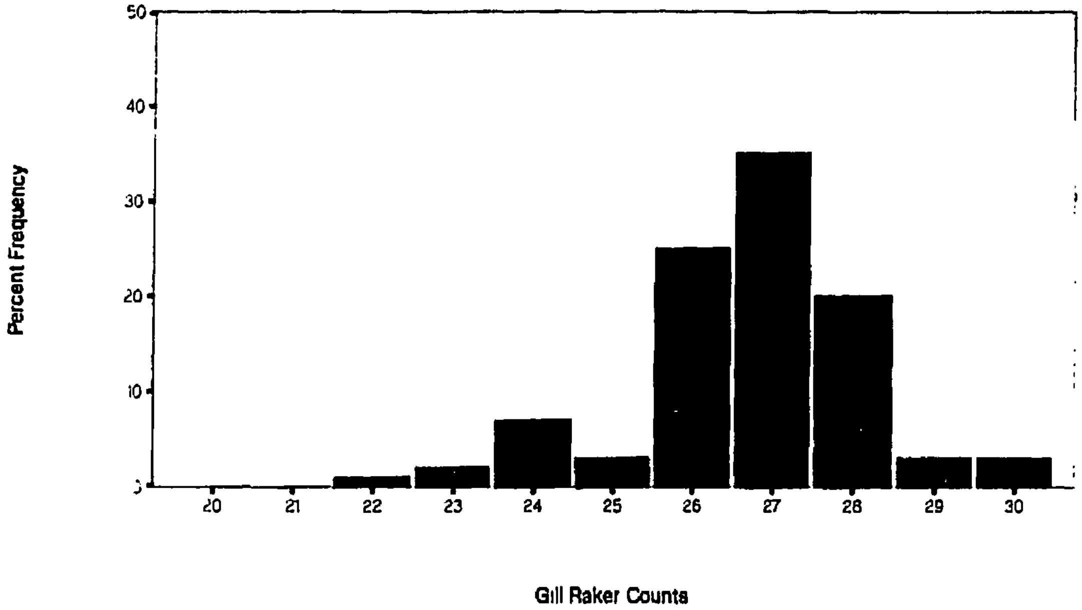


Figure 6. Gill raker count distributions
Simpson Lagoon

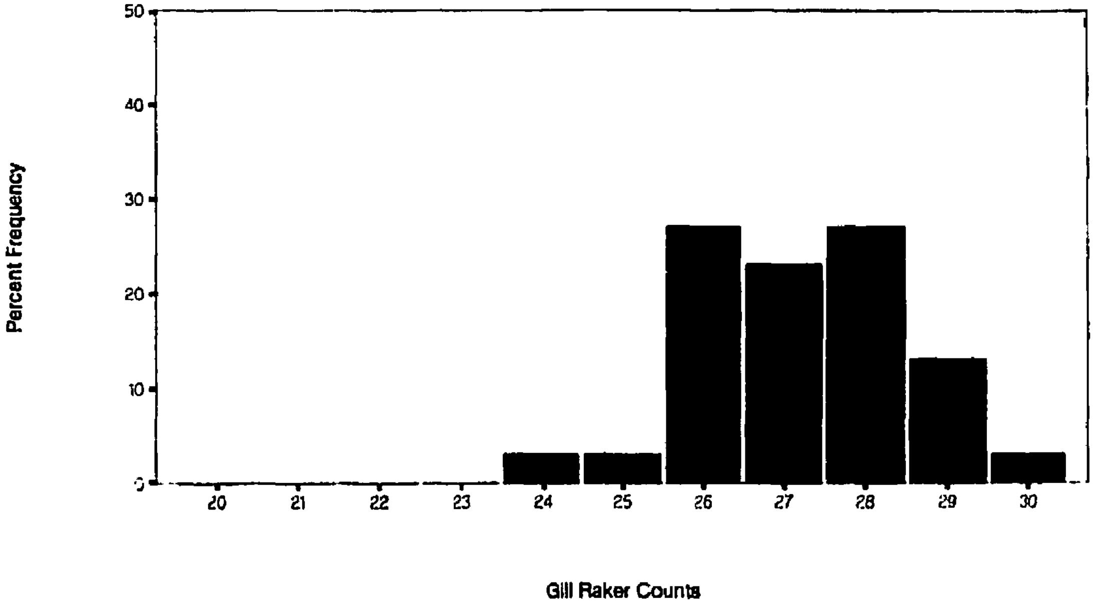


Figure 7. Gill raker count distributions

Barter Island

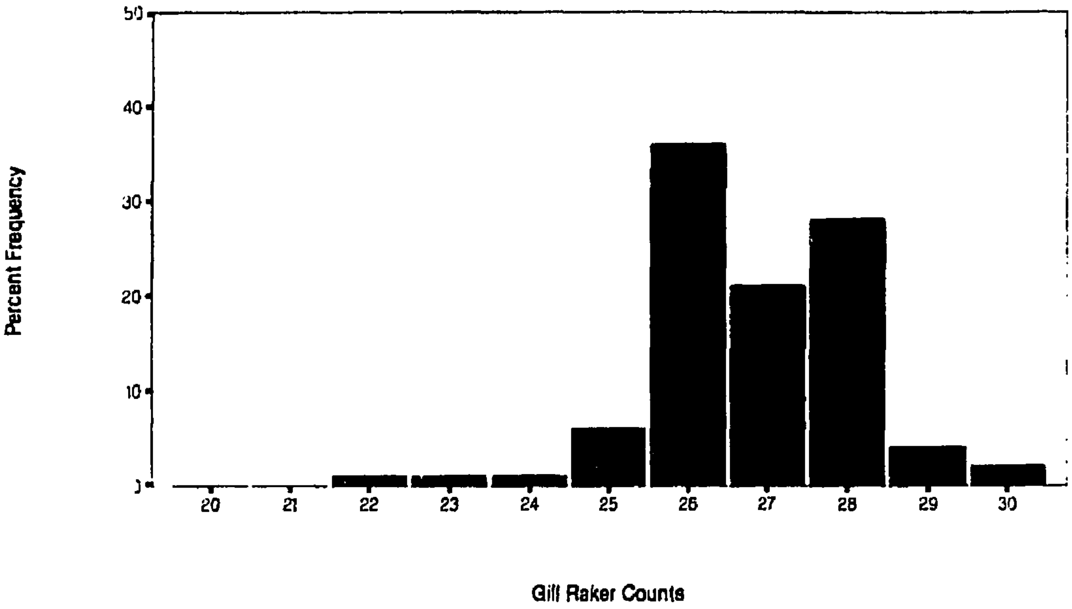


Figure 8. Gill raker count distributions

Phillips Bay (Mackenzie River)

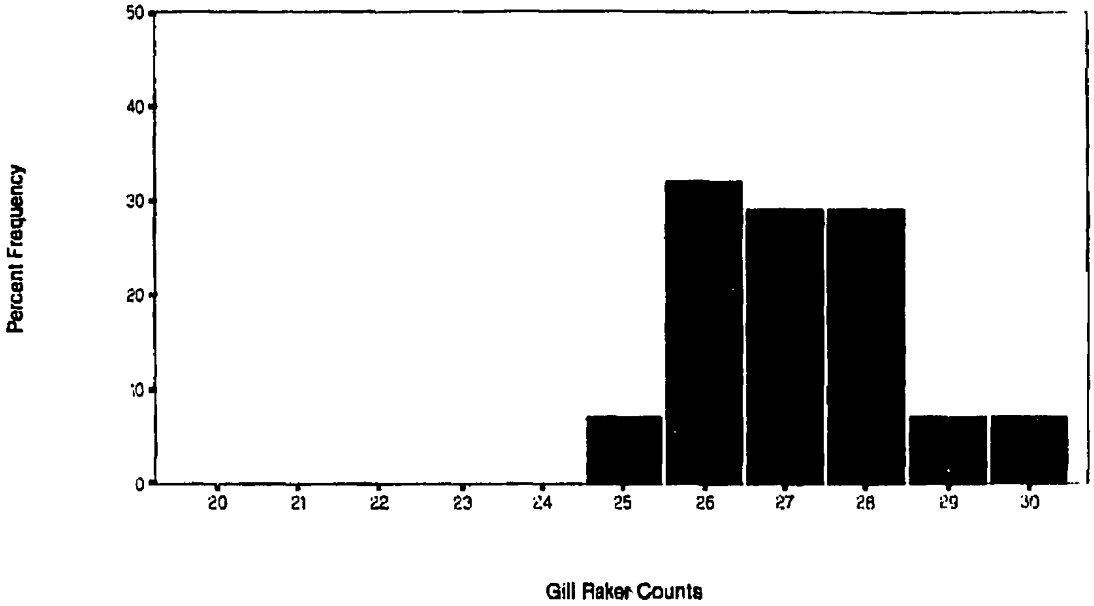


Figure 9. Gill raker count distributions

Peel River

DISCUSSION

4.1. Morphometric and meristic characteristics

The purpose of the morphometric analysis was to determine whether the Bering cisco and Arctic cisco could be separated on these criteria. If so, and reproductive isolation was maintained, it would be expected that the accuracy of classification found for each species in allopatry would be maintained in sympatry. If a great deal of hybridization takes place in the zone of sympatry, the pattern should be that of high classification success in allopatry and low success in sympatry. A third possibility is that of latitudinal variation, in the nature of a cline, with accuracy decreasing with increasing latitude.

A review of the literature concerning the use of morphometric analysis in fish taxonomic studies reveals the most serious biological problem to be that of environmental modification of the morphological variables in question. Growth rate, temperature, and feeding mode have all been implicated in the alteration of head and body characters (Smirnov, 1969; Kanep, 1975; Henault and Fortin, 1987). At least in regard to the first two factors, it would be expected that the effect of the latitudinal differences would be to increase the differences between populations.

The results seen in this study do not demonstrate the expected trends. If the morphometric differences found between the Yukon River and Mackenzie River fish had been strong enough to warrant considering them to be two separate species, the discriminant analysis should have produced an even greater level of correct classification. That latitudinal differences did not increase the level of correct classification to that of species level suggests that this is not a factor in the analysis. The inability of the discriminant analysis to distinguish the Bering cisco in the Colville River region suggests these fish are not a part of the Yukon River populations of Bering cisco that merely ranges that far north and east.

The data clearly show that the first hypothesis is not correct; the rate of classification success is not maintained in the zone of sympatry. As well, the second hypothesis is untenable, as classification success is quite variable, and is actually higher in the areas of sympatry than in some areas of allopatry.

The inability of the discriminant function analysis to distinguish known group members separated by considerable spatial distance at a rate of better than 80-85% indicates that the differences between the two populations are limited. It is entirely possible that, given the possibility of environmental modification of these morphometric characters, the observed differences were not due to genotypic variation at all. The absolute amount of difference measured, in light of other studies on single fish species, is at the level of stock separation (60-80%) rather than species or even subspecies separation (Mayr, 1969; Qadri, 1974; MacCrimmon and Claytor,1985).

The further inability of the discriminant function analysis to correctly identify fish in the area of purported sympatry suggests that: 1) the hypothesis of specific-level morphological distinctions, at least at the degree of precision used in this study, is untenable, and 2) as the result of this morphological similarity, gene exchange between the two populations is either continuing, or may have been stopped in geologically recent times (within the last one hundred thousand years) (Svardson, 1965).

With the present data it is not possible to determine whether gene flow is continuing. Heterozygosity of allele frequencies can be maintained between two fish species at a very low level of exchange. As the ability of these fish to undertake long movements has been well documented (Stein et al., 1973; Alt, 1973), it is not out of the realm of possibility to assume such events could take place.

Most of the meristic data has shown either insignificant differences between populations, or was found to be too easily influenced by environmental conditions to be of any use in taxonomic studies (McPhail, 1966). The exception to this has been gill raker counts, and even those are undergoing reconsideration as to their utility. The analysis of the distribution of gill raker counts across the sample area in this study suggests that the data used by McPhail (1966) represented an incomplete picture of the species. An increase in the number of fish analyzed has revealed that: 1) low gill raker count fish are not simply found in the Yukon River area, but are also found throughout the Mackenzie system; 2) high gill raker count fish of uncertain origin but which appear to be Arctic cisco are found in the Yukon River system; and 3) the percentage occurrence of these fish are internally consistent throughout each of the ranges. These data call into question the speciation pattern as interpreted by McPhail and suggest the presence of two allopatric populations of the same species. The frequencies of gill raker counts suggest the extension of the Mackenzie River population to at least the Colville River. The similarity of the gill raker count range for the two species in North America to that seen for the one species in the rest of its range suggests that the original separation was probably premature.

4.2. Zoogeography

The results of the morphometric and meristic data analysis suggests that the zoogeographic hypothesis of McPhail (1966) which followed from his systematic analysis should be reconsidered.

Walters (1955), in his study of the zoogeography of absence of gene exchange in approximately ten thousand years following the end of the glaciations (Ferguson et al., 1978). The diversity Svardson (1961) described in European species of coregonines was attributed to successive waves of formerly allopatric populations coming back into sympatry, none of which were considered as valid species. A second problem arises in the Bering Land Bridge bifuricating the range of Coregonus autumnalis. For this to have occurred, the range must first have been established to have contained spawning populations of the species in the river systems between the Yukon River and the Mackenzie River prior to the formation of the land bridge.

Wynne-Edwards (1952) stated that spawned-out Arctic cisco were reported to have been taken in the Colville River Delta and suggested that a spawning population might occur in the Colville River. No evidence for this has been found in a number of recent attempts to locate the spawning ground or find fish in spawning condition (Craig and Haldorson, 1981; McElderry and Craig, 1981). Mitochondrial DNA research by Bickham et al. (in press) has indicated that Arctic cisco from the Colville River and the Sagavanirktok River deltas belong to the same population as those from the Mackenzie River. Analysis of the distribution of gill raker counts for Arctic cisco confirms these data (present study). Arctic cisco, unlike other Coregonines (the least cisco Coregonus sardinella, for example), appear to inhabit only

Arctic fishes, thought that the major influence on the distribution of fishes in the region was the decrease in water levels during the Pleistocene glaciations. This exposed the Bering Land Bridge and isolated formerly contiguous (or nearly so) populations. The populations then evolved in allopatry. When the ice sheets retreated and the populations became sympatric once again, they might have diverged sufficiently so as to maintain reproductive isolation and could therefore be considered valid species. McPhail (1966) in his taxonomic analysis of the *Coregonus autumnalis* complex considered this to be the important factor in the separation of *Coregonus laurettae* and *C. autumnalis*. There are several problems with this scenario, both with the subfamily Coregoninae generally and with the species in question. The first problem involves the amount of time spent in allopatry. Ten to twenty thousand years, the approximate duration of the last Wisconsin glaciation is considerably less than the one hundred thousand years suggested as the amount of time for speciation to occur (Svardson, 1979). Indeed the amount of introgression that has taken place between species of *Coregonus*, both in Europe and North America (Smith, 1964; Svardson, 1965; and Behnke, 1972) suggests that the Wisconsin glaciation was probably not a long enough time for reproductive isolation to occur. If the long-isolated population of *C. autumnalis* in Ireland is considered, little divergence has taken place in the large rivers. On the Alaskan Arctic coast, the only rivers that fit this description are the Canning, the Sagavanirktok, and the Colville. All three rivers have been thoroughly investigated for spawning populations of Arctic cisco; none have been found (Craig and Haldorson, 1981; Griffiths, 1983; Griffiths et al. 1983). There is no question of a substantial run of three to eight year old Arctic cisco up the Colville River, but these fish are non-spawners (LGL U.S. Inc., unpub. data; this study). This means the Mackenzie is the only river system in which Arctic cisco spawn and strongly suggests that the distribution of Arctic cisco is not made up of a number of populations along the Arctic coast but instead consists of a single large migratory Mackenzie River population. These fish migrate along the coast as far west as Point Barrow, utilizing the barrier island lagoon systems in between as feeding areas in the summer and the river delta regions and Colville River as overwintering areas, then move back to the Mackenzie River system to spawn at age eight. This interpretation fits well with the data obtained by researchers in the Mackenzie delta who noted an absence of Arctic cisco aged two to eight years from that system (Hatfield et al., 1972; present study).

