CISCO (*COREGONUS* SPP.) DIVERSITY IN GREAT BEAR LAKE NORTHWEST TERRITORIES, CANADA

BY

MICHEL A. L. LECLAIRE

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Department of Environment and Geography
University of Manitoba
Winnipeg, Manitoba

ABSTRACT

Cisco display highly variable morphology and life history. Great Bear Lake provided an opportunity to observe Cisco diversity in a relatively pristine environment.

The study characterized the morphological differences among Cisco between geographic arms and depth strata, and determined the trophic positioning of various morphs, based on twelve years of capture data and specimens using morphological measurements, meristic counts, stomach contents, stable isotopes and fatty acids.

Two main Cisco morpho-types were identified, a shallow water form and a deep water form that mainly differed in traits associated with swimming and feeding. These results were reinforced by the results on trophic ecology of morphs that demonstrated that each morph occupied a distinct niche. Results showed that shallow water groups had a more varied diet with a high percentage of copepods being ingested whereas deep-water groups showed preferences towards mysids. Although a consistent pattern in differences among shallow and deep morphs was observed, there was some degree of variation among arms of the lake suggesting a degree of isolation and adaptation to local conditions in each area of the lake. For example, in Smith Arm, morphological and dietary differences were found such as narrower body depth and a dietary preference towards daphnia.

This lake-wide analysis of the Cisco diversity has shown that separation exists between the two distinct morphs, and thus should be treated differently with respect to conservation and preservation of important fisheries stocks of the lake.

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I must also thank my amazing support group at home and at work for allowing me to bore them without end with statistical problems, with long conversations about why Cisco are important, and with my absence from home or from work to dive deeper into the work below. The patience exhibited by each of you is astonishing; a full thank you.

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1.0 INTRODUCTION

Cisco have long been noted for their highly variable morphology and life history (Scott and Crossman 1998). Cisco in the Laurentian Great Lakes, in particular, have been shown to display a high degree of variability in habitat use and morphology (Pratt 2008, Pratt and Chong 2012) forming what is known as a species complex (Scott and Crossman 1998). However, studies of this species complex have been confounded due to the loss of unique stocks through fishing pressure and further declines as a result of invasive species (Bronte et al. 2010). To date, very little cisco research has been conducted in the more remote and relatively pristine northern lakes (Pratt 2008, Muir et al. 2009, Pratt and Chong 2012, Chavarie et al. 2013, Howland et al. 2013).

Great Bear Lake provides a unique opportunity to study fishes in a relatively pristine environment (Muir et al. 2012, Howland et al. 2013). Due to its remote location, the lake has had limited exposure to anthropogenic modification or manipulation (Johnson 1975a,b, Howland et al. 2013). Previous trophic ecology research in this system (mainly on the top predator (lake trout *Salvelinus namaycush*) has shown a great deal of polymorphism or variability in the habitat use and associated morphology and life history (Kennedy 1953, Chavarie et al. 2013, Howland et al. 2013). The ongoing collection of data on the fish community and various ecosystem components in this lake over the last decade provided an ideal opportunity to study the ecology of lower trophic level forage fish (e.g., cisco *Coregonus* sp.).Lower trophic level studies have been gaining popularity in recent years providing a holistic view of the ecosystems in question (e.g., Pratt 2008, Pratt and Chong 2012).

1.1 ISSUE STATEMENT

Committee on the Status of Endangered Wildlife in Canada (COSEWIC), has identified a gap in information surrounding the cisco complex in North America, particularly in the northern Great Lakes and therefore would benefit from this research which has the potential to expand current distribution maps of the various cisco species/morphs while also providing valuable baseline information to inform other subsequent studies. Furthermore, Fisheries and Oceans Canada (DFO) has made recommendations for the identification of designatable units (DU's) (DFO 2013). DU's are a recommended conservation strategy allowing for the conservation of unique stocks on an ecosystem by ecosystem basis; this strategy helps minimize the loss of diversity that could arise from the standard taxonomic species-based approach to conservation (DFO 2013). This approach allows strategies to be implemented for the explicit conservation of specialized or distinguishable species/morphs of ciscoes in a given system (DFO 2013). The purpose of the DU's outlined by DFO with respect to cisco acknowledge that unique morpho-types play a significant role in the functioning of ecosystems and are thus important for the maintenance of biodiversity and ecosystem integrity as a whole (DFO 2013).

1.2 BACKGROUND

1.2.1 Polymorphism

Polymorphism is the occurrence of two or more morphs or phenotypes of a given species occupying the same habitat at the same time (Svanback et al. 2008). Differences may include morphological variation, life history variation, colour variation, trophic positioning variation or any other type of observable variation between individuals of the same species (Svanback et al. 2008). Hutchinson (1965) commented that most species exhibit some type of polymorphism. Hutchinson was referring to individual populations of the same species that had adapted to take advantage of different niches given their specific environmental conditions and pressures. Moreover, Svanback and Persson (2004) state that populations can be delineated by their geographic location and/or by their niche occupancy when found in the same geographic location.

Resource polymorphism is especially common in newly formed (10,000-15,000 years old) lakes. These lakes formed by geological processes (e.g., volcanic influence, deglaciation of an area) provide the stage for species to coevolve (Smith and Skulason 1996). Newly formed lakes contain relatively low species diversity due to their past isolation and slow immigration of new species (Barbour and Brown 1974). The low diversity of biota can lead to open niches that have the potential to be filled by newly arriving species or by the present species that adapt their life histories to the new environmental conditions provided by the recently formed lake (Barbour and Brown 1974).

Numerous fish species exhibit polymorphism that can be attributed to different causes (Smith and Skulason 1996). The onset of polymorphism can be linked to habitat or environmental condition changes, differences in evolutionary history of the population or the system in which they are contained, or even phenotypic plasticity in biochemistry, morphology, physiology, life history or behavior of organisms (Smith and Skulason 1996, Whitman and Agrawal 2009). Some fishes display resource polymorphism under conditions where there is high intraspecific competition (Werner and Gilliam 1984). However, polymorphism can also occur due to a lack of ecological pressures such as relaxation of interspecific competition or the immigration of individuals into new habitats (habitat variability) (Smith and Skulason 1996). A good example of resource polymorphism occurs in Arctic Char (*Salvelinus alpinus*), which display different life histories, and morphologies depending on the waterbody or resource availability (Klemetsen 2010). Polymorphism has also been noted in Whitefish (*Coregonus*) which will often utilize both benthic and limnetic habitats in cases where those specific niches are not filled by other species (Kahilainen and Ostbye 2006).

Phenotypic plasticity is less common among organisms that can displace themselves from a less favorable environment to one which better satisfies their needs (Smith and Skulason 1996), however it is prevalent among freshwater fishes due to the physical boundaries of waterbodies that can limit dispersal. Factors such as depth, water temperature, water clarity and substrate composition can all limit a fish's ability to displace itself in search of more favorable conditions (Babour and Brown 1974).

Although polymorphism is typically considered within the context of differences in habitat use among mature individuals, there are also examples of polymorphism associated with ontogenetic changes where a single species will change its life history attributes depending on its age or period of development (Wimberger 1992). For example, many fish species progress from planktivory at first hatching, to insectivory with increased size, and finally maturing into piscivory. These life history changes do account for observed polymorphism but are better classified as ontogeny (Muir et al. 2013). Polymorphism of this type has long challenged researchers with the identification of new, yet closely related species. The difficulty of identifying ontogenetic variation lies in the scale of the study – evaluation of individual life histories can only supply snapshots of life history traits that an animal will exhibit throughout its life cycle. Thus, difficulties arise when small sample sizes or uneven age class distributions occur among sampled populations. Small sample sizes from a population can limit the observed variation among individuals and uneven age class distributions can result in missing age-specific life history variations in the life cycle thus resulting in the study of a population which has possible gaps in life stages.