The Bering cisco population probably has a similar life history, although the evidence is less conclusive. Spawning populations have only been found in the Yukon/Kuskokwin River systems. Alt (1973) took a total of 21 immature fish from the Port Clarence/Grantley Harbor area, however, it is not known whether these fish were coming from the Yukon or Kuskokwin Rivers or from a river such as the Koyuk. No information on Bering cisco is available for the river systems between this area and the Kokolik River near Point Lay, Alaska. Approximately four months of gill netting in the nearshore lagoon system and the Koklik River at Pt. Lay produced a total of eight Bering cisco and a single Arctic cisco, none of which were in spawning condition. No fish were found between there and Pt. Barrow. It can be inferred from these data that the range of Bering cisco does not extend sufficiently far north for it to be considered sympatric with Arctic cisco. The lack of any resident populations of Bering cisco in the Chukchi region has been attributed to the unsuitable riverine habitat in this area (Craig, 1989).

All fish captured were immature and taken in the marine environment, suggesting the lack of a resident population in the region. Fishes sampled in the Yukon River were almost exclusively C. lauretta<u>e</u> but several fish of indeterminate status were captured. At least two fish, including one obviously mature female, did not closely resemble either C. autumnalis or C. laurettae despite having the gill raker counts of C. autumnalis. The physical features of these fish displayed a strange combination of species characteristics. Their mouths were subterminal, as in C.

autumnalis, but the fins, rather than being immaculate had a great deal of dark pigmentation. Gill raker counts were 25 and 18 which fall well within the range for *C. autumnalis*, as well as for the closely related *C. artedii* and *C. sardinella*, which don't have subterminal mouths. An analysis of these fish using the discriminant function, developed above, groups them as *C. autumnalis*. If correct, this would represent a substantial southerly range extension of this species as well as provide a percentage occurrence similar to that noted for *C. laurettae* in *C. autumnalis* populations along the Beaufort Sea coast. The appearance of ten to twenty of these Arctic ciscoes in a total of 290 fish taken in the Yukon River gives a percent occurrence of between three and six. This could explain the apparently anomalous occurrence of a single *C. autumnalis* in the Pt. Lay region (present study), as well as the appearance of two *C. autumnalis* in the specimens originally described by Bean (McPhail, 1966). This latter situation was part of the rationale for McPhail to name a holotype in his redescription of *C. laurettae*.

It had formerly been concluded that the appearance of a single *C. autumnalis* at Pt. Lay during the present study was the result of straying from the Point Barrow region, as the numbers of fish in the Point Lay region were considerably lower than elsewhere. Alternatively, this fish may represent the approximate percentage of high gill raker fish seen in the Yukon River population, rather than a stray from the Mackenzie River population. Discriminant analysis of morphometric characters has indeed placed both this fish and the low gill raker count Yukon River fish in the *C. laurettae* group. It is possible that the Yukon River fish represents a potential hybrid between *C. autumnalis* and *C. sardinella*, which are sympatric in that system. If this is the case, the hybrid was a mature fish, ready to spawn, as no ciscoes taken in the Yukon River were immature. The appearance of so many mature hybrids would suggest that the distinction between the two species is considerably more blurred than had first been considered.

All the available evidence favors the following distributional picture. Bering cisco spawn in the Yukon/Kuskokwin region and range north to the Point Lay/Point Hope area, although in very small numbers. Arctic cisco spawn in the Mackenzie River system and range westward to Point Barrow, Alaska. The low gill raker count fish found along the Arctic coast are probably resident members of the Mackenzie spawning populations. Their numbers are maintained between six and ten percent of each sample taken which suggests a consistent number of low gill raker count fish throughout the range rather than just in a single area of sympatry. A similar distribution was noted by Burkhov and Solovkina (1975) for *C. autumnalis*. Fish from the Pechora River were found across both the Barents and Kara

Seas.

An alternative hypothesis to the isolation scenario presented by Walters (1955) and McPhail (1966) involves the possibility of fish transfer between the Mackenzie and Yukon River systems through a series of stream captures and flow reversals. It has been well documented that the Porcupine River was originally a tributary of the Mackenzie River flowing north through MacDougall Pass in the Richardson mountains (Hughes et al., 1969; Cumbaa et al., 1981). During the Illinoisan glaciation a lobe of the Laurentide glacier blocked this flow and diverted the river south into the Yukon River. It is not known whether or not this situation continued following the retreat of the glaciers. If the Porcupine resumed its former course, a similar event in the Wisconsin glaciations was sufficient to permanently change its flow to what is seen in the present day. The present evidence, although circumstantial, suggests that it is unlikely the Porcupine River was a pathway for cisco migration. The most telling point is the absence of either Bering or Arctic cisco from the upper Porcupine system (Elson, 1974). Bering cisco move at least as far up the Porcupine as Ft. Yukon, Alaska, where they are taken in fish wheels by commercial fishermen. It is possible that, due to the lack of research and commercial fish wheel effort between Ft. Yukon and Old Crow, these fish simply have not been caught by the commercial/subsistence fishing effort in

Old Crow which is directed at salmon and uses large mesh gill nets that will not capture ciscoes. Sets of appropriately sized gill nets in 1987, although of short duration, produced no Bering cisco at a time when movement up the rivers would have been expected (Dillinger, unpub. data). Extensive gill netting and seining in the early 1970's produced a similar result (Elson, 1974). The only Bering cisco reported above the Porcupine/Yukon confluence was a single immature fish taken in the Yukon River at Dawson, Y.T. in 1977 (DeGraaf, 1981).

A second argument against the Porcupine as a transfer system is the time available for the divergence. If the ciscoes diverged during the Illinoisian glaciation, considerable morphological differences would be expected between the populations, which is not seen. Divergence during the Wisconsin glaciation is more likely given the degree of difference. A great deal of the evidence for rejecting the Porcupine as a transfer point is circumstantial, however, and could change with increased research effort in this area.

Other potential sites for exchange exist. It has been hypothesized that the upper Peel River and the Eagle River were points of transfer of fishes during the Wisconsin glaciation (Bodaly and Lindsey, 1977). The Eagle River has been investigated (Dillinger, unpub. data) and found not to have played an important role in the movement of other fishes (specifically the longnose sucker, Catostomus catostomus) between the two systems. The Peel River has a stock of early-running Arctic cisco which moves into the Bonnet Plume River region, that could have been transferred to the Yukon from there. The timing of the upstream runs of these fish and Bering cisco from the Yukon River is coincident and can differ significantly from that occurring in the mainstream Mackenzie River and the Arctic Red River (Stein et al., 1973). Another possible area of exchange is the Liard River, which has a spawning population of Arctic cisco that runs well up the river (McLeod and O'Neil, 1983). The Liard River has long been suspected of having a great deal of historical influence on the Yukon River and numerous Pacific drainages in northwestern British Columbia (Lindsey, 1956; McPhail and Lindsey, 1970; Lindsey, 1975). Preliminary analysis of longnose sucker genetic data indicates the possibility of Mackenzie River (Mississippian Refugium origin) fish penetrating the upper Yukon River in this fashion (Dillinger et al., in prep.).

Another problem exists with the scenario envisioned by McPhail (1966) for the speciation of C. autumnalis and C. laurettae. In order for this speciation to have occurred as hypothesized by McPhail, C. autumnalis must have survived the Wisconsin glaciation in either of the following locations: 1) A portion of the Beringian refugium not influenced by the Yukon River, but north east of the Bering

Land Bridge (the Colville River area); and/or 2) a proposed but as yet unproven refugium in the region of the upper Peel River.

Considering these possibilities in reverse order, it is unlikely that populations of Arctic cisco could have populated the upper Peel at this time, as there are none presently found in this region. No evidence currently exists for the "refugium", but it is quite possible that some connection with the Yukon River was maintained throughout the Wisconsin glaciation. As for the first possibility, while it is true that the Mackenzie River population of Arctic cisco does not utilize the Colville River as spawning habitat, it is clearly suitable for spawning, as may be evidenced by the number of fish species taking advantage of it for that purpose (McElderry and Craig, 1981). It seems unlikely that a population of fish would spawn in a river system for 10,000 years, then abandon it as soon as it regained access to the Mackenzie River.

It is quite possible that the Arctic cisco instead spent the Wisconsin glaciation in the Mississippian refugium. Certainly a number of other whitefishes, _C. clupeaformis_, _C. nasus_, and _Prosopium cylindraceum_, did. Clarke (1973) stated that _C. autumnalis_ was of Beringian refugium origin, based on the lack of any evidence of present populations in the Mississippian region. This may be due to two mutually exclusive possibilities. The first that they indeed weren't there. The second possibility is that the C. autumnalis introgressed with the closely related and quite abundant Coregonus artedii. A similar hypothesis was erected by Behnke (1972) to explain the disjunct distribution of C. autumnalis in Europe. He hypothesized that introgression took place with C. lavaretus, and was one reason for the tremendous morphological diversity found in that species complex. Although the possibility of this introgression taking place has not been investigated, the characteristics of the two species overlap sufficiently as to allow the potential for mixing. This is a testable hypothesis, using genetic data, but is beyond the scope of the present analysis. Such introgression has, however, been documented at the subgeneric and species level in whitefishes as well as in other families (Smith, 1964; Nelson, 1968; Behnke, 1972; Dauble and Buschbom, 1981; Todd et al., 1981).

McPhail and Lindsey (1970) describe Coregonus artedii as a species complex with considerable geographic variation. Mouth characteristics are similar to those of C. autumnalis, the paired fins are usually immaculate, and ranges for fin ray and gill raker counts overlap or encompass those of C. autumnalis (dorsal fin ray 12-14 v. 10-12, anal fin ray 11-14 v. 12-14, gill rakers 18-27 and 14-18 v. 26-31 and 15-17). Clearly the necessary morphological similarity that would make introgression a possibility exists. As well, C.

artedii have been caught in the upper Mackenzie River system, making their ranges overlap, if only slightly.

The Coregonus autumnalis/C. laurettae species complex has only fulfilled a single requirement for species determination, that of reproductive isolation. This is the result of allopatry, rather than evolution in allopatry with reinforcement of isolation when in sympatry. This condition was met only if the high gill raker count fish from the Yukon River meant the presence of Arctic cisco in that system, and similarly for the low gill raker count fish in the Mackenzie River. This, given the penchant for introgression in the subfamily, is unlikely. The discriminant analysis was unable to sufficiently distinguish between the two species, and the meristic overlap, at least in a distributional sense, was greater than what would be expected. It is suggested, therefore, that C. laurettae be lumped into C. autumnalis, the position taken by Dymond (1943) and supported by the analysis done in this study.

SUMMARY

In summary, it has been determined that the original classification of the *Coregonus autumnalis* complex by Dymond (1943) was correct. McPhail's (1966) separation of *C. autumnalis* and *C. laurettae* was based on insufficient samples from the area of purported sympatry. The two fish are, at best, allopatric subspecies, based on gill raker count distributions, the results of the discriminant analysis, and the genetic data.

The original hypothesis, accounting for the separation between the populations, fails to take into account present distributional information. An alternative hypothesis involving headwater transfers may better fit the data.

THE LIFE HISTORIES OF COREGONINE FISHES

INTRODUCTION

The goal of this aspect of the study is to: 1) describe the life history for both Arctic and Bering populations of ciscoes; 2) to compare this life history with that of the sympatric least cisco, Coregonus sardinella, and other related coregonine species; and 3) to compare coregonine life histories on both latitudinal and continental bases to determine if bet-hedging strategies are seen on either level.

1.1. Life history analysis

Life history tactics have been defined as the "schedules" of fecundity and survivorship most suited to maximizing fitness in an individual's environment (Stearns, 1976; Thorpe et al., 1984). The investigation of these tactics and their relationship to environmental conditions has led to an increased understanding of the determination of reproductive fitness (Stearns, 1976, 1977, 1980, 1983 a,b). The concept that tradeoffs between reproductive growth and somatic growth occur when energy is limiting is an important point in life history theory. The premise that present reproduction may have a negative effect on future survival to reproduce and on fitness is especially important when considering teleost fishes (Stearns, 1976; Wootton, 1979) which for the most part, have indeterminate growth and a strong relationship between body size and reproductive output (Mann and Mills, 1979; Wootton, 1979).

The presence of tradeoffs in reproductive patterns of northern fishes has been investigated from two differing directions. Regions with a variable climatic regime are thought to give rise to tactics that tend to reduce the possibility of a year class leaving no descendants and/or population extinction, as well as those which would allow individuals access to resources previously unavailable (Mann and Mills, 1979). Mechanisms that enhance the former include bet-hedging strategies such as the presence of a non-migratory or precociously maturing proportion of the population, or iteroparous spawning. Variable maturation age can produce the effect of spreading out risk in a semelparous fish, conferring the advantages of interoparity (Mann and Mills, 1979). Mechanisms for the latter may include such tactics as anadromy or other migratory behavior, which enable fish to exploit the higher production found in the northern marine environment (Gross et al., 1988). These behavioral traits serve to increase size which can then influence fecundity if an allometric relationship exists between these two variables.

Density-dependent and independent models have been constructed to explain variation in life histories. Species with low juvenile mortality (high adult mortality) concentrate energy toward a single highly fecund reproductive event (semelparity) occurring early in life (early maturity). Species with high juvenile mortality (low adult mortality) concentrate efforts toward repeated reproductive events (iteroparity) later in life with low relative fecundity (Murphy, 1968). Originally, the terms "r" and "k" selection were used to identify these life history character suites and their associated environments (Pianka, 1970). Individuals that were considered to be r-selected were thought to maximize individual fitness by reproducing rapidly, with increased effort, in a relatively uncrowded environment. K-selected individuals maximized fitness by delaying maturity with a smaller reproductive output as populations were considered to be at or near carrying capacity (Pianka, 1970). Species were often characterized by their adherence to one or the other approach (Parry, 1981). Later, more detailed reviews of populations in the field found that r-k selection was not an either/or system but rather a continuum, and that organisms could be r-selected at one stage of their life cycle and k-selected at another (Adams, 1980). Recently, r- and k-selection have been restored to their position as a model of density dependent selection, one of many factors that may influence life history evolution (Boyce, 1984).

1.2. Analysis of the role of size and phylogeny in life history covariation

Stearns (1983a) thought that the existence of patterns of life history variation did not result from differing modes of population regulation, for several reasons. First, the patterns observed were not distinct when intra-population, intra-specific, and intra-generic comparisons were made. Second, a number of tests of this theory have shown that the patterns seen were more consistent with age-specific mortality rate models rather than with carrying capacity or population regulation models. Third, differing modes of age-specific selection pressures were found within density dependent and density independent selection.

Stearns (1983b, 1984) used broad scale life history studies to demonstrate the roles of taxonomy and body size relative to local adaptation. To test this, he applied principal components analysis to a total of 65 mammalian species, belonging to 14 orders and 30 families, using ten traits as variables (in one data set) and 162 species in 22 orders and 64 families using six traits, as a second data set (Stearns, 1983b). He found that, when order and family effects were removed, size, as determined by weight, accounted for less than 30 percent of the total variance. While Stearns recognized that a great deal of the mammalian variation scaled on a single axis ranging from early maturing, highly fecund, and short lived species at one extreme to late maturing, low fecundity, long-lived species at the other, could be accounted for by size (weight), the converse analysis (removal of weight) retained sufficient variance to lead him to propose that morphology imposed by phylogeny significantly constrained life history traits.

Similarly, Stearns (1984) looked at patterns of covariation in reptilian life histories. The resultant analysis led him to hypothesize that: 1) the patterns of covariation in reptilian life history traits appeared to be lineage dependent; 2) the effect of order was not as important in the reptiles as it was in the mammals, probably as the result of the numerous extinctions undergone in this class; 3) family effects were important in the reptiles but not as much as in the mammals; and 4) the strongest effects resulted from the fixation of a single trait (size).

Dunham and Miles (1985) reviewed Stearns' (1984) work on reptiles and presented the following criticisms of his analysis and technique: 1) serious mistakes were made in classification and body size; 2) the statistical methodology produced composites; and 3) annual variation in traits was not considered. They re-analyzed Stearns' data. considering the above points and including more data, and found that all traits varied significantly and that the order effects were removed with the removal of size differences; but the family effects remained. Dunham and Miles stated that, despite their criticisms, the attempt to partition out the effects of size and phylogeny had a great deal of merit.