1.2.2 The Cisco Complex in North America

The Salmonidae subfamily Coregoninae (i.e. Cisco) is characterized by immense variability within and between species (Scott and Crossman 1998). This subfamily has been described as being one of the most taxonomically confounding of the fishes found in the northern hemisphere (Scott and Crossman 1998, Muir et al. 2013). Moreover, its vast distribution adds further complications given the phenotypic plasticity of the group. This subfamily is divided into three genera (*Stenodus*, *Prosopium*, and *Coregonus*) of which approximately 18 species are known. The genera of interest for this study is *Coregonus*; among the approximately 14 species within this genus, a number are closely related and highly plastic creating taxonomic challenges. Difficulties in identification frequently arise when comparisons between waterbodies are done (Scott and Crossman 1998). Species-specific characteristics (e.g., size, morphology, age at maturity) tend to vary widely between waterbodies and thus create difficulties in the classification of any given species across waterbodies. Additionally, of these 14 species of coregonids, there are five that are thought to be exclusively endemic to the Laurentian Great Lakes (Scott and Crossman 1998), and more specifically to the deeper waters of these lakes. Dymond (1943, 1964) identified the five Great Lakes endemic species as Deep Water Cisco (*C. johannae*), Longjaw Cisco (*C. alpenae*), Shortnose Cisco (*C. reighardi*), Kiyi (*C. kiyi*) and Bloater (*C. hoyi*). Additionally, three more non-endemic species of ciscoes were identified in the Great Lakes by Dymond (1943) – Blackfin Cisco (*C. nigripinnis*), Shortjaw Cisco (*C. zenithicus*) and finally Cisco (formerly Lake Cisco and Common Cisco) (*C. artedii*). Few studies of this magnitude have been completed since this time.

The Cisco in particular (*C. artedii*) appears to be highly variable with respect to its life history and morphology as shown by recent studies from Muir et al. (2013) and Pratt and Chong (2008) who identified both shallow water and deep water forms. In addition to these two forms, Blackie et al. (2012) also distinguished adfluvial (spawning and rearing in rivers later migrating to lakes) and lacustrine (lake) forms. The coupling of high intraspecific variability and adaptability to a wide range of environments with a widespread distribution has added to the challenges surrounding the taxonomic delineation of this species.

1.3 CISCO RESEARCH IN LARGE LAKE SYSTEMS

1.3.1 Lake Superior

Currently, Lake Superior retains the most intact deep water Cisco assemblage of all the Laurentian Great Lakes with Bloater, Kiyi and Shortjaw Cisco (Pratt 2008). There has been a substantial loss of Cisco diversity in the other Great Lakes due to over exploitation of the commercial chub (Cisco) fishery and increased anthropogenic manipulation of the landscape surrounding the lakes (e.g., gravel extraction, gas drilling and sewage discharging) (Bronte et al. 2003). In addition to these three Deep Water Ciscoes the Common Cisco is also found in both the shallow and deep waters zones of Lake Superior (Pratt 2008, Pratt and Chong 2012). Despite having the most complete assemblage of ciscoes, two of the deep water forms are experiencing low populations – the Kiyi is listed as Special Concern and the Shortjaw Cisco is listed as Threatened by COSEWIC. Furthermore, there appears to have been a loss in the genetic diversity among species, likely due to population reduction and related hybridization among closely related species/morphs (Turgeon and Bourret 2013).

More recent studies of the lake's ecosystem by Pratt (2008) and Pratt and Chong (2012) have revealed the importance of ciscoes, and more specifically the importance of deep water ciscoes as a means of cycling nutrients from benthic invertebrate to pelagic predators (Schindler and Scheuerell 2002). This trophic link has been destabilized as a result of the low population numbers of deep water ciscoes in other Laurentian Great Lakes (Smith 2011). The continued study of Lake Superior's deep water food web is helping managers identify and mitigate the effects being felt from the loss of diversity in other large lakes (Schmidt et al. 2009).

1.3.2 Great Slave Lake

Great Slave Lake has been receiving more attention from researchers looking to find insight regarding the diversification of the Cisco species. Great Slave Lake is considered a young lake in geological time, having only recently been deglaciated (8000 – 12000 years b.p.) (Lindsey and McPhail 1986). Due to its relatively young age and remote location Great Slave Lake provides a good system for the study of speciation and phenotypic diversification; both of which are central to better understanding the Cisco complex (Blackie et al. 2012). Studies by Blackie et al. (2012) and Muir et al. (2009, 2012, 2013, 2014) have focused on identifying the Cisco diversity in Great Slave Lake and considered the associated ecological implications for the functioning of naturally occurring deep water fish and invertebrate communities.

Presently there have been five Cisco species/morphs identified in Great Slave Lake, these are the Least Cisco (*C. sardinella*), the Shortjaw Cisco, and the Common Cisco which has been subdivided into three distinct morphs - Lacustrine, Adfluvial, and Big-eye (Blackie et al. 2012, Muir et al. 2009, 2011, 2013, 2014). Each of these ciscoes can be distinguished by one or more characteristics including morphology, life history and/or trophic positioning within the waterbody. These characteristics, among others, have been compared to ciscoes from other large deep lakes (e.g., the geologically "older" Laurentian Great Lakes) to give researchers insight into the finer mechanisms of speciation and phenotypic diversification (Hutchinson 1965, Klemetsen

2010, Smith 2011). This type of comparison between “newer” lakes and “older” lakes allows researchers to identify critical inflection points in the overall functioning of the ecosystem as a whole (Engstrom et al. 2000). Furthermore, critical thresholds or important trophic connections can be identified, and thus mitigated for, in an attempt to maintain the full range of biodiversity.

1.3.3 Great Bear Lake

Great Bear Lake is the most recently deglaciated (“newest”), and the most pristine lake of those discussed thus far, and therefore provides the opportunity to examine trophic interactions which have had the least anthropogenic manipulation and alteration from their natural state. Moreover, this relatively unaltered system provides an opportunity to study an intact complex of ciscoes (Howland et al. 2013). Great Bear Lake is similar to Great Slave Lake with respect to geological time (Engstrom et al. 2000, MacDonald et al. 2004). Furthermore, Great Bear Lake is similar in size and limnology to both Great Slave Lake and Lake Superior thus providing the opportunity for cross-lake comparisons with respect to Cisco species diversity and associated trophic interactions. Differences in trophic interactions can be attributed to a variety of factors – time scale being the most prevalent (Engstrom et al. 2000). However, changes in trophic interactions can also be attributed to anthropogenic manipulation as documented in Lake Superior (Crossman and Cudmore 2009). Therefore, each of these lakes can provide an understanding as to how trophic interactions develop from one successional stage to the next (Engstrom et al. 2000).

Recent Great Bear Lake research has focused mainly on the morphological diversity of lake trout, the top predator, as it relates to the trophic ecology of the lake (Chavarie et al. 2013). Better defining these trophic interactions, particularly with respect to Cisco, the main fish prey species, is the next logical step in gaining a better understanding of the ecosystem functioning and nutrient cycling in the lake (Howland et al. 2013). Expanding the current knowledge of trophic ecology can help mitigate future changes in the ecosystem. More specifically, understanding the deep water trophic structure of Great Bear Lake can help us understand what the best course of action should be when attempting to restore other troubled ecosystems such as the Laurentian Great Lakes.

The observed Cisco diversity in large deep lakes is thought to be related to the ability of these fish to become highly specialized in a given niche (Kahilainen et al. 2011). To date, a preliminary investigation into the diversity of ciscoes for Great Bear Lake has been undertaken within two regions of the lake (Howland et al. 2013). These analyses suggest that Great Bear Lake contains at least two distinct Cisco species or morphotypes; Common Cisco, and a variation of the Shortjaw Cisco (Howland et al. 2013), however both genetic and morphological studies suggest that there may be more extensive variation at a lake wide scale (Howland et al. 2013, Turgeon and Bourret 2013). This preliminary research has identified a need to study the Cisco diversity of the lake in more detail to document the extent of variation and better characterize the Cisco complex within Great Bear Lake (Howland et al. 2013). Understanding the diversity of ciscoes present in Great Bear Lake along with each of their respective life histories will assist in the understanding of the trophic structure together with the nutrient cycling between deep and shallow zones of the lake.

1.4 OBJECTIVES

The research has two main objectives;

1) Identify the morphological variation among Cisco found in Great Bear Lake to assess whether (Chapter 2):

   a) unique morpho-types/species can be identified

   b) and describe morphology and habitat type (depth and lake arm),

2) Characterize the trophic ecology (trophic positioning) of the different morphs/populations of Cisco identified in Great Bear Lake (Chapter 3) to describe possible:

   a) mechanisms driving differentiation and niche partitioning among morphs/populations

   b) consequences of niche partitioning and differential habitat use

Both objectives 1 and 2 will be analysed as individual research questions. Objective 1 involves the use of morphometrics and meristics to classify the various morphs/populations of ciscoes. Objective 2 encompasses the analysis of habitat utilization of different Cisco morphs using capture location information, and diet information (stomach contents, stable isotopes and fatty acid analyses).

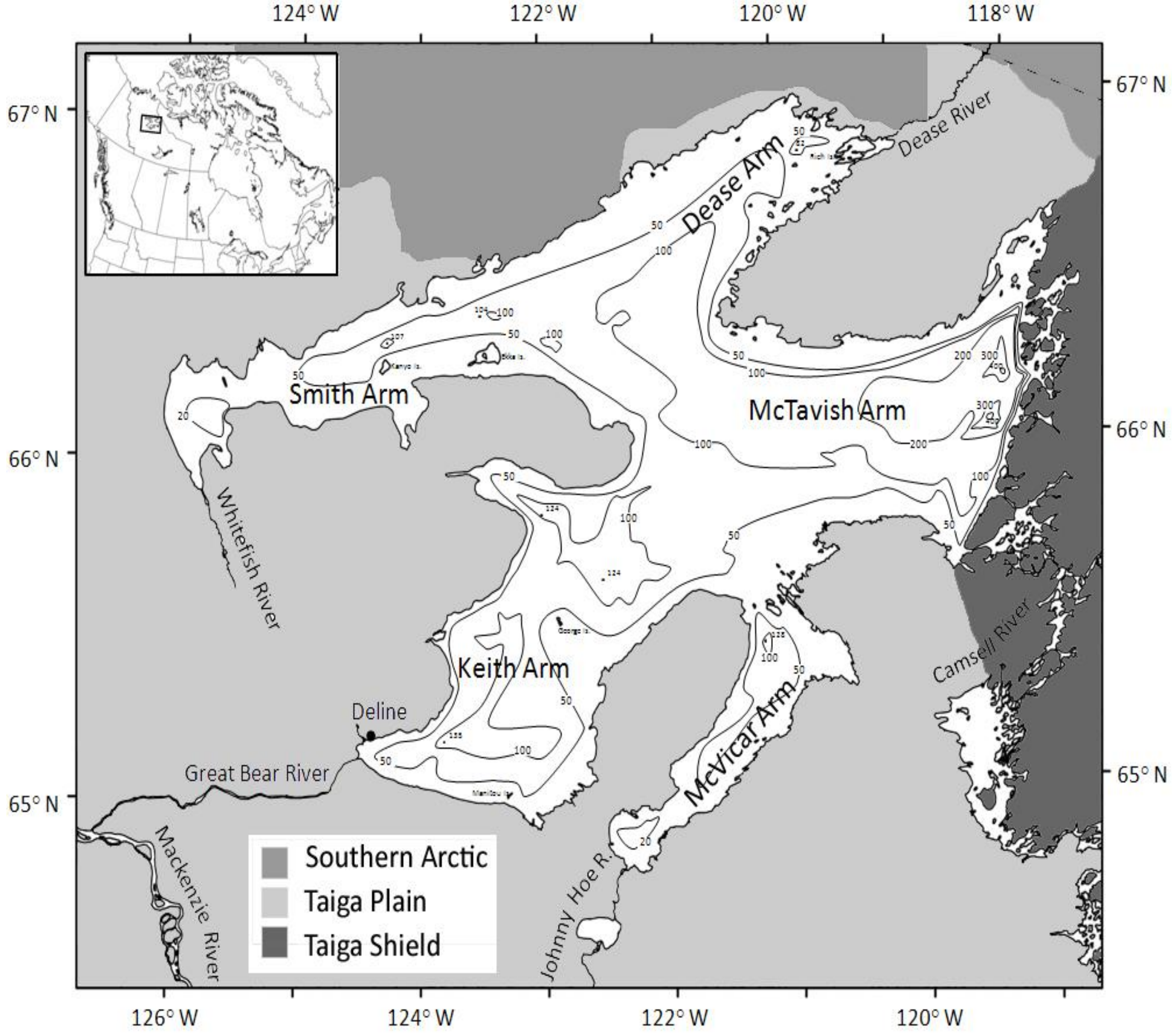
To address these objectives, I have utilized a combination of existing Cisco samples and data that have been collected through DFO stock assessment studies on Great Bear Lake over the last 9 years (2003 – 2011), together with supplemental samples that have been collected from 2012 to 2014 as part of a larger ecosystem study on the lake.

1.5 STUDY AREA

Great Bear Lake is described as highly oligotrophic with low species diversity resulting in a relatively simple food web (Johnson 1975a, Muir 2012, Howland et al. 2013). Great Bear Lake is located in the Northwest Territories of Canada and is the most northerly in a chain of remnant proglacial lakes that extends northwest from the Laurentian Great Lakes (Figure 1-1).

The lake has a central basin with five clearly distinct radiating arms: Keith, McVicar, McTavish, Dease, and Smith. Each of these arms are large enough to potentially function as independent waterbodies and may harbour unique assemblages of fish and invertebrates. The geographic isolation and unique geological inputs to each of the arms provides a setting in which different morphs of highly variable species (e.g., Cisco) may have had the opportunity to develop *in situ*. Great Bear Lake ranks ninth largest worldwide for surface area (Johnson 1975a) at 31,153 square kilometres. Great Bear Lake is the largest lake situated entirely in Canada, and the fourth largest in North America (Johnson 1975a). Great Bear Lake has an average depth of 90 metres, however the depth varies significantly among arms (Johnson 1975a, Howland et al. 2013). The greatest recorded depth in the lake was 446 metres near Port Radium in the McTavish Arm (Johnson 1975a) (Figure 1-1). The lake has approximately 3,000 kilometres of shoreline which includes island shorelines (Johnson 1975a). The lake is bisected by the Arctic Circle at its northerly end in Dease Arm. Despite its size, the lake's drainage basin is relatively small at only 145,870 square kilometres (Johnson 1975a).

Figure 1-1. Map of Great Bear Lake, located in the Northwest Territories, Canada showing diffrent lake arms, the town of Deline, and the general ecozones.



(taken from Chavarie et al. 2013).

Great Bear Lake has a central basin with five clearly distinct radiating arms: Keith, McVicar, McTavish, Dease, and Smith covering a wide range of ecozones and underlying geologies, which may contribute to differences in habitat/aquatic communities among arms.

The lake occurs within three different ecozones; the Southern Arctic ecozone to the north, the boreal plains (Taiga Plains) to the south and west, and the boreal shield (Taiga Shield) to the east (Johnson 1975a) (Figure 1-1). Each of these zones is characterized by differences in geology and plant communities (Johnson 1975a) and likely runoff and nutrient inputs. These differences of inputs and geology combined with the specific morphometry of the lake may contribute to differences in habitats/niches among arms of the lake. Furthermore, the differences among arms and their isolation from each other may allow for distinct aquatic food webs to become established in the different arms.

The Southern Arctic zone (mostly in the Dease Arm vicinity) is underlain with Ordovician sedimentary rocks such as limestone, dolomite and sandstone (Johnson 1975a), and the plant community is mostly comprised of sprawling shrublands, wet sedges and grassy meadows all typical of northern climes (Johnson 1975a, Muir 2012). The boreal (taiga) plains are similar in geology to the northern areas of the lake, however they are covered with a thick layer of glacial till which has been shifted into landforms such as glacial moraines (Johnson 1975a). The vegetation in this area is typical of the boreal forest with a high percent of the vegetation made up of black and white spruce (*Picea mariana* and *P. glauca*) (Johnson 1975a). These features extend from the lower half of Smith Arm to Keith Arm and through to the western shores of McVicar Arm.

The boreal (taiga) shield area in McTavish and southern shores of Dease Arms have typical geology of the Precambrian shield, characterized by high mineral richness (Johnson 1975a). Minerals such as silver, cobalt, nickel, copper and gold can be found in this region. Moreover, large uranium deposits were mined from this area (Port Radium) (Johnson 1975b). The vegetation is typical of the boreal forest also found to the east and south (Johnson 1975a, Muir 2012).