Hutchings and Morris (1985) evaluated covariation in the family Salmonidae using seven life history traits. The approach, used to evaluate the effects of phylogeny, size and behavior, was a modification of Stearns (1983, 1984) methodology. Their analysis identified three principal components of salmonid life history strategies. The first ranked forms as ranging from large, early maturing, semelparous individuals bearing few large, rapidly developing eggs, to the opposite. The second component (anadromy) was thought to be related to growth. The third component (delayed reproduction with slowly developing eggs) appeared to have a seasonality component (fall spawning-spring hatching). The authors concluded that: 1) phylogeny provided some constraint but not as much as in other classes; 2) size had little effect, probably the result of relatively small intrafamilial size ranges; and 3) anadromy influenced covariation of life history traits to a great degree, such that the greatest influence was that of behavior. The analysis of coregonine life histories in relation to latitude in this study will use similar analytic procedures.

1.3. Latitudinal differences in life histories

The greatest number of life history studies in fishes have been done at the generic, specific or intra-specific levels and have dealt with variation in these traits associated with latitude.

Life histories have been seen to covary with latitude within such species as American shad Alosa sapidissima (Leggett and Carscadden, 1978), Pacific herring Clupea harengus pacificus (Paulson and Smith, 1977), Atlantic salmon Salmo salar, (Schaeffer and Elson, 1975; Thorpe et al., 1984; Saunders and Schom, 1985), and boreal smelt Osmerus mordax, (Haldorson and Craig, 1984).

Leggett and Carscadden (1978) analyzed the life history of American shad (Alosa sapidissima) throughout its range along the Atlantic coast and found that iteroparity increased and fecundity decreased, independent of growth, with increasing latitude. The factor determining these strategies is apparently the thermal regime of the natal river system. The harsh and variable regime found in northern streams forced the fish to allocate energy reserves into post-spawning survival which reduced the amount available for reproduction. In comparison the southernmost populations were able to allocate a large amount of energy to reproduction and dispense with repeat spawning.

Paulson and Smith (1977) analyzed latitudinal variation in the Pacific herring (Clupea harengus pallasi). Statistical comparisons suggested that an inverse relationship between fecundity and latitude at body size occurred but that this was countered by the presence of larger females at higher latitudes and correspondingly increased fecundity with increased body size.

Schaffer and Elson (1975) looked at the variations in life history strategies in local populations of anadromous Atlantic salmon (Salmo salar) by analyzing differences in fish weight (age at first spawning) from different river systems and determined that these differences were dictated by riverine migration distance. The further a fish had to swim, the greater its weight. Recently, however, Myers and Hutchings (1987) re-analyzed these data and concluded that errors in the statistical treatment invalidated the conclusion.

Haldorson and Craig (1984), in their investigation of rainbow smelt populations in the Alaskan Beaufort Sea, compared the life history of the Pacific-Arctic subspecies (containing these populations) with that of the Atlantic subspecies. The two subspecies are known to have experienced considerable amounts of genetic divergence since they became disjunct in the Wisconsin glaciation (McPhail and Lindsey, 1970). It was found that the Pacific-Arctic fish were longer-lived, matured later, and grew more slowly than the Atlantic form.

Baltz (1984) looked at life history variation in surf perches (Family Embiotocidae) in California and detected three possible strategies; a small, high fecundity form, a medium to large form showing delayed maturity, and a low to moderate fecundity form of small to medium size. He determined that the northern populations showed greater longevity, higher fecundity, and larger young aside from greater body size and delayed maturation. The increase in reproductive variables was hypothesized as a compensatory mechanism for the slower growth and later maturity at higher latitudes. The fecundity variation seen in all populations was thought to be important as it maintained age at first maturity. Brood size in the small forms was found to vary inversely with environmental predictability.

1.4. Tradeoffs and bet-hedging in fishes

The conditions found in northern environments have been shown to force a delay in maturation that allows the fish to achieve a size sufficient to reproduce. Shorter lived fishes produce larger broods, while longer lived fishes spread their reproductive efforts over a greater amount of time and produce a greater number of smaller broods. Egg size is generally larger in iteroparous individuals because the fish, maturing later, has a correspondingly greater body size and more material is available to be allocated to each egg, while producing a smaller number of eggs (Mann and Mills, 1985).

Thorpe et al. (1984) studied the relationship between developmental rate, fecundity, and egg size in Atlantic salmon and found that reproductive strategies had an environmental component that seemed to fit the hypothesis of trading reproduction off rapid growth and small eggs against slower growth and larger eggs.

Another strategy is the production of both migratory, late maturing and non-migratory, early maturing offspring. Jonsson and Sandlund (1979) found that a population of brown trout (Salmo trutta) in Norway contained both migratory and non-migratory individuals. Similar mixed populations have been seen in Alaskan arctic char, Salvelinus alpinus, (McCart and Craig, 1971, 1973; Mann, 1974) and may also exist in populations of S. salar in Newfoundland (Leggett, 1969) and other portions of maritime Canada (Saunders and Schom, 1985). Precocious spawning also occurs in members of the genus Onchorhynchus on the Pacific coast; precocious forms may be either early returning anadromous fish or fish that have not yet gone to sea (Gross, 1984). All of these mechanisms serve to "spread out" reproductive effort, important in variable environments, as well as to maintain genetic diversity and the existence of small populations (Saunders and Schom, 1985). The production of individuals from the same year class that mature at different ages is a mechanism by which an essentially semelparous fish, like S. salar, can gain the advantages of iteroparity and also serves to spread out effort (Mann and Mills, 1979). The presence of a non-migratory form means some individuals avoid potentially high at-sea mortality, in return for a reduced fecundity which result from smaller size.

1.5. Northern coregonine life histories

Life history research on northern whitefishes has, for the most part, had a taxonomic or fisheries orientation (Walters, 1955; Lindsey, 1962, 1963a,b; McPhail, 1966; Muth, 1969; Alt, 1969, 1973, 1979). In a number of instances, a great deal of baseline life history information has been gathered for small populations (Cohen, 1954; Wohlshlag, 1954; Alt, 1969, 1973; Bond, 1982; Bond and Erickson, 1985) without any theoretical context.

In Eastern Canada, Morin et al. (1980, 1981, 1982) examined life history variation in three species of coregonine fishes, Coregonus artedi, C. clupeaformis, and Prosopium cylindraceum from the James-Hudson Bay system. It was found that in Prosopium cylindraceum (round whitefish) life history varied with latitude (decreased fecundity and late maturity), C. clupeaformis (lake whitefish) showed some changes (lower fecundity, later maturation and slower growth) and C. artedi (lake cisco) exhibited changes in reproductive age and growth rate but no reductions in fecundity, respectively, with increasing latitude. It was concluded that the patterns displayed by ciscoes represented the consequences of the physiological constraints produced by the harsh environment rather than an adaptive strategy as would be predicted by life history theory.

In this study, life histories of Arctic and Bering cisco, as well as other coregonines, will be examined to determine: 1) intrapopulation or intraspecific characteristics; 2) latitudinal patterns within and between sympatric populations and species; 3) patterns of variation, both intraspecific and interspecific between latitudes, using variables from North American, European, and Eurasian populations. This final analysis should also determine the potential effects of phylogeny on life history plasticity.

MATERIALS AND METHODS

Life history data collected from individual fish included fork and standard length, body and gonad weight, fecundity, egg diameter and age. Length measurements were made using standard techniques (Hubbs and Lagler, 1958). Fecundity was calculated using gravimetric techniques in which the total mass was first weighed, and three subsamples removed, weighed, the eggs counted and a mean calculated. Mean egg diameter was calculated using measurements of a random sample of ten eggs per fish. Maturity was based on a ten-point qualitative description of gonadal development according to the following scale (Bond and Erickson, 1985).

Female	Male	
1	6	Immature
2	7	Maturing (non-spawning)
3	8	Mature
4	9	Ripe
5	10	Spent

0 Sex indistinguishable

Age was determined by the otolith method. Otoliths were taken from fish, broken, ground if necessary for clearer resolution, and growth rings counted. Population level life history information (number of broods, total lifespan, age at maturity, etc.) was obtained using a combination of the above information and data from the literature where appropriate. Age at maturity was that age at which 50 percent of the females in the population were mature. Number of broods was calculated by subtracting age at maturity from total lifespan, and dividing this by the inter-brood interval. Fecundity values were maximum values reported. Length at maturity values were generally reported in the literature as mean values for each age class. Maximum age and length values were as reported.

All analyses were performed using SPSS^x (ver 3.0). Values used in subfamily comparisons were first $\log_{10}$ transformed then adjusted for length effects by the use of linear regression and subtraction of the slope times maximum length from all values (Stearns, 1983, 1984; Hutchings and Morris, 1985) for use in subsequent analyses. The data used in the other multivariate comparisions were first $\log_{10}$ transformed.

The broad-scale analysis was done using principal components analysis. A principal components analysis is an ordination technique that reduces a large number of variables to a smaller set incorporating most of the variance and is designed to locate the "hidden" factors responsible for variation. Principal components analysis partitions the total variance (the sum of variances for the original variables) by finding the linear combination of the variables which will account for the maximum amount of this total (y_1).

The procedure next finds a second linear combination, uncorrelated with the first that, after the first component has been removed, accounts for the next largest amount of variance (y_2). The components are then interpreted using factor loadings which represent the component variable correlations. These correlations may be positive, negative, or both if the factor is bipolar. The relationships of the variables within the factor are then determined, which serves to identify the factor (Stevens, 1986).

Other analyses were performed using univariate techniques (analysis of variance-ANOVA and analysis of covariance-ANCOVA). An analysis of covariance allows the adjustment of means to what they would be if all groups in question were standardized on the covariate. This allows the analysis of samples with inequalities in body size, for example, and produces a comparison of the variability throughout the entire population. The assumptions are those of analysis of variance, ie. independence, normal distribution and equality of variances, as well as the existence of a linear relationship between the dependent variables and the covariable, the homogeneity of the regression slopes and measurement of the covariate without error. The covariate can be any variable that is significantly correlated with the dependent variable. The null hypothesis in analysis of covariance is that the adjusted population means are equal. Significant differences, sometimes obscured by ANOVA, may often be noted, but not deemed to be damaging to the overall analysis.

determined by using ANCOVA (Stevens, 1986). In this study, fork length was used as the covariate in all analyses.

Univariate analysis of variance evaluates differences in group means. Multiple analysis of variance and covariance allow the use of several dependent variables. This enables the determination of interactions between the variables and allows their use in the analysis.

Three indices were calculated, using fecundity data, to compare populations. Relative fecundity (fecundity divided by body weight) provided an estimate of the relationship between egg production and somatic (body) tissue production. Gonadosomatic index (G.S.I.) the body weight divided by the gonad weight multiplied by 100, gave the proportion of body weight utilized for reproductive purposes. Eggs per gram of gonad weight (fecundity divided by gonad weight) gave an indication of the relative productivity of each fish.

These indices allowed inter and intra-population comparisons to be made, as well as inter and intra-age comparisons. The indices, despite the problems associated with ratio data, still provide an effective determination of characteristics involving gonad weight. Were these the only characteristics to be analyzed it might be more appropriate to use gonad weight as a covariate and do an ANCOVA. However, G.S.I., for example, does provide a proportional measure not easily attainable through ANCOVA. The statistical problems associated with this use of indices are

RESULTS

3.1. Arctic cisco life history strategies

The Arctic cisco population along the Beaufort Sea coast has the following life history structure. Female age of maturation is eight. Males appear to mature at age six. This has been demonstrated, not only in the present study but in previous work by Craig and Haldorson (1981), Bond (1982), and Bond and Erickson (1985). An analysis of the Colville River population reveals it to be composed of fish that are either immature (three to six years) or mature fish that will not spawn in the coming year (ages seven to fourteen). No mature spawning females have been taken in the Colville River or surrounding area since the spawned out fish reported by Wynne-Edwards (1952). The population apparently spawns only in the Mackenzie River system.

The sex ratio of spawning fish appears to favor males. Samples taken in Phillips Bay, Yukon Territories during the summer of 1985 comprised 35 mature females and 60 mature males, from a total of 300 fish. In 1986, the Peel River, Yukon Territories, sample had three mature females and 27 mature males. A sample taken in the lower Peel River, N.W.T. in 1988, yielded six mature females and seven males. The numbers of mature females and males taken in the Arctic Red River, Northwest Territories in 1987, were the same as the Peel River, six and seven. The timing of the sampling may have influenced the wide disparity in numbers seen in Phillips Bay. The age structure of the Mackenzie River sample of mature fish ranged from eight to fourteen years, with the modal distribution at ten years. Mean fecundity values ranged from 10,975 at age six (n=2) to 29,130 at age twelve (n=11), mean egg size from .85 to 1.2 mm., mean eggs per gram of gonad weight from 851 to 1448, and G.S.I. from 3.8 to 5.2 (Table 1). Mean fecundity increased with body size, but not significantly (Table 1). A linear regression analysis confirmed this ($r^2 = 0.03$). A non-significant increase was seen with age. Eggs per gram of body weight also showed a slight increase with age. Between age comparisons of mean values revealed no significant differences between fecundity, eggs per gram of gonad weight, or G.S.I. (Table 2).

Table 1. Mean reproductive variables by age class - Arctic cisco-Mackenzie River.

Age	Fecundity	Egg Diameter	G.S.I	Eggs/gram gonad	n
6	10975	0.9	3.8	1073	2
8	20682	1.2	5.2	851	8
10	25896	1.1	4.6	1335	18
12	29130	1.0	3.5	1249	11
14	27375	1.1	3.8	957	6

Table 2. One-way analysis of variance - Arctic cisco reproductive variables (between ages 6-14).

Variable	d.f.	F-value	Significance (p=.05)
log Fecundity	5,39	1.24	N.S.
log Egg diameter	5,39	1.10	N.S.
log Eggs per gram gonad weight	5,39	0.32	N.S.
log G.S.I.	5,39	1.04	N.S.

It is not certain whether the two mature six year old females represent early maturation or errors in aging. The small size, low fecundity, and low G.S.I., coupled with a moderate eggs per gram gonad weight value would suggest early maturation, although the sizes of these fish do fall within the range for older age classes. Bond (1982) reported finding a small number of mature six year old females in Tuktoyuktuk harbor. The small sample size may account for the lack of a significant difference between this age class and the others.

The Yukon River form (Bering cisco) appears to mature at age four, and unlike the Arctic coast form, spawns every year (Alt, 1973; present study). Fish in this population ranged from four to ten years old (Table 3). Of the 182 fish caught in this study, 181 were mature spawners. The female to male ratio was 1:4. A single young-of-the-year fish was captured in a 48 hour experimental mesh gill net set. The heavy preponderance of mature fish may have been the result of sampling using a fish wheel. While this certainly skewed the distribution toward larger fish, it is probable that smaller fish, if present, would have been captured, as the smaller sized least cisco, C. sardinella, were taken in the wheel. No significant differences in fecundity at age were obtained. Linear regression produced a similar non-significant relationship with length (r^2 = 0.07). Similarly, no significant differences were obtained in egg diameter, or eggs per gram gonad weight (Table 4). G.S.I. values declined with age and significant differences were detected between the first three age classes and the last four (Table 4).

Table 3. Mean reproductive variables (by age) - Bering cisco.

Age	Fecundity	Egg diameter	G.S.I.	Eggs/gram gonad	n
4	28522	1.7	14.0	401	2
5	26254	1.7	14.0	401	9
6	25975	1.7	13.7	377	11
7	31028	1.6	9.8	581	17
8	31516	1.6	6.0	307	20
9	20210	1.6	6.3	364	3
10	34166	1.6	6.0	399	2

Table 4. One-way analysis of variance - Bering cisco reproductive variables (between ages 4-10).

Variable	d.f.	F-value	Significance (p=0.05)
log Fecundity	5,32	1.57	N.S.
log Egg diameter	5,32	1.29	N.S.
log Eggs per gram gonad weight	5,32	0.75	N.S.
log G.S.I.	5,32	7.968	Significant

It may be seen from Tables 1 and 3 that the Bering form of the cisco has a greater mean G.S.I. value per age class than corresponding Arctic forms. This is indicative of earlier maturation in the Bering form and a greater allocation of resources toward gonad development rather than somatic growth as the result of the smaller mean size at age in the Arctic form (Fig. 1).