Great Bear Lake has only one permanent settlement on its shores; the town of Deline which maintains approximately 800 year-round residents (Kenny-Gilday 2014). The majority of residents are Sahtu Dene who have a long history in this area. Other seasonal settlements include 3-6 sport fishing lodges which have operated at various times since the 1950's and have mainly sought lake trout (Howland and Tallman 2005). Mining operations have also occurred along the lake's periphery or on watercourses that flow into the lake. The most substantial is Port Radium in McTavish Arm that extracted uranium from 1932 to 1962 (Johnson 1975b), and had a small community which housed a general store, a hotel, and a Royal Canadian Mounted Police post at its peak (Johnson 1975b). These were abandoned once the mine closed. The mine was reopened to extract silver from 1962-1982 (Kenny-Gilday 2014).

1.6 METHODS

1.6.1 Field Data Collection

Field work from 2012 through 2014 was completed during the open water season (approximately mid-July to late-August) and involved setting of multi-mesh gillnets in a random depth stratified design to capture a representative sample of the fish community, including the Cisco populations. All ciscoes captured were frozen in the field (using a freezer powered with a generator) and transported to Winnipeg for further processing (morphometrics, meristics, and trophic analyses). Additional information about the water quality and habitat were collected by taking water quality profiles (temperature, dissolved oxygen, pH, turbidity and chlorophyll *a*), benthic grab samples (ponar grab) and zooplankton tows in the vicinity of each gillnet set. Although the water quality and habitat information are not the focus of this research, these data will be analysed as part of the larger ecosystem study on Great Bear Lake and have been available for use in interpreting the findings (e.g., how habitat differences are related to the diets of different types of Cisco) and for use in trophic analyses.

The above described data were complemented with relevant Cisco data and samples from previous stock assessment studies by DFO (2003 through 2011; see Howland 2013 for details on collection methods). These data together with the more recent data collected from 2012 to 2014 are the foundation of the morphometric and trophic analyses included in this thesis.

1.7 ORGANIZATION

This thesis is organized in four chapters, with the two data chapters (2 and 3) formatted as journal article submissions to enhance the opportunity for graduate student publication upon completion. Chapter 1 provides background and a general introduction, Chapter 2 examines the morphological variations of Cisco found in Great Bear Lake, Chapter 3 describes the different trophic patterns and positions of the Cisco in Great Bear Lake andChapter 4 provides a holistic interpretation of all the results from the full study concluding in further recommendations for the evaluation of Cisco in Great Bear Lake.

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CHAPTER 2:

MORPHOMETRIC AND MERISTIC EVALUATION OF THE CISCO OF GREAT BEAR LAKE

ABSTRACT

The Coregoninae subfamily has been described as being one of the most taxonomically confounding of the fishes found in the northern hemisphere. Great Bear Lake is the last and most northerly of the major proglacial lakes where the Cisco diversity has yet to be fully understood. The objective of this study was to characterize morphological differences between Cisco caught in Great Bear Lake at various locations and depths to determine the number of unique morpho-types/species present and if a link exists between morphology and habitat type.

Twenty morphometric measures and six meristic counts along with the premaxillary angle were recorded for Cisco collected from two depths of capture (<50 metres and >50) in each of six lake areas. Discriminant function analyses of these variables were used to evaluate the fit of individuals to predetermined location-depth groups and mainly separated groups by depth of capture and by arm of capture with the latter having lower classification success. A shallow water morph and a deep water morph were clearly identified. Two additional groups were also observed; one group was a distinct deep water variant found in Smith Arm area only. The other showed traits that were intermediate between shallow and deep water groups. Further research is needed to determine to what extent these latter two groups vary from the others found around the lake.

2.0 INTRODUCTION

The Salmonidae subfamily Coregoninae is characterized by immense variability within and between species (Scott and Crossman 1998). This subfamily has been described as being one of the most taxonomically confounding of the fishes found in the northern hemisphere (Scott and Crossman 1998, Muir et al. 2013a, Muir et al. 2014). Moreover, its vast distribution adds further complications given the phenotypic plasticity of the group. The Cisco (*C. artedii*), in particular, appears to be highly variable with respect to its life history and morphology as shown by recent studies from Muir et al. (2013a) and Pratt and Chong (2012) who identified both shallow water and deep water forms. In addition to these two forms, Blackie et al. (2012) also distinguished adfluvial (spawning and rearing in rivers later migrating to lakes) and lacustrine (lake) forms. To date, very little research has been conducted on this species complex in the more remote and relatively pristine northern lakes (Pratt 2008, Muir et al. 2009, Pratt and Chong 2012, Chavarie et al. 2013, Howland et al. 2013).

Great Bear Lake is the last and most northerly of the major proglacial lakes where the Cisco diversity has yet to be fully understood. Great Bear Lake provides a unique opportunity to study fishes in a relatively pristine environment (Muir et al. 2012, Howland et al. 2013). Moreover, the unique lake morphometry provides a setting where fish populations may develop independently from each other through geographic isolation. Great Bear Lake has a central basin with five clearly distinct radiating arms: Keith, McVicar, McTavish, Dease, and Smith. Each of these arms is large enough to potentially function as independent waterbodies and may harbour unique assemblages of fish and invertebrates. The geographic isolation and unique geological inputs to each of the arms provide a setting in which different morphs of highly variable species (e.g., Cisco) may have had the opportunity to develop *in situ*.

To date, a preliminary investigation into the diversity of ciscoes for Great Bear Lake has been undertaken within two regions of the lake (Howland et al. 2013). These analyses suggest that Great Bear Lake contains at least two distinct Cisco species or morphotypes; Common Cisco, and a variation of the Shortjaw Cisco (Howland et al. 2013), however both genetic and morphological studies suggest that there may be more extensive variation at a lake-wide scale (Howland et al. 2013, Turgeon and Bourret 2013). Understanding the diversity of ciscoes present in Great Bear Lake along with each of their respective life histories will assist in the understanding of the trophic structure together with the nutrient cycling between deep and shallow zones of the lake. Svanback and Persson (2004) state that populations can be delineated by their geographic location and/or by their niche occupancy when found in the same geographic location thus this chapter will focus on the delineation of Cisco morphs/populations of Great Bear Lake by characterizing the morphological variation among Cisco found in Great Bear Lake to determine:

c) the number of unique morpho-types/species present and

b) if a link exists between morphology and habitat type (depth and lake arm).

2.1 STUDY AREA

Refer to Chapter One for detailed study area description.

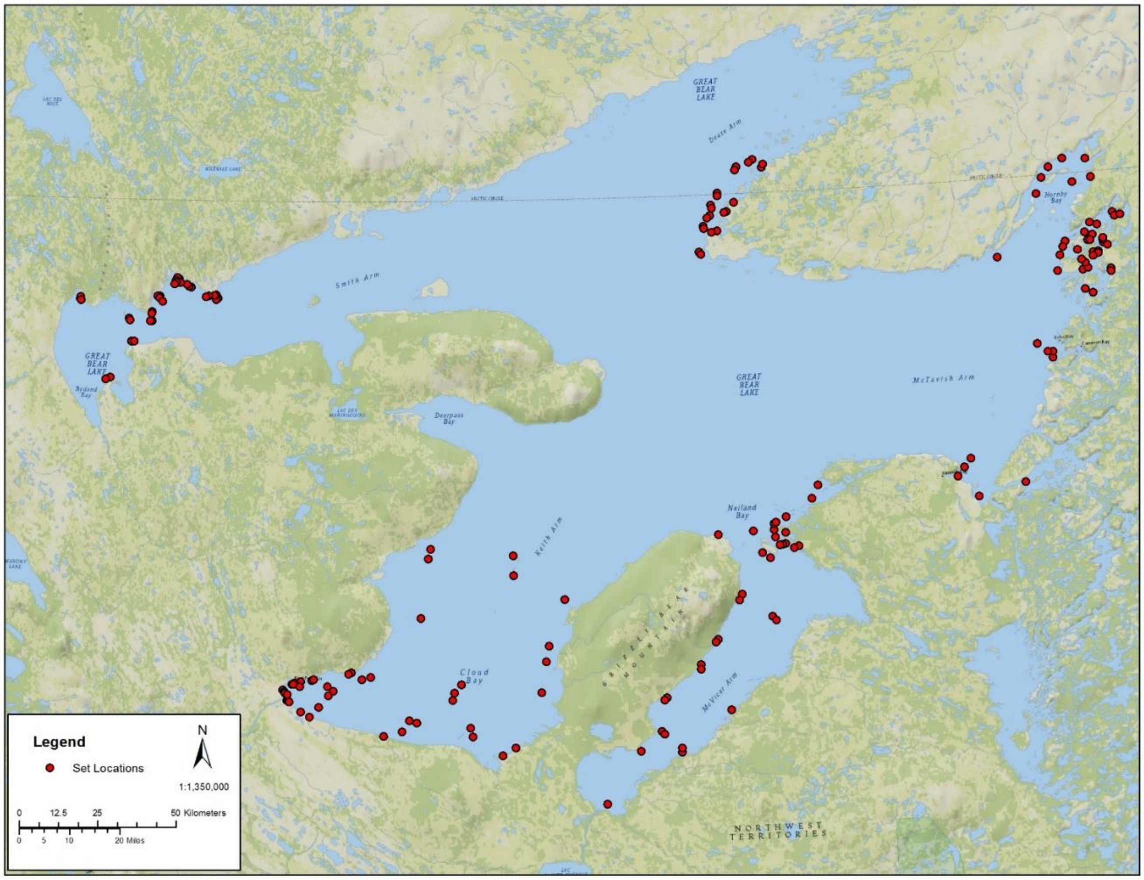
2.2 METHODS

2.2.1 Field Collection Methods

Cisco were mainly captured using bottom-set multi-mesh experimental gillnets (stretched mesh sizes ranging from 25.4 millimetres to 101.6 millimetres) at a range of depths from 5 to 150 m, generally fished for a 24-hour period during July and August over a 12 year period from

2003 to 2014 (Table 2-1). However, between 2012-2014, some samples were also collected using mid-water and surface set nets of the same configuration. Due to the large size of Great Bear Lake a rotational approach was taken where one of each of the five arms was fished per year (Table 2-1, Fig 2-1).

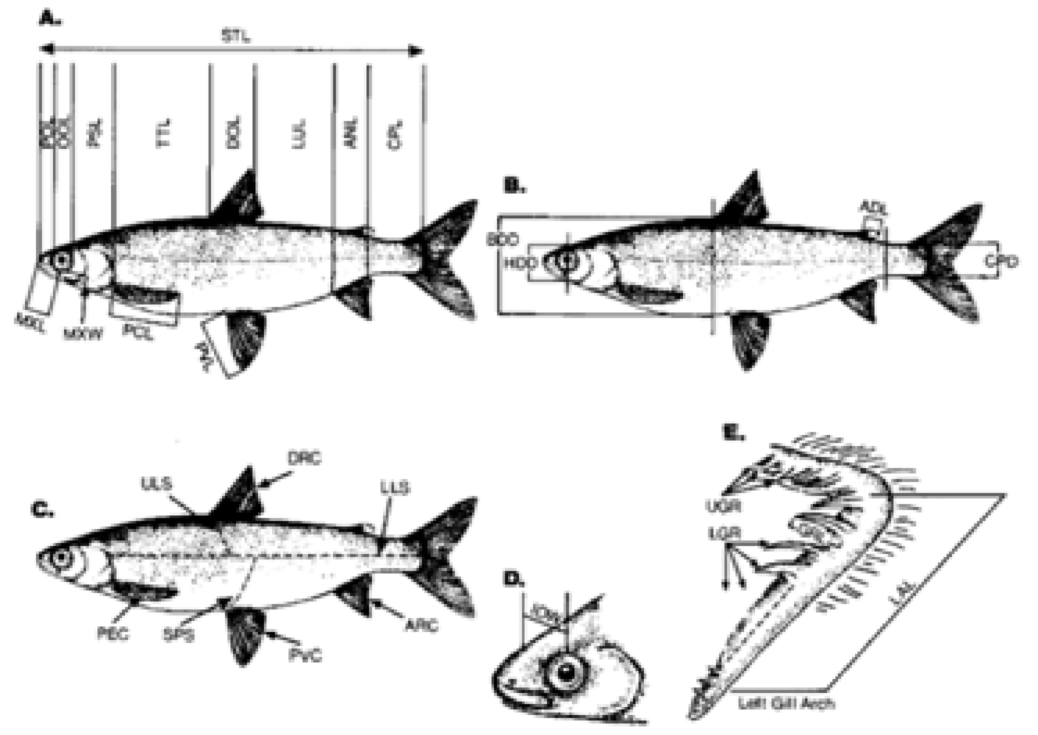
Figure 2-1. Map of Great Bear Lake showing fishing locations from years 2003 through 2014.



2.2.2 Laboratory Methods

Individual Cisco were thawed and 20 morphometric measures plus seven meristic counts were taken as described by Vuorinen et al. (1993) (Figure 2-2); the premaxillary angle was also measured as described by Clarke (1973). All morphometric characters were measured to the nearest 0.1 millimeter, the premaxilla angle to the nearest degree and the standard length to the nearest 1.0 millimeter using digital calipers.

Figure 2-2. Morphometric and meristic features tabulated for discriminant function analysis.



MORPHOMETRICS	**PCL – pectoral length**
	PVL – Pelvic length
STL – Standard length	**ADL – Adipose length**
POL – Pre-orbital length	**GRL – Middle gillraker length**
OIL – Orbital Length	**LAL – Lower arch length**
PSL – Postorbital length	**PMA – Pre-maxillary angle**
TTL – Trunk length	
DOL – Dorsal length	**MERISTICS**
LUL – Lumbar length	
ANL – Anal length	**DRC – Dorsal ray count**
CPL – Caudal peduncle length	**ARC – Anal ray count**
HDD – Head depth	**PRC – Pectoral ray count**
BDD – Body depth	**VRC – Pelvic ray count**
CPD – Caudal peduncle depth	**UGR – Upper gillraker count**
IOW – Interorbital width	**LGR – Lower gillraker count**
MXL – Maxillary length	**LLS – Lateral line scales**
MXW – Maxillary width	

Source: Modified from Vuorinen et al. 1993.

2.2.3 Morphometric and Meristic Statistical Analysis Methods

Morphometric data from all captured ciscoes were combined and individuals with missing morphometric data were removed. In addition, only Cisco of ≥100 millimeters (the smallest observed mature fish) were used for all subsequent morphometric and meristic analyses as this was the smallest size at which mature Cisco were observed based on a previous study by Howland et al. (2013). Males and females were grouped together and treated the same in all subsequent analyses based on previous studies which did not find significant differences between sexes for these traits (Kennedy (1949, Howland et al. 2013). Visual inspection of individual linear regressions of standard length and each morphometric variable were initially used to compare samples among years within arms. With the exception of Keith Arm, variables were similar among years and thus samples were pooled within a given arm. Samples from Keith Arm showed variability among years, which may have been due to the larger geographic extent of this arm and the use of different capture locations in different years. These samples were therefore sub-divided by within-arm capture location; Manitou Island deep and shallow water groups were teased out from the rest of the ciscoes from Keith Arm and included in all subsequent results.

Previous studies of Cisco diversity in Great Bear Lake showed that no correlations exist between body size and any of the meristic variables including one morphometric variable – premaxillary angle, however strong correlations were found between body size and each the other morphometric variables (Howland et al. 2013). Therefore in the current study all morphometric variables were size-adjusted using the methods outlined by Reist (1986). Visual inspection of regressions of each variable on standard length were evaluated to determine if heterogeneity existed between slopes for all samples collected from each arm of Great Bear

Lake. Since heterogeneity was found, the common within-group size-adjusting method (Reist 1986) was used.

For all subsequent comparisons, ciscoes from each area of the lake were allocated to a priori shallow versus deep water groupings based on reported depth preferences among Cisco morphs in other systems (Pratt and Chong 2012, Pratt 2012, Muir et al. 2013) and utilized in previous studies on Great Bear Lake by Howland et al. (2013). Cisco caught in ≤ 50 meters were allocated to the shallow water group and those caught at depths > 50 meters were allocated to the deep water group. In some cases nets were set either at the 50 meter mark or crossing the 50 meter mark; for these instances Cisco were allocated to the shallow water group. The total sample sizes for each of the a priori groups is shown in table 2-1, together with the years of capture for each of the groups.