A comparison of reproductive characteristics using multiple analysis of covariance for each population reveals significant differences in both slope and adjusted means (Table 5). This indicates that latitude may produce both modifications of the growth variables (age at maturation, and total lifespan) and reproductive variables. The lack of significant differences between age groups within populations, but presence of differences between populations, differs from that of Nikolsky (1969) who found that values of relative fecundity varied within populations during development and between populations as well. He also found that despite great year to year fluctuations in

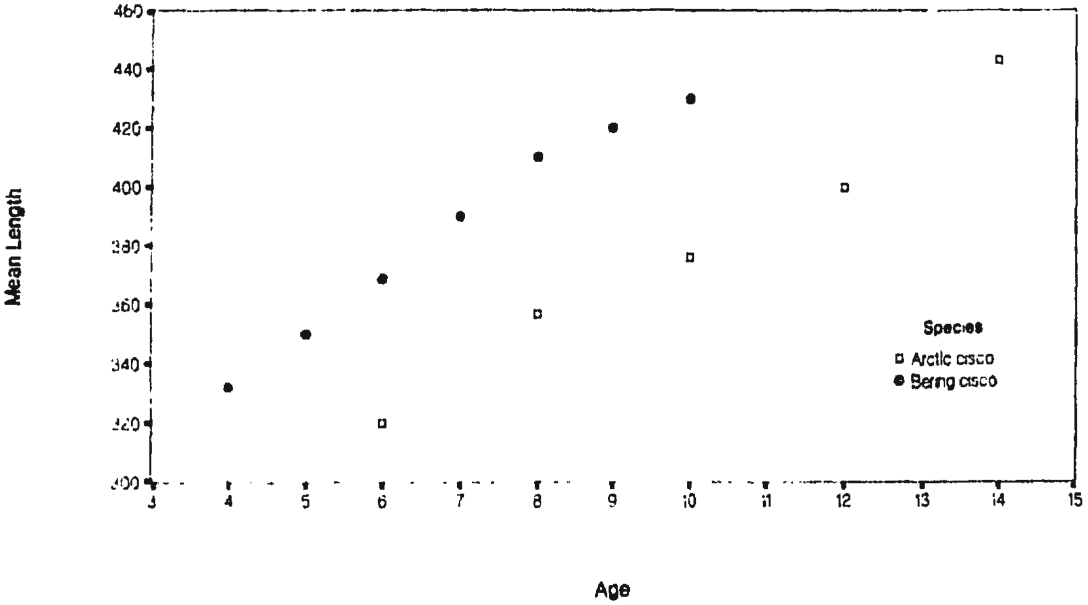


Figure 1. Mean length at age

Arctic and Bering ciscoes

fecundity in two species of whitefish (C. peled, C. muksun) the character still increased as the fish grew, although at a reduced rate. A similar result was seen in C. albula populations in Poland. Although fecundity appeared to be closely correlated with length (but not with age) year to year variations appeared to be significant irrespective of growth in some locations (Zawisa and Backiel, 1970).

Table 5. Multiple analysis of covariance - Arctic cisco and Bering cisco populations.

Effect	Wilk's Multiple test of Sig	Exact F	Hypoth. d.f.	Error d.f.	Sig
species by log fork length	.88430	4.31756	3	99	.007
species	.87938	4.52651	3	99	.005

Egg size differences are difficult to determine, if at the time of collection significant reproductive timing differences exist between populations. It is not known, since no one has collected ripe Bering or Arctic ciscoes, whether this difference is carried on to the final stage of egg maturation. There was a lag of about one month between the two collections made in this study.

The fact that eggs are produced in both populations following spawning, but that the northern population is unable to reach the egg development threshold in order to spawn the following season, suggests the alternate year spawning of the northern population may be the result of the physiological restriction of an annually spawning population. The converse would be that the annually spawning Yukon River population is the result of the release from the physiological restraint seen in the Mackenzie River population. Moskalenko (1971) noted the same response to arctic conditions in colder Eastern Siberian waters for a number of whitefish species, and attributed them to a similar mechanism.

3.2. Least cisco life history strategies

The life history strategies of the least cisco, Coregonus sardinella, present a similar picture to that seen in the Coregonus autumnalis complex. An analysis of covariance of fecundity, egg diameter and grams of eggs per gram of gonad weight showed significant differences between latitudinal populations, similar to what is seen in the C. autumnalis complex from the same locations (Table 6).

Table 6. Results of multiple analysis of covariance between least cisco populations.

Effect	Wilk's Multiple test of Sig	Exact F	Hypoth. d.f.	Error d.f.	Sig
location by log fork length	.89	1.64	3	41	.194
location	.89	12.50	3	42	.000

A multiple analysis of variance within locations between ages found no differences between the age groups present in the sample from each population (Table 7).

Table 7. Results of multiple analysis of variance (between ages) for each population of least cisco.

Location	Effect	Value	Approx F.	Hypoth. F.	Error d.f.	Sig.
Yukon R.	Age	.65	.82	6	18	.570
Mackenzie R.	Age	.50	3.37	3	10	.060

This suggests that, as in the _C_. _autumnalis_ complex, there is probably no significant difference between ages in regard to life history variables. Linear regression analysis confirmed this (r^2 = 0.09 Fec N, r^2 = 0.02 GW N, r^2 = 0.30 GW S, r^2 = 0.23 Fec S). Similarly, it is probable that when reproductive maturity is reached, a threshold number of eggs is produced, and increases very little through time, despite the continued growth of the fish. Other studies have shown that growth in this species becomes asymptotic around nine to ten years in northern populations and age seven in southern populations (Craig and Haldorson, 1981). Maturity is reached at around six to eight years for fifty percent of the population in the north (Mann, 1974) and at around four years for the Yukon River population. The change in gonadosomatic index values with age tends to support the contention that production of gonadal tissue declines after maturity is reached, although a slight increase is seen in Mackenzie River populations (Table 8).

Table 8. Mean G.S.I. values for least cisco.

Yukon River		Mackenzie River	
Age	Value	Age	Value
4	11.4	6	6.4
5	11.8	8	4.4
7	8.8	10	4.8

The appearance of alternate year spawning in northern populations adds weight to the hypothesis that energy reserves are limited and must therefore be allocated, at least during the growth phase. This presence of alternate year spawning is seen in the appearance of fish of a size and age greater than that of first maturity which show gonadal development insufficient to be considered to be spawning that season.

In looking at both populations of C. sardinella, again there were significant differences between age groups in terms of some life history variables. Reproduction begins at an earlier age in southern fish than in the northern population (age four vs. age eight), probably the result of faster growth. Reproduction appears to be annual in the south, as no fish of reproductive age were found in a non-spawning condition. This probably means that energy is not allocated in a manner similar to that in the northern populations, which are alternate year spawners. At this level the strategies are similar to those of the C. autumnalis complex. The major difference is the longer lifespan and greater number of broods in C. sardinella populations. Egg size doesn't differ between groups, the same situation seen in C. autumnalis, but fecundity is lower in the more northerly population. This fits the pattern seen in a number of marine, freshwater, and anadromous species: that of reduced fecundity with increased life expectancy. Egg size generally varies with latitude in these species as well, but in the case of C. sardinella as in C. autumnalis, egg diameter appears to be constrained and shows little fluctuation about the mean. One of the major problems with this assumption is the lack of comparative data. Accurate data on egg size usually requires a presence on the spawning grounds, a logistic difficulty in the Canadian and U.S. arctic and subarctic.

3.3. Within latitude comparisons of Coregonus sardinella populations

A survey of fecundity (the only life history variable measured in all populations) in six populations of least cisco along the Beaufort Sea coast (Mann, 1974; present study), demonstrates that life histories comparisons may be influenced by behavioral traits, such as anadromy (Table 9).

The analysis includes two lakes that contained both normal and dwarf populations (Mann, 1974; Mann and McCart, 1981). Five of the populations are lake residents and one is an anadromous riverine population. The anadromous population reaches a larger size, and is more fecund (Table 9).

Table 9. A comparison of size, weight and fecundity for least cisco populations.

Variable	Location	Mean	Maximum
Fork Length			
Anadromous	Mackenzie River	330	380
Non-anadromous	Trout Lake (normal)	299	320
Non-anadromous	Trout Lake (dwarf)	96	111
Non-anadromous	Peters Lake (normal)	241	258
Non-anadromous	Peters Lake (dwarf)	125	130
Non-anadromous	Lake 105	242	311
Weight			
Anadromous	Mackenzie River	409	470
Non-anadromous	Trout Lake (normal)	283	336
Non-anadromous	Trout Lake (dwarf)	8.7	19
Non-anadromous	Peters Lake (normal)	148	183
Non-anadromous	Peters Lake (dwarf)	18.5	20
Non-anadromous	Lake 105	154	345
Fecundity			
Anadromous	Mackenzie River	35917	76422
Non-anadromous	Trout Lake (normal)	12059	19261
Non-anadromous	Trout Lake (dwarf)	409	672
Non-anadromous	Peters Lake (normal)	5250	9505
Non-anadromous	Peters Lake (dwarf)	974	1080
Non-anadromous	Lake 105	5286	13821

No significant differences were detected in log fecundity, using multiple analysis of covariance (Table 10). It would appear from this, that three life history types are found in Beaufort Sea *C. sardinella*: 1) lake resident dwarf forms which are short-lived, small fish with few eggs; 2) lake resident normal fish of moderate length, fecundity, and lifespan; and 3) long-lived anadromous forms which are longest and most fecund.

Table 10. Analysis of covariance of log fecundity for all North Slope least cisco populations.

Source of variation	SS	DF	MS	F	Sig
log fork length by location	.09	6	.01	.95	.462
location	.09	6	.01	.91	.488

It is clear from the differences between anadromous and non-anadromous normal and non-anadromous dwarf populations, that behavioral traits play a role in determining life history strategies in a fashion similar to that seen in Hutchings and Morris' (1985) review of salmonid life history strategies.

The role of anadromy as a life history strategy has been pointed out by a number of authors (most recently, Thorpe, 1981; Gross et al., 1988). It appears from this analysis that the exposure to a more abundant food source in the marine environment has enabled anadromous *C. sardinella* populations to grow larger and increase fecundity. What is most interesting, however, is the lack of any difference when fecundity is "adjusted" for length (ANACOVA). This suggests that anadromy may supply an advantage in increasing reproductive output, as a function of increasing size. The variation in fecundity takes place on the basic template provided by phylogeny. The "jumbo" lake dwelling form of least cisco reported by Lindsey and Kratt (1982), while apparently not anadromous, may represent a fourth life history type, however no population characteristics have been reported for this population.

3.4. Within latitude comparisons of sympatric North Slope coregonines

A number of species of coregonines are found sympatrically along the Alaskan North Slope (Beaufort Sea Coast). Due to the variation in the quality of the data collected from these populations, the only reproductive variable comparable across the species is gonad weight. This variable was used in an analysis of covariance with fork length as the covariate. This analysis for broad whitefish (Coregonus nasus), humpback whitefish (Coregonus pidschian), round whitefish (Prosopium cylindraceum), least cisco (Coregonus sardinella), Arctic cisco (Coregonus autumnalis), and the Arctic grayling (Thymallus arcticus) revealed no significant differences (Table 11). This suggests, at least in one important reproductive variable, that no particular pattern exists within the Coregoninae at that latitude, with the grayling acting as an outgroup in the analysis, but that a similar pattern in the relationship between somatic and gonadal growth may exist for these sympatric salmonids. This pattern is probably one of slow growth and delayed maturation resulting in alternate year reproduction, when compared with more southerly populations.

Table 11. ANCOVA for all North Slope fish.

Variable	d.f.	F-value	Significance
log fork length by species	1,56	.56054	.692
gonad weight by species	1,56	.55402	.697

DISCUSSION

The differences in the life histories between the two Arctic cisco populations (Arctic and Bering) demonstrate the apparent inability of this species to respond to the physiological stress of life at the higher latitude. The differences seen in the non-anadromous C. autumnalis pollan (Wilson and Pitcher, 1984) suggest that, given enough time and a greater divergence in habitat type and behavior, life history can change with the environmental conditions in a manner similar to that seen in numerous other fish species. The seeming inability of the Arctic cisco in this study to compensate for, decreased yearly reproductive output, which decreases the total lifetime output by either increasing the number of broods or increasing the size of eggs, suggests that these characters are not plastic. As is evident from the literature, this case is atypical, even among the whitefishes (Moskalenko, 1971). The only other whitefish species demonstrating a similar life history strategy is the round whitefish, Prosopium cylindraceum, which shows no apparent compensatory reproductive changes, in Alaska (present study).

The differences in Coregonus sardinella and C. autumnalis life histories may either be the result of evolution in separate refugia during the Wisconsin glaciation or the result of physiological responses to environmental stresses encountered post-glacially. If the North American range of each species is examined, it may be seen that C. sardinella extends considerably further south than C. autumnalis (Scott and Crossman, 1973). The inability of northern C. autumnalis to compensate for reduced fecundity by either increasing broods or egg size, as is seen in C. sardinella suggests differing abilities in responding to the physiological problems induced by higher latitude conditions. The reason for this could be a combination of phylogeny and physiological responses to a more stressful environment, with C. sardinella consisting of two populations that underwent evolution in two different refugia, becoming sympatric following the retreat of the glaciers. The present-day distribution of C. sardinella is more representative of one that could have been more easily influenced by the Bering land bridge. The analysis of coregonine life history strategies as a whole has shown that such a pattern may be possible (present study). This would allow the retention of sufficient intraspecific variability to enable it to adapt to a wide variety of conditions and still maintain its reproductive output. Clarke (1973) suggested that C. autumnalis spent the Wisconsin glaciation in the Beringian refugium. In opposition to this, as was pointed out in the discussion of Arctic cisco life history tactics, it would appear that the strategy seen in the northern population is a restriction of "normal" strategies, due to the physiological constraints imposed by the environment. This would argue against the notion of evolution in different refugia. The only variables that do show the expected response to changes in latitude are growth and growth related variables such as age and length at maturity, and total age and length. This result is not surprising as the restriction of energy available for uptake by the fish in these environments necessitates tradeoffs.

Also of interest is the maintenance of alternate year spawning in northern populations with an asymptotic growth pattern. If alternate year spawning arose as a result of the necessity to allocate scarce energy resources between gonadal and somatic development, as is likely, it seems that once the need for such allocation ended, when growth reached the asymptotic value, alternate year spawning would be discarded. It may be that in the case of C. autumnalis, the number of spawnings remaining for an individual fish is negligible, as these fish live only to an age of fourteen years. In the case of C. sardinella, which may live to be as old as twenty-one years, there remains a considerable time. Survivorship to this old age may be considerably reduced, and the total contribution to the population of these older fish may be, as in the case of C. autumnalis, quite small. Population structure analysis appears to bear this out (Craig and Haldorson, 1981).

4.1. Continental and latitudinal analyses of coregonine life histories

Based on the results of the previous analysis, it was of interest to determine whether differences in life history existed among populations of coregonines from a wider range, and if differences were found, could they then be attributed to changes in latitude or to phylogeny.

A multiple analysis of covariance was first done to determine whether any large-scale differences attributable to latitude could be detected in 67 populations from four genera or subgenera and 23 species. The variables analyzed were: age of maturity, number of broods, total life span, fecundity, and egg size (diameter). Maximum length was used as the covariate. Few data sets existed which documented life history variables over a continuous latitudinal range. Therefore, a decision was made to evaluate populations as North/South on a case-by-case basis rather than set an arbitrary baseline for such a determination. This allowed for flexibility in determining relationships on a geographical basis. For example, a population of _Prosopium williamsoni_ from Alberta was classified as northern, when compared with the same species in Utah. _P_. _coulteri_ populations from Alberta were considered southern, when compared with those in Alaska. No significant differences were found between latitudinal populations (Table 12).

Table 12. Results of multiple analysis of covariance

Effect	Value	Exact F	Hypoth. d.f.	Error d.f.	Sig.
log max length by latitude	.89392	1.50311	6	76	.189
latitude	.877	1.79724	6	77	.111

A nested multiple analysis of variance and a multiple regression analysis were also run using these data and produced no significant differences.

Despite the results of the previous multivariate analysis, a principal components analysis was done to look at the responses of individual populations to changes in latitude by examining component scores.

Univariate regressions were first done on each trait as it varied with maximum length. This was done to determine if length had a significant effect on traits to obscure their covariation. These regressions indicated that the relationship between log maximum length and log length at maturity, log age at maturity, and log fecundity was strong enough that a correction factor was applied to the data (Figs. 2-5 and Table 13). This correction factor was the same as that used by Stearns (1983, 1984) and Hutchings and Morris (1985). The slope of each trait regressed on maximum length was multiplied by maximum length and subtracted from that trait. A principal components analysis was then done.