Table 2-1. Sample size and year(s) of capture for each of the a priori location-depth groups of Cisco used in comparisons of morphometric and meristic traits within Great Bear Lake

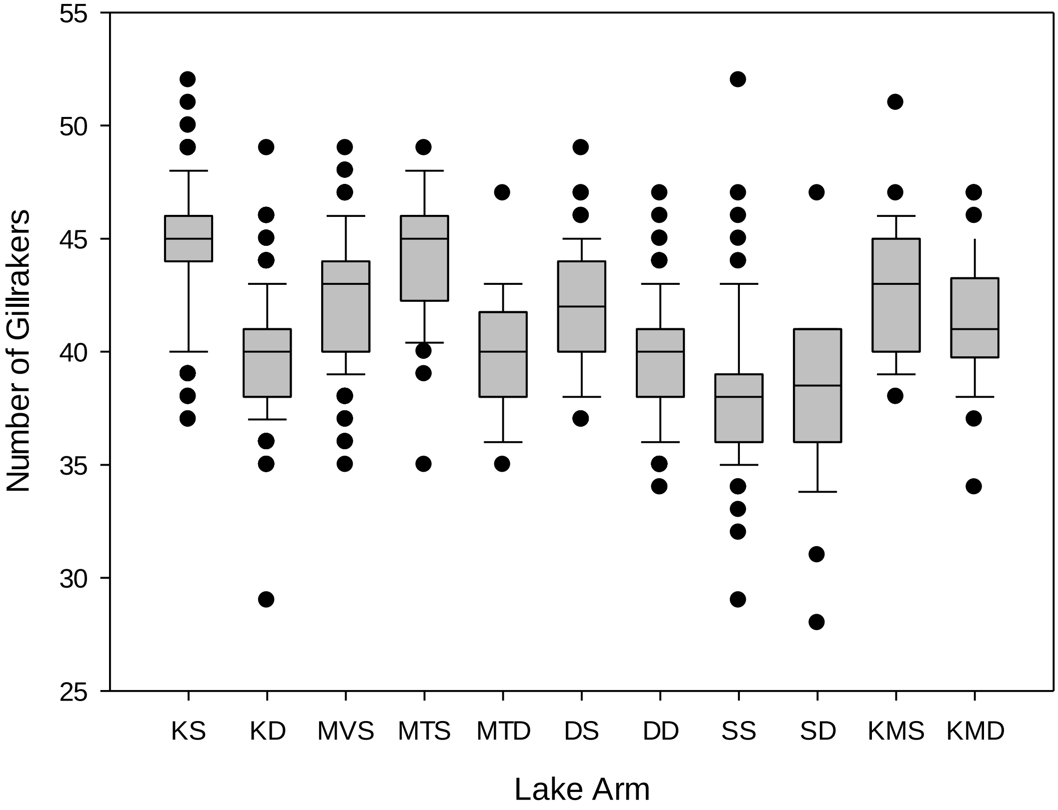
Location	**Sample Size**	**Years of Data Collection**
Keith shallow	231	2005, 2007, 2012
Keith deep	196	2003, 2004, 2008, 2012
McVicar shallow	250	2008, 2013
McVicar deep	0	
McTavish shallow	39	2004, 2009
McTavish deep	15	2004, 2009, 2014
Dease shallow	72	2005, 2010
Dease deep	178	2010
Smith shallow	84	2006, 2011
Smith deep	22	2011
Keith Manitou shallow	40	2012
Keith Manitou deep	45	2012

An initial exploratory comparison of total gillraker counts distributions among different location-depth groupings was conducted using box plots as this has traditionally been used as the primary attribute in distinguishing among Cisco species and morphs (Scott and Crossman 1998, Smith and Todd 1992, Todd and Smith 1992). Box plots were also used to visually evaluate each of the morphometric variables individually across all groups in order to quickly determine possible variances between groups which would ultimately aid in the interpretation of the multivariate analysis that followed and all meristic variables were evaluated in the same manner. Linear discriminant function analyses (LDA) of morphometric and meristic variables were used to evaluate the fit of individuals to predetermined location-depth groups. These two types of variables were evaluated separately because morphometric data were continuous whereas meristic data were discrete. Discriminant function scores were plotted to visualize relationships between groupings along the first two canonical axes. Classification success was determined by the percent of individuals assigned to the correct predetermined group using jackknife cross-validation. Lastly, the discriminant loadings were used to assess the relative influence of each variable in discriminating between groups. All statistical analyses were run in “R” (R Core Team 2013).

2.3 RESULTS

Mean and modal gillraker counts generally differed between Cisco captured in deep and shallow water habitats, with the shallow water groups having more gillrakers than those from the deep water habitats (Figure 2-3). An exception was in the Smith Arm area where Cisco from the two habitats had similar gillraker counts, that were interestingly the lowest observed anywhere in the lake. Although consistent patterns were generally observed, this trait alone was not always a good indicator of habitat type because of the large degree of overlap in distributions for some arms/locations (Figure 2-3).

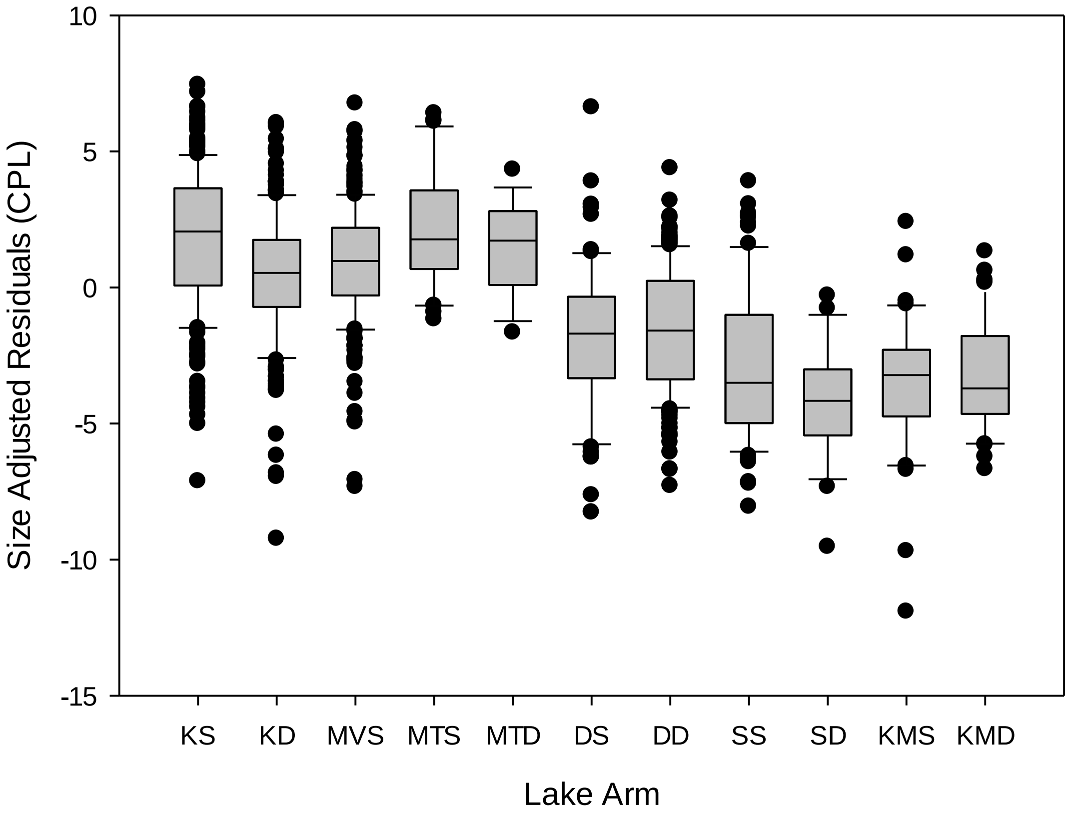
Figure 2-3. Boxplots illustrating the distribution of total gillraker counts of shallow (≤50 metre) and deep (>50 metre) water Cisco in each of the arms/locations of Great Bear Lake.