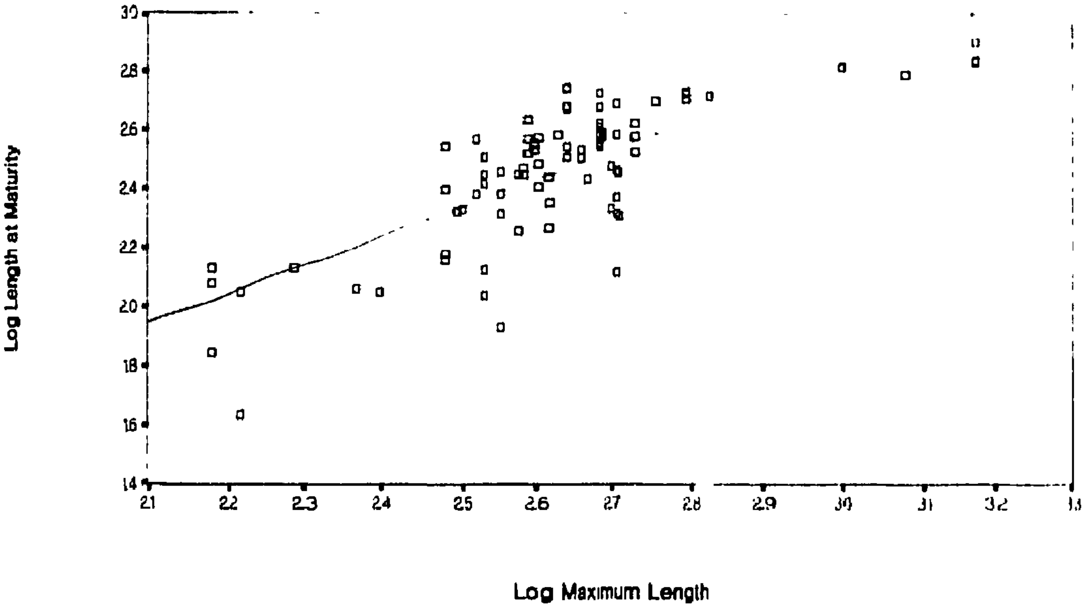


Figure 2. Linear regression - effect of log maximum length on log length at maturity

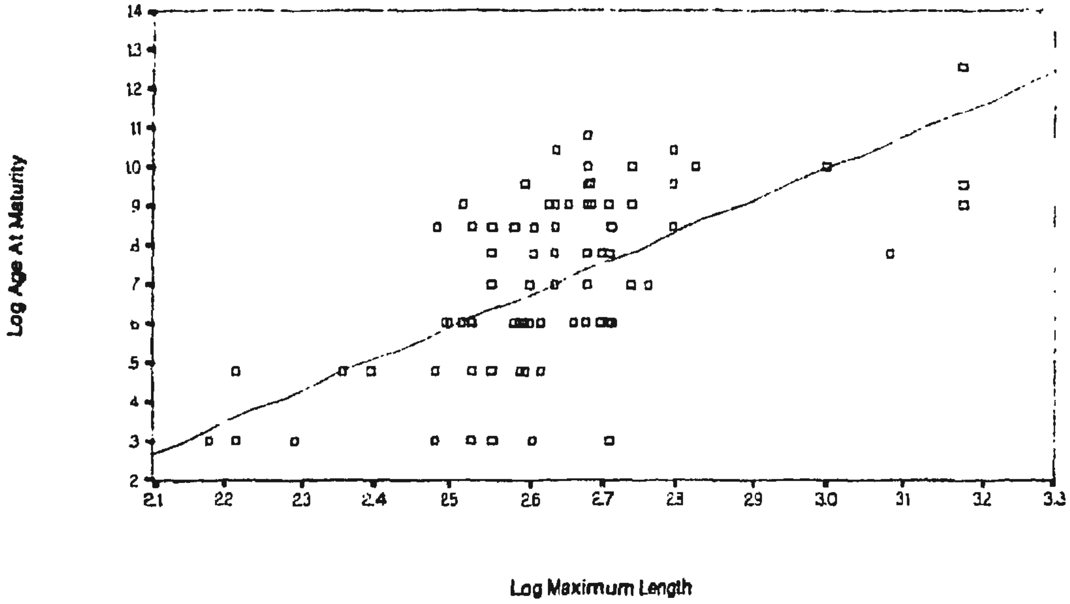


Figure 3. Linear regression - effect of log maximum length on log age at maturity

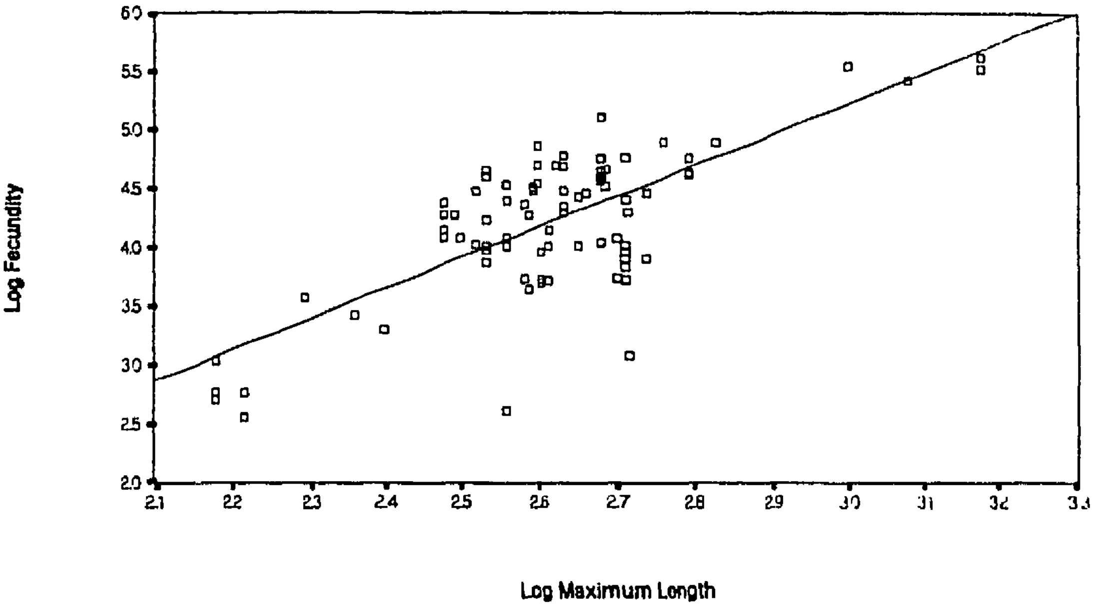


Figure 4. Linear regression - effect of log maximum length on log fecundity

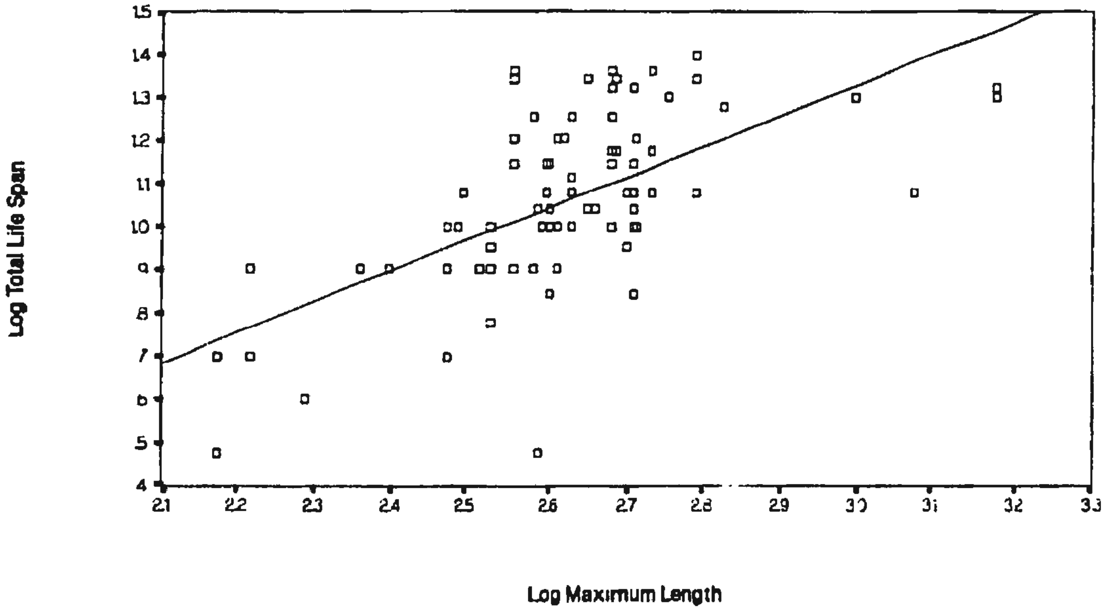


Figure 5. Linear regression - effect of log maximum length on log total life span

Table 13. Regression equations for life history variables.

Variable	Equation	r^2
log age at maturity	lam = -1.45 + .810 log max length	.47
log length at maturity	llm = -0.056 + .951 log max length	.64
log fecundity	lfec = -2.47 + 2.54 log max length	.61
log egg size	les = .197 + .0368 log max length	.003
log total life span	ltls = -.775 + 0.698 log max length	.44
log number of broods	lnb = -0.226 + .405 log max length	.14

Variable loadings were determined to be significant if their loading was greater than 0.64 (Stevens, 1986). The initial analysis extracted two components: Factor 1 described a strategy ranging from short lived, early maturing fish with low fecundity to long lived, late maturing, highly fecund fish with large eggs. Factor 2 described a strategy ranging from semelparous fish with small eggs to iteroparous with large eggs (Table 14).

Table 14. Factor loadings.

Variable	Factor 1	Factor 2
log length at maturity	.97	-.05
log age at maturity	.88	-.08
log max length	.88	.21
log total life span	.77	.32
log fecundity	.86	-.08
log number of broods	.39	.77
log egg size	-.27	.75
Total variance explained	56.3	17.6

When the analysis was run with maximum length removed, the amount of variance explained by Factor 1 drops two percent (56-54%)(Table 15). This suggests that maximum length is not extremely important in the life history of coregonines.

Table 15. Factor loadings, size removed.

Variable	Factor 1	Factor 2
log length at maturity	.90	-.03
log age at maturity	.89	-.06
log total life span	.84	.35
log fecundity	.84	-.06
log number of broods	.34	.80
log egg size	-.27	.68
Total variance explained	54.0	20.0

As a subfamily, coregonines scored generally positively for both factors. Northern coregonines as a group tended to be larger at maturity with higher fecundity which did not correlate well with what was seen in some other fish species, but did have a slightly greater tendency toward a greater number of broods with larger eggs (Appendices 2-5). That the southerly populations showed a similar, although considerably weaker, trend in reproductive traits independent of body size characters suggests that coregonine life history strategies may be more constrained by phylogeny than by environmental effects encountered with latitude. To determine this, the species in the analysis were divided into four genera which reflected the earlier, now discredited, taxonomic relationship. This allowed the differences between the ciscoes as genus Leucichthys and whitefishes as genus Coregonus to be considered more clearly.

Regression analysis of the effect of latitude on each component indicated little statistical and biological significance. For the subfamily, r^2 values for components 1 and 2 were .20 and .04 respectively. Values for individual genera were as follows: Coregonus (.01 and .37), Prosopium (.001 and .03), Leucichthys (.14 and .20), and Stenodus (.45 and .12). Values of .20 and greater were statistically significant, but little of the variation in a biological sense was explained by any of them. The number of populations of Stenodus (n=4) made these values biologically non-significant.

Populations of each species were scored positive, negative, or neutral in their relationship with the regression line of the effect of latitude on each component. While few of these lines had any statistical significance, and explained little of the biological significance, this eliminated the arbitrary decision made in earlier tests as to whether a population was northern or southern.

4.2 Intrageneric comparisons

Coregonus spp.

Populations of the genus Coregonus (Coregonus) are generally large, late-maturing fish on both continents (Table 16, Fig. 6). Where the genus differs is in egg size and number of broods. The North American forms are negative in these characters, while European/Eurasian forms have large eggs and many broods (Fig. 7). The regressions, while not biologically significant, did show increases in both traits with latitude. The strongest relationship was seen in component 2. A great deal of the influence in the European/Eurasian forms of this genus comes from C. lavaretus. All negatively loaded populations for both components come from this species (Table 16). This apparent lack of plasticity in component 1 stands in contrast to its noted diversity and morphological variation.

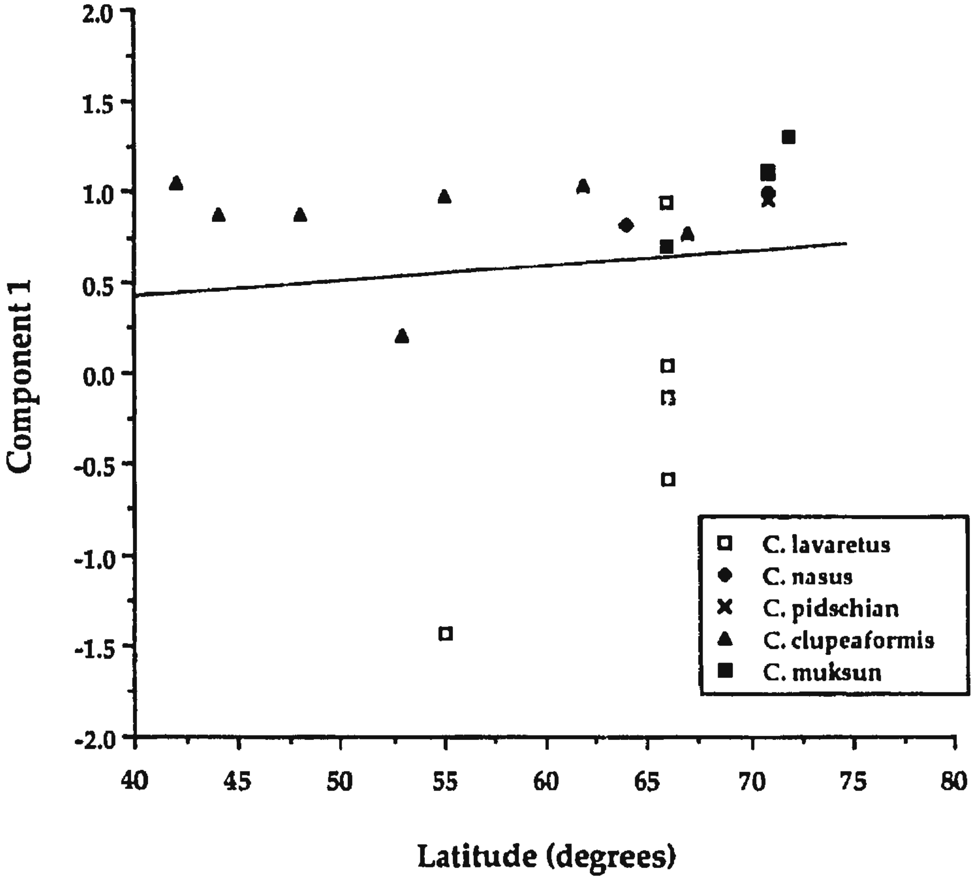


Figure 6. **Plot of component 1 scores against latitude for the subgenus Coregonus (coregonus) spp.**

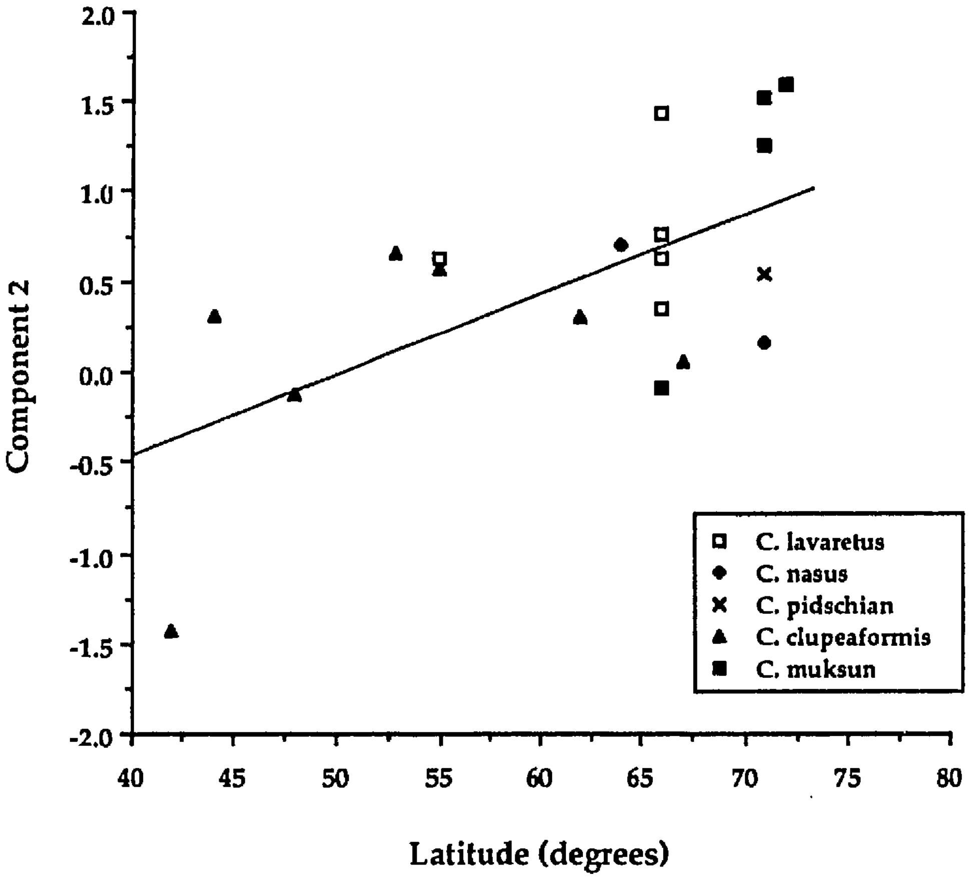


Figure 7. Plot of component 2 scores against latitude for the subgenus Coregonus (Coregonus) spp.

Table 16. Factor loading totals for Coregonus.

	Component 1			Component 2		
	Pos.	Neg.	Neut.	Pos.	Neg.	Neut.
Genus						
N. America	9	1	0	3	6	1
Europe	5	4	0	7	2	1
C. nasus						
N. America	3	0	0	0	1	0
Europe	1	0	0	1	0	0
C. clupeaformis						
N. America	6	1	0	3	3	1
C. pidschian						
N. America	1	0	0	0	1	0
C. muksun						
Europe	3	0	0	3	0	1
C. lavaretus						
Europe	1	4	0	3	2	0

Prosopium spp.

The genus contains a total of seven species, three of which are confined to a single lake, Bear Lake, Utah (*P. abyssicola*, *P. gemmiferum*, and *P. spilnotus*). The remaining species are more widespread although the populations of *P. coulteri* and *P. williamsoni* are confined (with one exception: *P. coulteri* in Lake Superior) to western and northwestern North America. *P. cylindraceum* is widespread across the northern portion of the continent. As a genus *Prosopium* are more long-lived and fecund, although this is accounted for solely by *P. cylindraceum* and *P. williamsoni*. The other genera are all short-lived and have a lower fecundity (Table 17, Figs. 8 and 9). There is no latitudinal trend for these factors for any of the species. A regression of this component with latitude produced an r-value of 0.1, which was not statistically significant. The regression line showed an inverse (non-significant) relationship with latitude.

Table 17. Factor loading totals for *Prosopium*.

	Component 1			Component 2		
	Pos.	Neg.	Neut.	Pos.	Neg.	Neut.
Genus	12	8	1	5	10	3
P. cylindraceum	8	1	1	3		3
P. coulteri	0	4	-	0	4	-
P. williamsoni	4	0	-	2	2	-
P. gemmiferum	-	1	-	1	-	-
P. spilnotus	-	1	-	1	-	-
P. abyssicola	-	1	-	1	-	-

Scores for egg size and number of broods showed an inverse relationship to latitude, although this was not significant. *P. coulteri* had fewer broods and smaller eggs. *P. williamsoni* and the Bear Lake forms scored generally higher on these traits, with the Wyoming population of *P. williamsoni* scoring especially high (Fig. 9). *P. cylindraceum* was intermediate. No data from Eurasian populations of *Prosopium* were found.

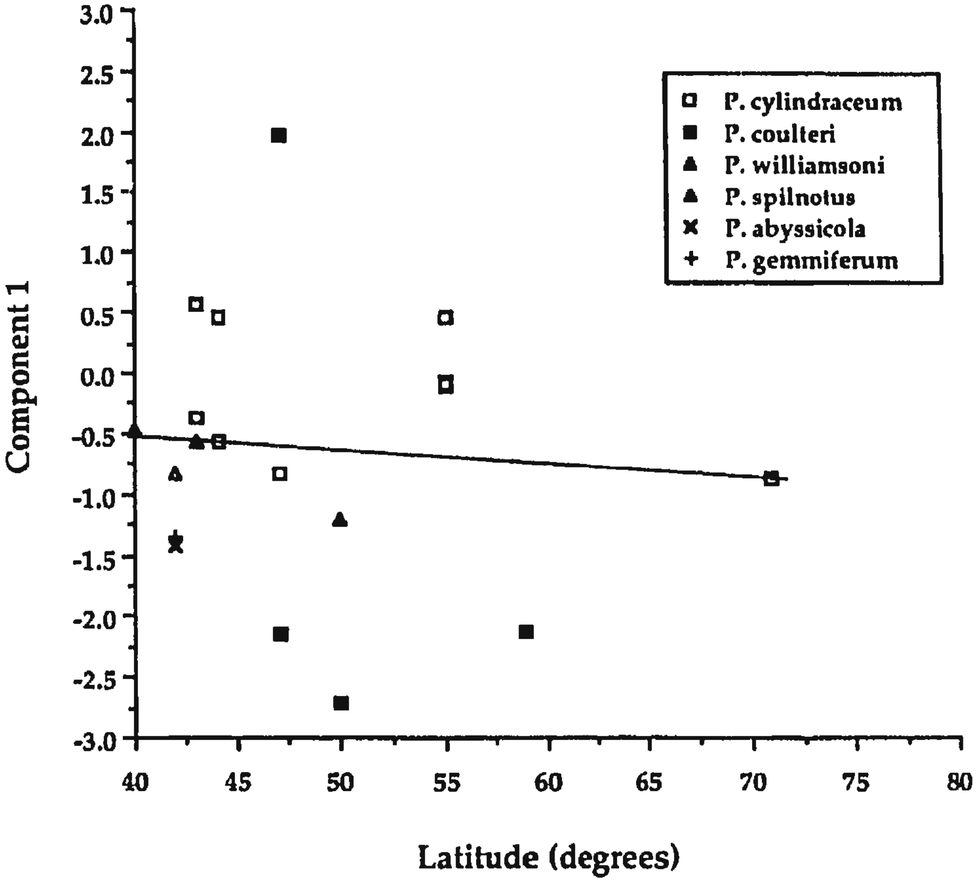


Figure 8. Plot of component 1 scores against latitude for the subgenus <u>Prosopium</u>

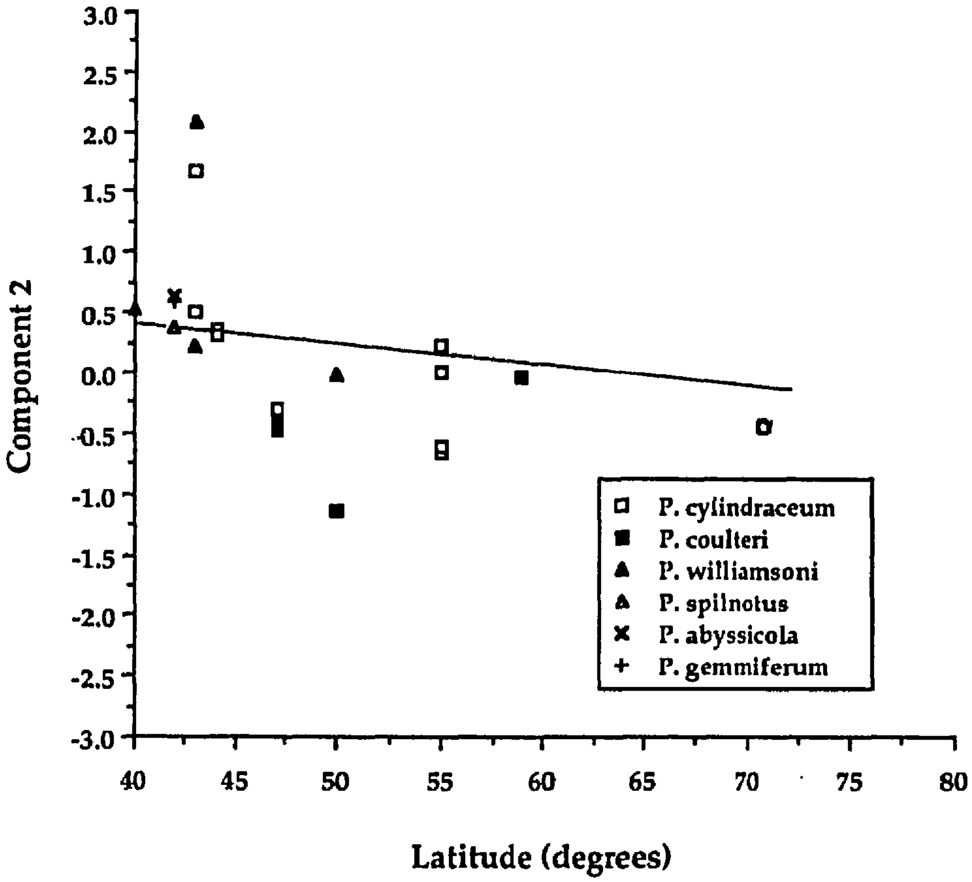


Figure 9. Plot of component 2 scores against latitude for the subgenus Prosopium

Members of the subgenus <u>Coregonus</u> (<u>Leucichthys</u>) were also generally large fish of high fecundity and late maturity, overall, on each continent (Table 18, Figure 10).

Table 18. Factor loading totals for <u>Leucichthys</u>.

	Component 1			Component 2		
	Pos.	Neg.	Neut.	Pos.	Neg.	Neut.
N. America	10	3	0	9	3	(1)
Europe	7	10	1	8	9	0
<u>C</u>. <u>autumnalis</u>						
N. America	2	0	0	1	1	0
Europe	2	2	(1)	1	4	0
<u>C</u>. <u>sardinella</u>						
N. America	4	2	0	5	1	0
Europe	2	2	0	3	1	0
<u>C</u>. <u>hoyi</u>						
N. America	2	0	0	2	0	0
<u>C</u>. <u>artedii</u>						
N. America	2	1	0	1	1	(1)
<u>C</u>. <u>albula</u>						
Europe	0	5	0	3	2	0
<u>C</u>. <u>peled</u>	3	0	0	1	2	0
<u>C</u>. <u>tugun</u>	0	1	0	0	0	1

This trait also showed a non-significant increase with latitude. Populations from Europe tended to load negatively for egg size and brood number, especially <u>C</u>. <u>autumnalis</u> and <u>C</u>. <u>peled</u>. North American populations were strongly positive. In both regions the strongly positive relationship between latitude and this component seen in *C. sardinella* influenced the totals. *C. albula* tended to be more like the North American ciscoes *C. artedi* and *C. hoyi* in this regard. *C. albula* were strongly negative, however, for the first component, and were early maturing, smaller fish, with fewer eggs. *C. autumnalis*, on the other hand, were similar to their North American conspecifics in this extent (Fig 11).

The monotypic genus, *Stenodus*, the inconnu or sheefish, is the only fish to remain consistent in Component loadings between latitudes and continents (Table 19). In almost all cases (based on only five populations) *S. leucichthys* evenly split in loadings for both components. The single North American population was intermediate in size-related characters but strongly positive for egg size and number of broods. The European populations were evenly split, but showed a trend toward increasing size with decreasing latitude but decreasing egg size and brood number. Both of these trends were non-significant (statistically and biologically) due to the small sample size (Figs. 12, 13).

Table 19. Factor loading totals for *Stenodus leucichthys*.

	Component 1			Component 2		
	Pos.	Neg.	Neut.	Pos.	Neg.	Neut.
North America	0	0	1	1	0	0
Europe	2	2	0	1	2	1

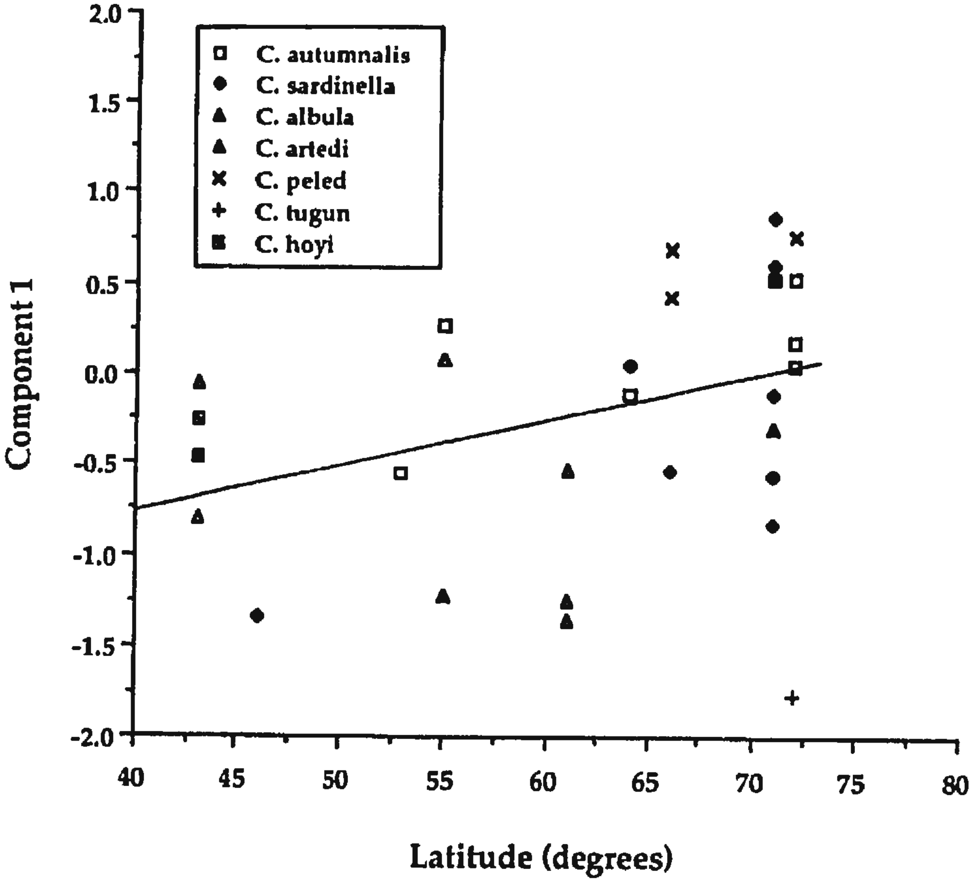


Figure 10. Plot of component 1 scores against latitude for the subgenus Coregonus (Leucichthys) spp.

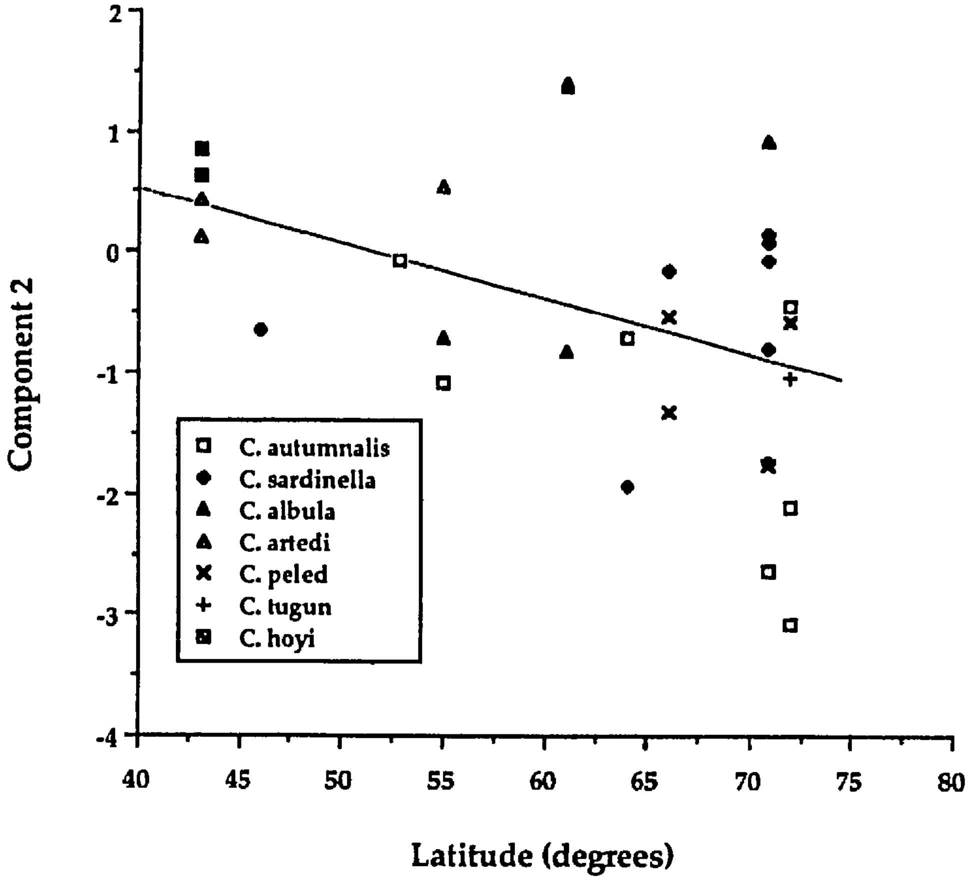


Figure 11. Plot of component 2 scores against latitude for the subgenus <u>Coregonus</u> (<u>Leucichthys</u>) spp.