Note: Population codes along the X axis are as follows; KS-Keith shallow, KD-Keith deep, MVS- McVicar shallow, MTS- McTavish shallow, MTD- McTavish deep, DS- Dease shallow, DD- Dease deep, SS - Smith shallow, SD- Smith deep, KMD- Keith Manitou deep, KMS- Keith Manitou shallow

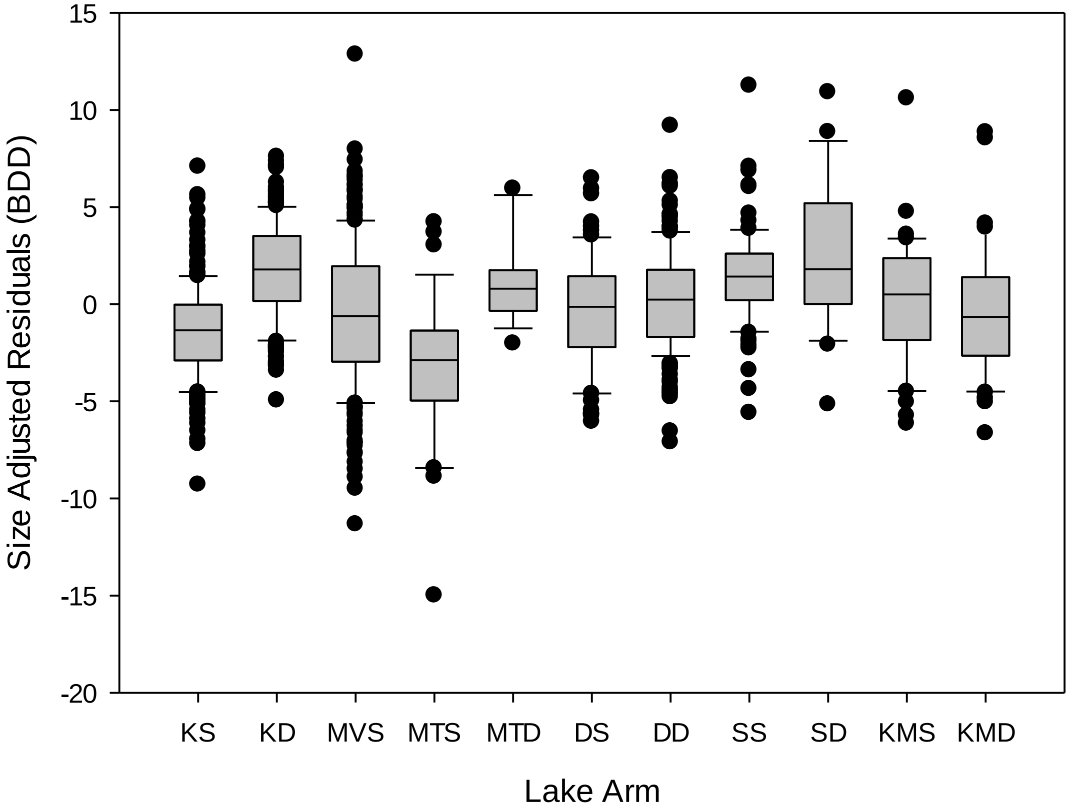
Other morphometric variables of interest via the visual evaluation of box plots were caudal peduncle length, body depth, and pectoral length (Figure 2-4 to Figure 2-6). These variables varied the most across all groups and therefore were expected to help differentiate individuals between groups. Caudal peduncle length appeared to vary widely across all groups with little recognizable pattern, body depth was generally greater in deep water groups whereas pectoral fin length showed trends towards shorter fin lengths in shallow water groups and longer fin lengths in deep water groups.

Figure 2-4. Boxplots illustrating the distribution of size adjusted caudal peduncle length of shallow (≤50 metre) and deep (>50 metre) water Cisco in each of the arms/locations of Great Bear Lake.



Note: Population codes along the X axis are as follows; KS-Keith shallow, KD-Keith deep, MVS- McVicar shallow, MTS- McTavish shallow, MTD- McTavish deep, DS- Dease shallow, DD- Dease deep, SS - Smith shallow, SD- Smith deep, KMD- Keith Manitou deep, KMS- Keith Manitou shallow

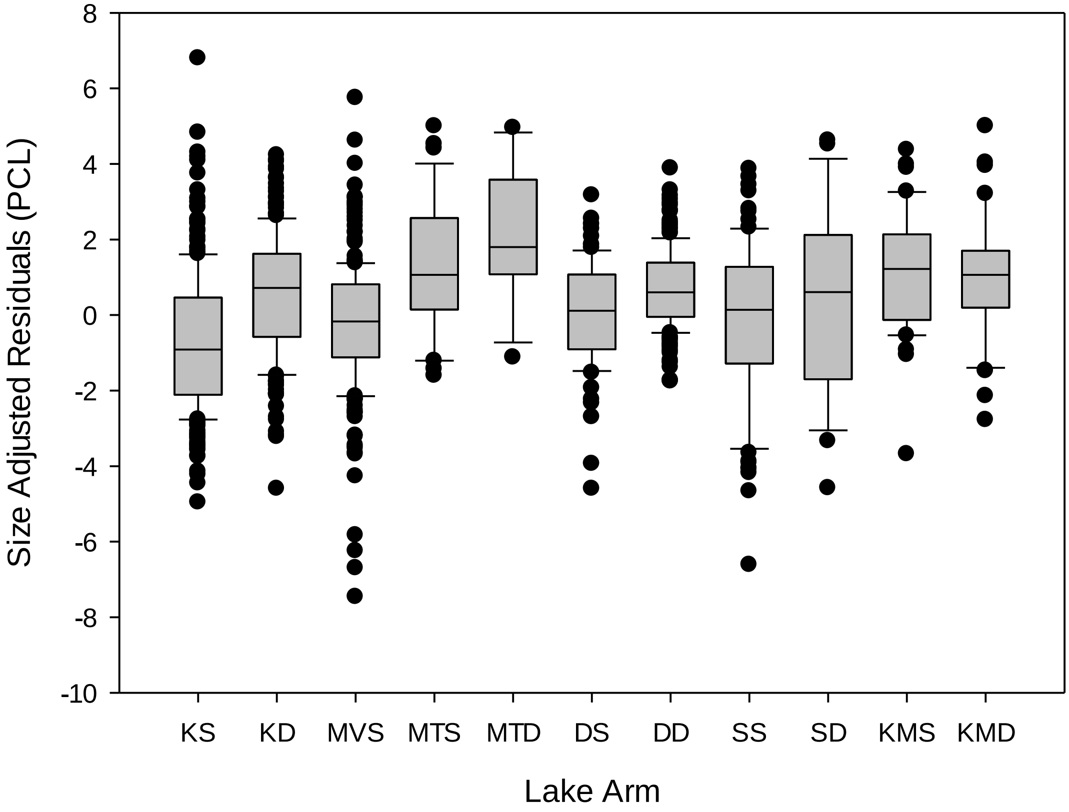
Figure 2-5. Boxplots illustrating the distribution of size adjusted body depth of shallow (≤50 metre) and deep (>50 metre) water Cisco in each of the arms/locations of Great Bear Lake.



Note:

Note: Population codes along the X axis are as follows; KS-Keith shallow, KD-Keith deep, MVS- McVicar shallow, MTS- McTavish shallow, MTD- McTavish deep, DS- Dease shallow, DD- Dease deep, SS - Smith shallow, SD- Smith deep, KMD- Keith Manitou deep, KMS- Keith Manitou shallow

Figure 2-6. Boxplots illustrating the distribution of size adjusted pectoral length of shallow (≤50 metre) and deep (>50 metre) water Cisco in each of the arms/locations of Great Bear Lake.