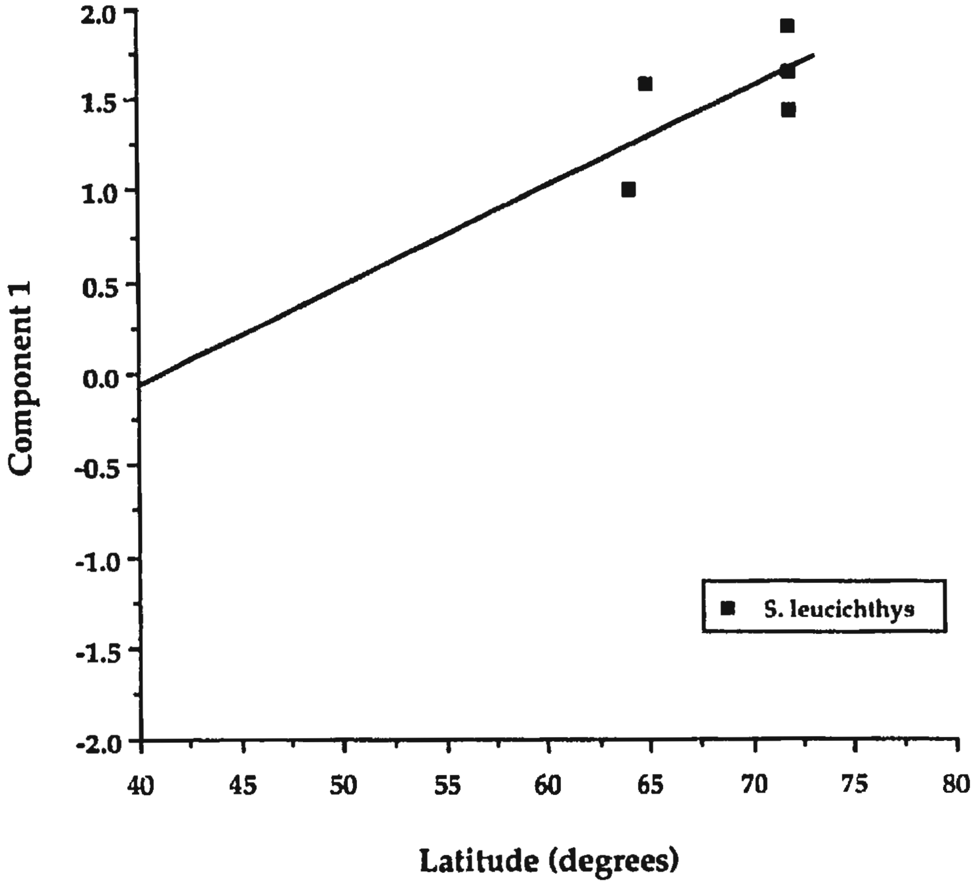


Figure 12. Plot of component 1 scores against latitude for the subgenus Stenodus leucichthys

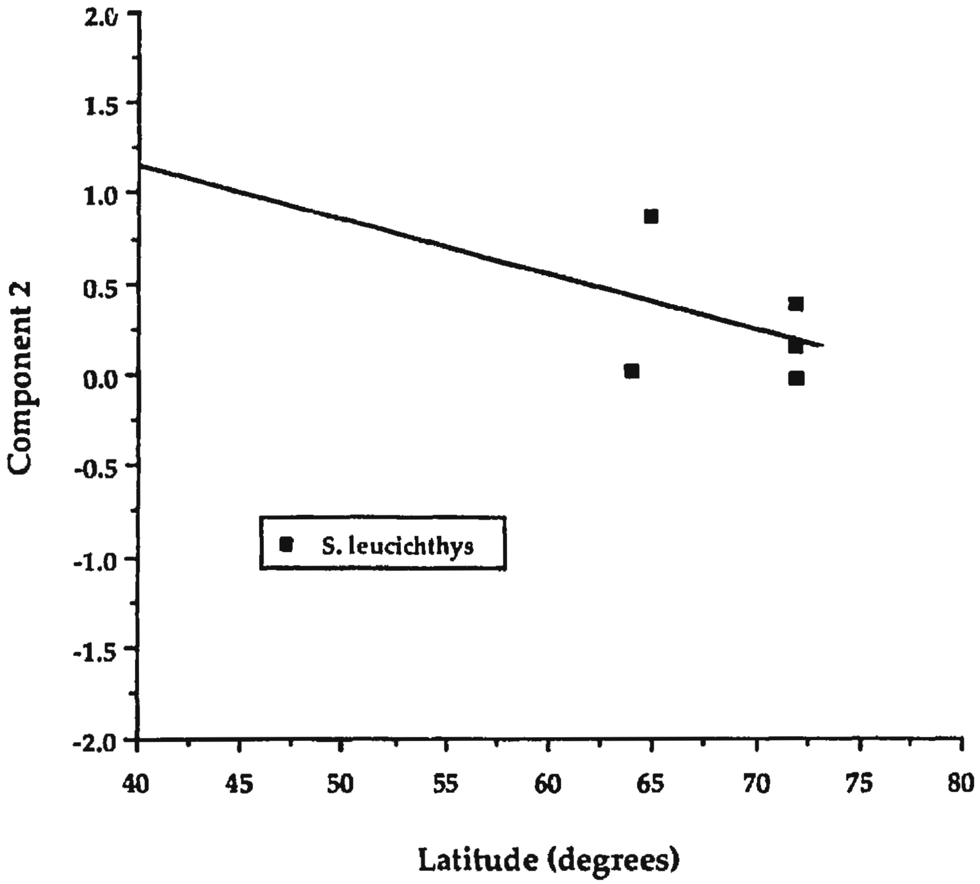


Figure 13. Plot of component 2 scores against latitude for the subgenus <u>Stenodus</u> <u>leucichthys</u>

4.3 Discussion of latitudinal trends in life history variables

In most genera and subgenera, the variation between latitudes was not great as that within latitudes, especially at the more northerly latitudes. The genus Stenodus, and most species of both Prosopium and Coregonus (Coregonus) seem to demonstrate consistent patterns in component loading throughout their range especially those in Europe and Eurasia. The North American forms of Coregonus (Coregonus) were similarly consistent in being large fish of relatively high fecundity. Coregonus clupeaformis, the lake whitefish, accounted for most of the positive loadings for egg size and number of broods.

It is not surprising that Coregonus clupeaformis differs slightly from the other members of its subgenus. Jensen (1985) noted the variability in life history traits seen in this species and thought this showed a flexibility for persistence in differing environments. A number of the populations also show the effects of exploitation: increased fecundity, earlier maturity, and smaller egg size (Bidgood, 1974; Healey, 1978; Jensen, 1982).

The subgenus Coregonus (Leucichthys) spp. showed North-South disparities in factor loadings. This suggests that life histories are plastic in most members of the subgenus. Coregonus sardinella seems to demonstrate an ability to respond to environmental conditions. Southerly populations scored negatively for Component 2 in Europe and North America. This is probably due to the lack of variation in egg size seen in these populations, as well as the shorter life span which cuts down on the number of broods. This information concurs with the earlier comparisons for C. sardinella (this study), that the latitudinal populations have different fecundities, but similar egg sizes. This was not seen in North American C autumnalis, which differed only slightly in component scores. This further suggests that a lack of flexibility can be strong among members of the subgenus with the most plastic life histories.

At the level of subfamily, it appears that the most consistent life history variable throughout is that of egg size (Appendix 1). Some variability is seen in species between latitudes and continents, but the majority show very little difference. The most variability in egg size seems to be between lake whitefish populations which includes those undergoing exploitation (Healey, 1978; Jensen, 1982, 1985). The plasticity seen in these populations may be indicative of human exploitation-induced life history changes. The remainder of traits appear to be able to be influenced by latitude, or perhaps behavior (anadromy). Alternate year spawning in northern populations, in general, is compensated for, at least in some C. (coregonus) spp. groups (C. nasus and C. pidschian), by both an increased lifespan and increased fecundity. This means, a larger reproductive output over the lifetime of the northern fish. This trait could be the result of a northern origin for the species. This would account for what appears to be the ability to completely compensate for reproductive losses resulting from environmentally induced late maturation, and lower fecundity. Coregonus (coregonus) spp. were considered to be lake dwelling northwest Eurasian in origin (Smith, 1957), but the members of the subgenus showing these compensating traits are generally anadromous in habit, demonstrating the possibility of the confounding influence of behaviour on life history strategies.

The genus Stenodus is unusual in that, of all the coregonine genera, it has what would be considered to be only "northern" populations. As in the whitefishes, component loading values suggest a northern strategy of reduced growth rate, increased broods and increased fecundity. The nucleus area, or area of apparent origin, and indeed the area of widest occurence and greatest plasticity for Stenodus is Siberia (Smith, 1957).

Prosopium represents a genus with a more southerly origin. Smith (1957) felt that the nucleus area of the genus Prosopium was in the rivers of northwestern North America. This region is certainly where the greatest diversity in the genus is found (Lee et al., 1980). Northern Alaskan populations had lower fecundities and the number of broods decreased from what was seen in the south. The factor loadings appear to be those expected for a southern species. Indeed, the only truly "northern" species in terms of distribution in this genus is P. cylindraceum, although the range of P. coulteri does extend as far north as southern Alaska. P. cylindraceum, in Alaska, does not exhibit the characteristics suggested by other studies as being those of a northern fish species, with its low fecundities and low numbers of broods. The non-anadromous nature of Prosopium cylindraceum probably accounts for its inability to compensate for its later maturity, alternate-year spawning and decreased number of broods in the north. The riverine habitat it occupies is of limited productive capacity, when compared with that of the marine environment (Craig and Haldorson, 1981). In northern Quebec, Morin et al. (1982) found that P. cylindraceum was able to compensate in a manner similar to of other fishes (Paulson and Smith, 1977; Leggett and Carscadden, 1978; Haldorson and Craig, 1984). It may be the result of a better habitat (larger river systems), a lower latitude, or both (Craig, 1989).

The ciscoes are the most interesting group in terms of constraint. The population level life history analysis of the Arctic cisco revealed what was interpreted to be physiological restraints on somatic growth and maintenance constraining reproductive effort. This also differs from previous studies which found decreased fecundity, but increased egg size and number of broods in northern fish (Leggett and Carscadden, 1978). However, a similar condition was detected in the lake cisco, C. artedii, from James Bay, Quebec, by Morin et al. (1982). This is not unexpected as C. artedii is considered to be a "southern" cisco, although it does also penetrate the upper Mackenzie River system.

It was Smith's (1957) hypothesis that cisco evolution at least in North America, was based on a C. artedii-like progenitor and had as its "nucleus area" the lakes of northeastern North America, presumably the Great Lakes. If this southern origin were indeed the case, it is no wonder that, as the species moved north, its life history characteristics would be those of a fish that has reached its physiological limit. This is definitely the case in C. artedii.

The life histories of the least cisco differ, with compensation for reduced annual reproductive output by increased lifetime output, and therefore an increased number of broods. As well, the effect of anadromy, which enables an increased reproductive effort through access to increased energy supplies, was seen in the intra-latitudinal comparisons of fecundity. This is not an uncommon occurrence in the Salmonidae and other families that demonstrate this behavior (Thorpe, 1981). It has been shown to increase the amount of energy available for growth and reproduction (Gross et al., 1988). This species also contained the only known "dwarf" and "giant" populations, which have been hypothesized as life history types for spreading risk, or "bet-hedging", in other species (Gross, 1984). They may be, at least in the case of the "giant" form, merely growth types, but may also imply a plasticity in life history forms characteristically seen in the other Salmonids (Gross, 1984). The comparison of the non-anadromous forms of *C. autumnalis* (*C. a. pollan* and *C. a. migratorius*) (the southern European forms in Figs. 10 and 11), supports the hypothesis that this life history tactic allows for increased growth and fecundity. However, the effect does not seem as pronounced as that seen in *C. sardinella*.

SUMMARY

The Arctic cisco, Coregonus autumnalis, belongs to a sub-family which has a great deal of diversity, in terms of both morphology and life history characteristics. Despite this "pedigree" and its wide range across both Palearctic and Neararctic, this species shows little variation among its populations. Morphologically the members of this species show little or no divergence. A slightly greater variability exists in life history strategies, but the constraints of phylogeny appear to be quite strong.

Arctic and Bering cisco populations show no significant intra-population differences in reproductive characteristics such as fecundity or gonad weight but inter-population differences are found. A difference was seen as well in egg size, but this may be due to timing of collections.

Least cisco populations from the same area showed similar intra- and inter- population trends. Sympatric least cisco populations showed variation in life history traits brought about by the influence of behavioral traits, such as anadromy, but this variation took place on a shared template such that when size differences were removed there were no significant population differences.

Similar analyses of sympatric whitefishes from the North Slope of Alaska demonstrated no significant differences in gonad weight, suggesting that a similar reproductive strategy was being followed. An analysis of life history traits from North Americ and Europe was done, to determine if similar responses to latitudinal (environmental) constraints existed within the subfamily. A multiple analysis of covariance revealed no differences between latitudes. A principal components analysis of the individual populations showed different responses within and between genera. It was determined that, in some reproductive characters, the influence of phylogeny was such that adaptations to latitude were constrained. While the analysis reveals that coregonines are, in general, large, long-lived, fecund individuals, a number of species fail to fit the mold.

GENERAL DISCUSSION

The Coregoninae appear to demonstrate a plasticity of life history that rivals the plasticity of their phenotypic characteristics. While the effects of phylogeny may be seen in some members of the subfamily, superimposed upon this are the adaptations resulting from responses to conditions encountered through wide scale dispersal into other latitudes in other species. This dispersal has brought the populations into regions with probably much more (or less) extreme differences in climate and/or food supply. The apparent ability of members of the subfamily to occupy these habitats is attributable to this plasticity. In addition to physiological plasticity, behavioral traits such as anadromy have served to modify some traits by increasing the amount of energy available for growth and reproduction. In at least some populations, exploitation may modify life history characters by decreasing age (and therefore size) at maturity but increasing fecundity (Jensen, 1985).

The differing levels of data analysis provide insight into the details of coregonine life history. Unlike most of the species cited in the introduction, coregonines as a group show no consistent trend in life history variation with changes in latitude. For example, C. autumnalis appears unable to alter other aspects of its life history (such as increased number of broods) to compensate for decreased reproductive output, but C. sardinella not only shows latitudinal differences between its populations but behavioural differences as well. When such variables as fecundity and gonad weight are investigated among coregonine populations at a similar latitude no differences are seen across genera, and even sub-families. This analysis would seem to indicate that, once size-related differences are removed, all species appear to be working under similar restrictions. This further suggests that phylogeny may play an important role in determining the amount of plasticity in the group. Conversely, the role of latitude-related effects may not be as strong in all groups. The situation is probably similiar to that seen by Morin et al. (1982) in the James Bay region of Quebec, Canada. Two species of whitefish demonstrated an ability to adjust reproductive output to counter adverse environmental effects on somatic variables, while the third, a cisco, could not.

The responses of coregonine fishes to latitudinal change involve, in part, their great degree of plasticity. The subfamily demonstrates a wide range of both size and age-related alterations with latitude, yet doesn't have the expected responses for reproductive variables based on allometric relationships with body size variables. Changes occur based on the broad template provided by phylogeny, (as in the latitudinal populations of C. sardinella) as would be expected from any group, but compensation for reproductive losses (through older maturation and smaller brood size) such as larger egg size and more broods, are not always seen. The analyses seem to suggest that exposure to environmental extremes may be a recent phenomena in the phylogenetic history of at least some of the coregonines. The fact that Prosopium cylindraceum, probably the most ancient species in the genus (Booke, 1968,1970; but see Norden, 1970), is unable to compensate for northern conditions despite its wide distributional range, suggests a strong genetic control over certain reproductive characteristics. A similar tendency is demonstrated by C. autumnalis. The trends pointed out by the principal components analysis, when used in conjunction with the population characteristics, support this. The data set is not complete, but it appears, at least in the European ciscoes, that a greater ability to compensate for adverse latitudinal conditions exists. This may be due to the plasticity seen in C. albula, considered to be the "progenitor" of the European forms (Behnke, 1972).

The members of the subgenus Coregonus (Coregonus) show opposing trends. North American fish tend to be large, slow-growing, late-maturing fish of great fecundity, but small egg size and brood number. European forms are smaller fish but with larger eggs and more broods. This is probably due, to a large extent, to the composition of the faunas on each continent. The North American data set is dominated by

C. clupeaformis, a large, widely distributed species, while the European fish are mainly *C. lavaretus* and *C. muksun*, which are not nearly so large.

The available evidence suggests that there is no latitudinal life history gradient in coregonine fish populations. Latitudinal population differences exist for the least cisco, *Coregonus sardinella* in the manner seen in other fishes, but not between latitudinal populations of the Arctic cisco, *Coregonus autumnalis*. Predictions opposite to those expected may also be found in both the broad whitefish *Coregonus nasus* and the round whitefish, *Prosopium cylindraceum*.

Population differences within a latitude also exist. The presence of at least three sympatric life history strategies in the least cisco (*C. sardinella*) confirms several predictions. Clearly, anadromous populations grow larger and are more fecund than either lake dwelling normal or lake dwelling dwarf populations. The plasticity seen in the least cisco, when compared to Arctic cisco, is further evidenced by population distributions. *C. sardinella* is found in many, if not most, of the streams and larger lakes and ponds along the Arctic coast, while *C. autumnalis* is found only in the largest river systems. What is generally seen, however, is a tendency for coregonine fishes to be large, late maturing fishes of relatively high fecundity. The outliers appear to be fishes of suspected southern origin, ie. the genus *Prosopium*, *Coregonus artedii*, *Coregonus autumnalis*, and the Great Lakes ciscoes, or fish undergoing environmental problems. An excellent example of this occurs in two Alberta populations of *C. clupeaformis*, found at a similar latitude and with grossly similar habitat features. Populations in one lake are quite dense, which affects life history traits, bringing about smaller, earlier maturing, less fecund fish than in the other lake.

GENERAL SUMMARY

An analysis of the characteristics of the Coregonus autumnalis species complex determined that the division of this group into two species, C. autumnalis and C. laurettae by Bean (1882) and McPhail (1966) does not represent its true nature. The morphological differences between the widely separated populations were not sufficient to distinguish the two fish at the species level. The morphometric analysis determined that, in the two originating river systems, classification rates were between 80 and 85 percent. A classification rate of greater than 95 percent is considered indicative of species-level differences. Classification rates in other sample sites were quite variable, suggesting no clear pattern. An analysis of gill raker counts, the characteristic used by McPhail (1966), revealed a different pattern than that used to split the complex. The bimodal distribution of gill raker counts used by McPhail to re-separate the two species was probably a function of the small sample size used. An increased number of samples and sample locations revealed a small, consistent pattern of low gill raker count fish in all Arctic cisco sample areas. It was proposed that the view of Dymond (1943), that these fish belong to a single species, Coregonus autumnalis, be upheld. It is possible that the Yukon River population originated from the

Mackenzie River populations through stream capture, rather than by a land bridge bifuricating the original species range, as was put forth by McPhail (1966).

An analysis of life history strategies, both within and between species has revealed differing responses to changes in latitude in the coregonines. Sympatric populations of C. autumnalis and C. sardinella demonstrated the ability of one species (C. sardinella) to adjust its reproductive output through a variety of conditions. Anadromy was seen to increase body size, and thereby increase fecundity, but not to change the basic template. When the effect of size was removed no significant difference in fecundity was seen between anadromous and non-anadromous fish. Arctic cisco did not show a similar ability to compensate for later reproduction, due to its shorter lifespan. The dichotomy seen here is carried on through the other species in the subfamily. Prosopium and Coregonus reflected, to a greater or lesser extent, the restriction of their ability to compensate for decreased fecundity and later maturity resulting from latitudinal differences in energy availability, by phylogeny. The genus Prosopium, despite the widespread distribution of P. cylindraceum, demonstrated the attributes of a southern species unable to compensate for northern conditions. A similar condition was seen in the whitefishes, Coregonus (Coregonus) where, with the exception of a single southerly population of C.

clupeaformis, no change was seen in egg size or number of broods, with latitude. A similar condition was seen in age and size variables, with the outlier belonging to C. lavaretus.

The ciscoes, Coregonus (Leucichthys) showed a decline in reproductive variables (egg size and number of broods) with latitude. A slight increase was noted for age and size variables. This demonstrated the lack of a consistent trend within the subgenus for variation with latitude, and suggests that the role of phylogeny may have been more important in reproductive variables than in morphology.

It was concluded that the plasticity seen in coregonine morphologies is not necessarily mirrored in their life histories.

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Appendix 1. Life history variables for Coregonine populations

Species	C.	A.	Le.	F.	E.	Li.	No.	Ma.	La.
C. nasus	N.A.	09	378	46234	1.9	22	07	485	71
P. cylindraceum	N.A.	02	255	5000	2.7	11	09	400	71
P. cylindraceum	N.A.	07	285	20000	1.8	16	09	513	44
C. autumnalis	N.A.	08	350	22271	2.0	12	02	430	71
C. autumnalis	N.A.	04	330	30243	2.0	10	06	390	64
C. sardinella	N.A.	07	280	23374	1.9	18	06	380	71
C. sardinella	N.A.	04	260	44693	1.9	8	04	340	64
C. clupeaformis	N.A.	12	476	44331	2.5	18	06	800	62
C. clupeaformis	N.A.	09	419	40321	2.1	15	06	800	67
C. clupeaformis	N.A.	05	350	11112	1.9	18	13	450	53
C. clupeaformis	N.A.	08	531	57330	2.1	14	06	800	48
C. clupeaformis	N.A.	07	551	110700	1.3	12	05	800	42
C. clupeaformis	N.A.	07	420	62750	1.8	23	16	800	44
C. clupeaformis	N.A.	08	354	67200	1.8	19	11	635	55
C. nasus	N.A.	08	390	33170	1.9	15	07	485	71
C. pidschian	N.A.	08	380	29000	2.0	15	07	540	71
C. sardinella	N.A.	05	240	34033	1.9	22	09	360	71
C. sardinella	N.A.	03	085	12059	1.9	14	11	360	71
C. sardinella	N.A.	06	205	00412	1.9	23	09	360	71
P. coulteri	N.A.	02	120	00508	2.4	05	03	150	47
P. coulteri	N.A.	02	135	01084	2.4	05	03	150	47
C. autumnalis	Eur.	03	370	32000	1.5	10	07	390	72
P. coulteri	N.A.	02	070	00580	2.4	03	02	150	50

Species	C.	A.	Le.	F.	E.	Li.	No.	Ma.	La.
P. coulteri	N.A.	02	112	00580	2.4	05	04	165	59
P. cylindraceum	N.A.	06	235	9100	2.0	12	06	510	55
P. cylindraceum	N.A.	02	305	9100	2.0	07	05	400	47
S. leucichthys	Eur.	08	690	335000	2.4	20	06	1500	64
P. cylindraceum	N.A.	04	235	05330	2.0	12	08	510	43
P. cylindraceum	N.A.	04	300	05500	2.0	09	05	500	44
C. clupeaformis	N.A.	04	350	11112	1.9	18	09	480	53
C. clupeaformis	N.A.	06	470	49114	1.8	18	09	430	45
P. coulteri	N.A.	03	043	00362	2.0	08	06	165	59
P. williamsoni	N.A.	03	280	04401	2.1	03	08	385	50
C. artedi	N.A.	06	290	8000	2.1	14	08	510	55
P. cylindraceum	N.A.	06	305	9100	2.0	10	04	400	55
S. leucichthys	Eur.	18	680	420000	2.4	20	06	1500	72
P. williamsoni	N.A.	03	225	14000	2.1	10	08	411	40
C. sardinella	Eur.	04	240	10500	2.2	08	05	330	66
C. sardinella	Eur.	04	180	5400	2.2	08	05	380	71
C. sardinella	Eur.	07	320	17000	2.2	10	04	340	72
C. autumnalis	Eur.	08	370	29900	1.7	08	01	330	72
C. autumnalis	Eur.	09	430	32400	1.7	10	02	390	72
C. autumnalis	Eur.	07	350	19000	1.7	10	04	300	55
C. muksun	Eur.	07	510	57000	2.3	12	06	620	66
C. muksun	Eur.	09	540	43100	2.3	22	14	620	71
C. muksun	Eur.	11	530	41300	2.3	25	14	620	71
C. lavaretus	Eur.	08	490	25600	2.3	21	14	510	66
C. lavaretus	Eur.	04	294	18800	2.3	11	08	385	66

Species	C.	A.	Le.	F.	E.	Li.	No.	Ma.	La.
C. nasus	Eur.	05	500	78900	2.3	20	08	570	64
C. peled	Eur.	05	361	73500	1.2	14	09	396	72
C. peled	Eur.	05	340	50000	1.2	12	08	396	71
C. peled	Eur.	04	353	34900	1.2	12	09	396	66
C. tugun	Eur.	02	135	3732	2.0	04	03	195	72
P. cylindraceum	N.A.	07	376	5318	1.2	14	08	400	55
P. cylindraceum	N.A.	08	320	10300	2.4	22	14	450	43
C. pidschian	N.A.	10	419	29000	2.3	23	07	540	71
P. williamsoni	N.A.	04	276	10235	2.7	08	05	410	43
P. williamsoni	N.A.	03	185	5180	2.7	16	14	410	43
S. leucichthys	Eur.	09	800	420000	2.5	21	07	1500	72
S. leucichthys	N.A.	10	656	350000	2.5	20	10	1000	65
C. autumnalis	Eur.	03	250	14000	2.0	08	06	300	53
C. hoyi	N.A.	04	210	18768	2.8	10	07	310	43
C. albula	Eur.	03	260	39908	2.0	06	04	340	61
C. lavaretus	Eur.	04	279	7386	3.0	09	06	340	66
C. artedi	N.A.	02	241	10250	1.9	08	07	360	43
P. cylindraceum	N.A.	06	215	12000	2.0	12	07	500	55
C. albula	Eur.	02	150	24000	2.0	05	04	300	55
C. lavaretus	Eur.	06	385	10425	2.5	11	06	510	66
C. muksun	Eur.	10	520	78000	2.7	19	10	670	72
C. albula	Eur.	02	133	9405	3.0	09	08	340	61
C. albula	Eur.	02	109	10189	3.0	09	08	340	61
C. sardinella	Eur.	02	144	12200	2.0	05	04	300	46
C. albula	Eur.	04	207	58230	3.0	10	07	510	71

Species	C.	A.	Le.	F.	E.	Li.	No.	Ma.	La.
C. lavaretus	Eur.	02	131	6807	2.6	07	06	510	55
C. peled	Eur.	05	385	129000	1.2	10	06	480	66
S. leucichthys	Eur.	06	620	264000	2.2	12	07	1200	64
P. spilnotus	N.A.	04	203	1200	2.0	10	07	515	42
P. abussicola	N.A.	03	112	2000	2.5	08	06	250	42
P. gemmiferum	N.A.	03	115	2657	2.5	08	06	230	42
C. artedi	N.A.	04	272	29000	2.1	11	08	460	43
C. hoyi	N.A.	04	213	12045	2.0	12	09	315	43

Legend

C.	Continent	Li.	Life span
A.	Age at Maturity	No.	Number of Broods
Le.	Length at Maturity	Ma.	Maximum length
F.	Fecundity	La.	Latitude
E.	Egg size		

Appendix 2. Factor loadings for the genus *Coregonus* (*Coregonus*).

Species	Continent	Latitude	Component 1	Component 2
C. nasus	N. America	N 71	1.01	0.14
	Eurasia	S 64	0.82	0.68
C. pidschian	N. America	N 71	0.97	0.53
C. clupeaformis	N. America	N 62	1.03	0.29
	N. America	N 67	0.78	0.05
	N. America	S 53	0.21	0.64
	N. America	S 48	0.87	-0.13
	N. America	S 42	1.05	-1.43
	N. America	S 44	0.87	0.30
	N. America	S 55	0.98	0.55
C. muksun	Eurasia	S 66	0.70	-0.10
	Eurasia	S 71	1.12	1.50
	Eurasia	N 72	1.31	1.58
	Eurasia	N 71	1.11	1.24
C. lavaretus	Eurasia	N 66	0.95	1.41
	Eurasia	N 66	-0.13	0.62
	Eurasia	S 55	-1.43	0.61
	Eurasia	N 66	-0.53	0.75
	Eurasia	N 66	0.04	0.33

endix 3. Factor loadings for the genus *Prosopium*.

	Continent	Latitude	Component 1	Component 2
Prosopium cylindraceum	N. America	S 44	0.46	0.36
	N. America	N 55	-0.10	0.01
	N. America	S 43	0.56	1.66
	N. America	N 55	-0.07	0.21
	N. America	S 47	-0.83	-0.31
	N. America	S 43	-0.37	0.51
	N. America	S 44	-0.57	0.31
	N. America	N 55	-0.09	-0.65
	N. America	N 71	-0.87	-0.35
	N. America	N 55	0.47	-0.62
P. coulteri	N. America	S 47	-2.15	-0.42
	N. America	S 47	1.96	-0.49
	N. America	S 50	-2.72	-1.13
	N. America	N 59	-2.13	-0.05
P. williamsoni	N. America	N 43	-0.56	0.22
	N. America	S 40	-0.49	0.52
	N. America	N 50	-1.20	-0.02
	N. America	N 43	-0.58	2.08
P. spilnotus	N. America	S 42	-0.83	0.38
P. abyssicola	N. America	S 42	-1.43	0.63
P. gemmiferum	N. America	S 42	-1.36	0.60

Appendix 4. Factor loadings for the genus *Coregonus* (*Leucichthys*).

Species	Continent	Latitude	Component 1	Component 2
C. autumnalis				
	N. America	N 71	0.53	-2.64
	N. America	S 64	-0.12	-0.71
	Eurasia	N 72	0.05	-0.46
	Eurasia	N 72	0.17	-3.08
	Eurasia	N 72	0.52	-2.11
	Eurasia	S 55	0.26	-1.08
	Eurasia	S 53	-0.55	-0.08
C. sardinella				
	N. America	N 71	0.86	-1.75
	N. America	S 64	0.04	-1.95
	N. America	N 71	0.60	-0.08
	N. America	N 71	-0.57	0.14
	N. America	N 71	-0.12	0.08
	N. America	N 71	0.52	-0.80
	Eurasia	N 66	-0.54	-0.16
	Eurasia	N 71	-0.83	-0.07
	Eurasia	S 46	-1.35	-0.66
C. albula				
	Eurasia	N 61	-0.54	-0.83
	Eurasia	S 55	-1.23	-0.72
	Eurasia	N 61	-1.26	1.37
	Eurasia	N 61	-1.36	1.39
	Eurasia	N 71	-0.30	0.91
C. artedii				
	N. America	S 43	-0.06	0.42
	N. America	S 43	-0.80	0.12
	N. America	N 55	0.08	0.54
C. peled				
	Eurasia	N 72	0.76	-0.58
	Eurasia	N 71	0.57	-1.77
	Eurasia	S 66	0.42	-0.55
	Eurasia	S 66	0.68	-1.33
C. tugun				
	Eurasia	N 72	-1.77	-1.05
C. hoyi	N. America	S 43	-0.46	0.85
	N. America	S 43	-0.26	0.62

Appendix 5. Component loadings for *Stenodus leucichthys*.

Species	Continent	Latitude	Component 1	Component 2
S. leucichthys				
	Eurasia	S 64	1.00	0.02
	Eurasia	N 72	1.45	0.14
	Eurasia	N 72	1.91	-0.03
	Eurasia	N 72	1.66	0.38
	N. America	S 65	1.59	0.86

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