Note:

Note: Population codes along the X axis are as follows; KS-Keith shallow, KD-Keith deep, MVS- McVicar shallow, MTS- McTavish shallow, MTD- McTavish deep, DS- Dease shallow, DD- Dease deep, SS - Smith shallow, SD- Smith deep, KMD- Keith Manitou deep, KMS- Keith Manitou shallow

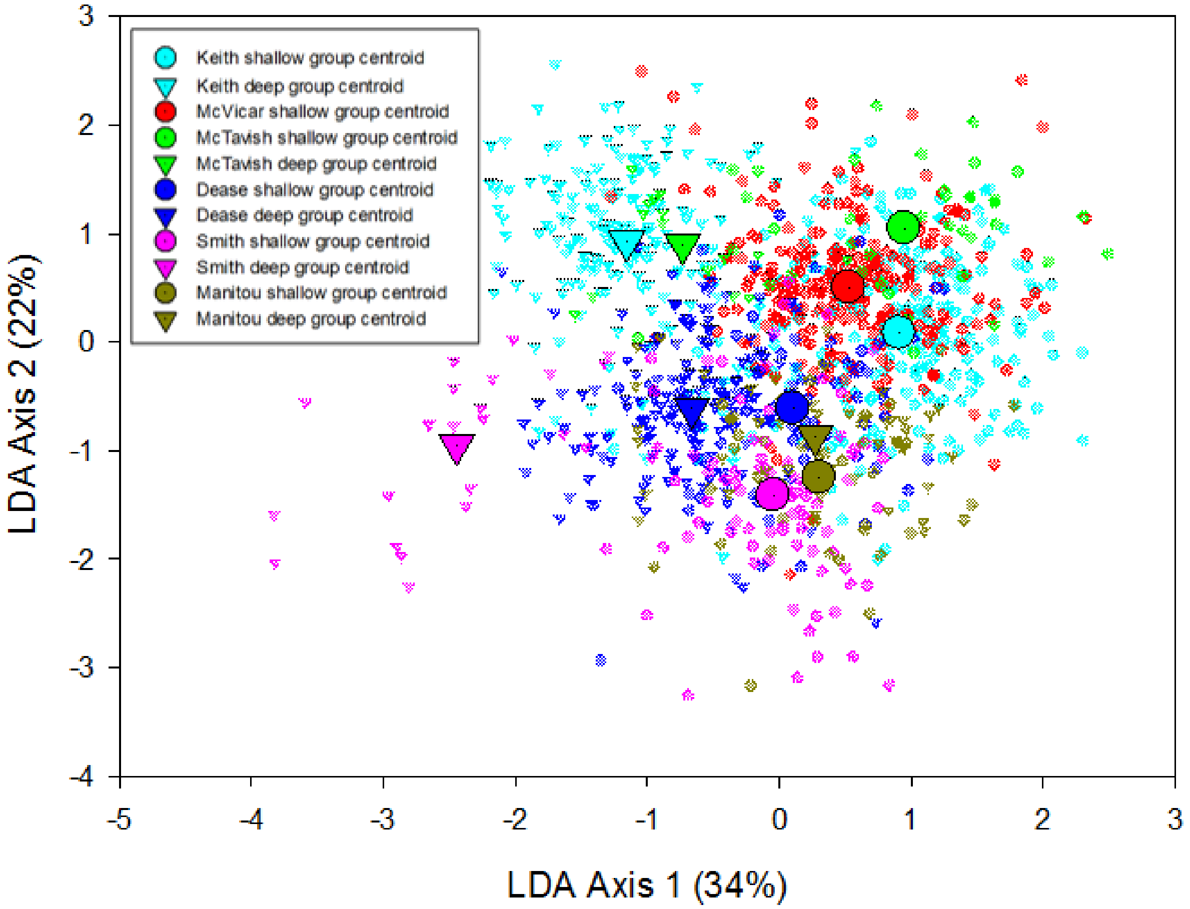
2.3.1 Morphometrics

The predetermined depth-location groupings were reasonably well supported by the LDA. The first two axes together accounted for 56% (LD1 34%, LD2 22%) of the variance in morphometry between groups (Wilks' Lambda = 0.022 and Chi-squared P-value < 0.001) with an overall classification success of 75.6% (Figure 2-7). Axis one mainly separated groups from shallow and deep water habitats whereas axis two loosely separated groups by arms of capture. Axis one had high positive loadings for maxillary length, head depth and pre-orbital length and high negative loadings for gillraker length, maxillary width and caudal peduncle depth (Table 2-2). Cisco from shallow water habitats generally had longer maxillary length, pre-orbital length, greater head depth, shorter gillraker length, smaller maxillary width and caudal peduncle depth. Axis two had high positive loadings for pre-orbital length, dorsal fin length, gillraker length and high negative loadings for lower arch length, caudal peduncle length, and interorbital width (Table 2-2). Shallow and deep water Cisco from Keith (excluding those from Manitou), McVicar and McTavish Arms generally had shorter pre-orbital, dorsal fin and, gillraker lengths and longer lower arch and caudal peduncle lengths. Cisco from Dease, Smith and Keith Arm Manitou showed the opposite in all above-mentioned traits.

Table 2-2. Discriminant function loadings for the morphometric analysis of Cisco in Great Bear Lake.

Loadings		
Morphometric Code	Axis 1	Axis 2
PMA	-0.05624	-0.30433
POL	-0.20817	-0.19984
OIL	-0.02574	-0.1384
PSL	0.118305	-0.09114
TTL	0.096424	-0.25872
DOL	0.1239	-0.298
LUL	0.352243	-0.20258
ANL	0.133828	-0.15833
CPL	0.318267	0.349903
HDD	-0.28759	0.089438
BDD	-0.1634	-0.01673
CPD	0.186029	-0.12497
IOW	-0.12172	0.132116
MXL	-0.23128	-0.02919
MXW	0.096494	0.039542
PCL	-0.00412	0.120379
PVL	-0.02581	0.068996
ADL	-0.01089	0.002209
GRL	0.285563	-0.14765
LAL	0.032817	0.37641

Figure 2-7. Graphical results of the discriminant function analysis on 20 morphometric variables for Cisco caught in Great Bear Lake, Northwest Territories, Canada.



From these discriminant function results a broad conclusion of the possible number of morphs/populations found within Great Bear Lake can be made. Four distinct groupings are visible from the plotted group centroids; first Keith deep and McTavish deep form a group in the upper left quadrant. Second, Keith shallow, McVicar shallow, and McTavish shallow form a group in the upper right quadrant. Below is a third group made up of the Manitou shallow and deep, Dease shallow and deep, and the Smith shallow. The fourth group is made up entirely of a single morph/population; the Smith deep group which does not appear to resemble any other group described here.

The reclassification success for individuals back to their predetermined depth- and location-specific groups from highest to lowest was Smith deep (100%), Dease deep (89%), McTavish shallow (87%), McTavish deep (86%), McVicar shallow (85%), Keith deep (83%), Smith shallow (79), Keith shallow (78%), Manitou shallow (55%), Dease shallow (45%), and Manitou deep (42%) (Table 2-3). Seventeen percent of Cisco from the Manitou shallow group reclassified into the Manitou Deep group, whereas only eight percent of the Cisco from Manitou deep reclassified into the Manitou shallow group; however, 28% of the Cisco from the Manitou deep group reclassified into the Dease deep group and similarly 15% of the Manitou shallow group reclassified into the Dease deep group.

Table 2-3. Reclassification success of the 11 Cisco groups from Great Bear Lake based on 20 morphometric variables using a discriminant function analysis.

	Keith shallow	**Keith deep**	**McVicar shallow**	**McTavish shallow**	**McTavish deep**	**Dease shallow**	**Dease deep**	**Smith shallow**	**Smith deep**	**Manitou shallow**	**Manitou deep**
Keith shallow	**182** **78%**	0	14 6%	1 <1%	1 <1%	2 <1%	14 6%	3 1%	0	4 1%	10 4%
Keith deep	3 1%	**163** **83%**	5 2%	0	8 4%	0	15 7%	0	0	0	2 1%
McVicar shallow	12 4%	3 1%	**213** **85%**	7 2%	1 <1%	3 1%	4 1%	2 <1%	0	1 <1%	4 1%
McTavish shallow	1 2%	0	1 2%	**34** **87%**	2 5%	0	1 2%	0	0	0	0
McTavish deep	0	1 6%	1 6%	0	**13** **86%**	0	0	0	0	0	0
Dease shallow	7 9%	3 4%	10 13%	1 1%	0	**33** **45%**	10 13%	6 8%	0	2 2%	0
Dease deep	1 <1%	4 2%	1 <1%	0	0	7 3%	**159** **89%**	1 <1%	0	4 2%	1 <1%
Smith shallow	1 1%	1 1%	2 2%	1 1%	0	5 5%	0	**67** **79%**	0	5 5%	2 2%
Smith deep	0	0	0	0	0	0	0	0	**22** **100%**	0	0
Manitou shallow	1 2%	0	1 2%	0	0	2 5%	6 15%	1 2%	0	**22** **55%**	7 17%
Manitou deep	6 13%	0	0	0	0	3 6%	13 28%	0	0	4 8%	**19** **42%**

2.3.2 Meristics

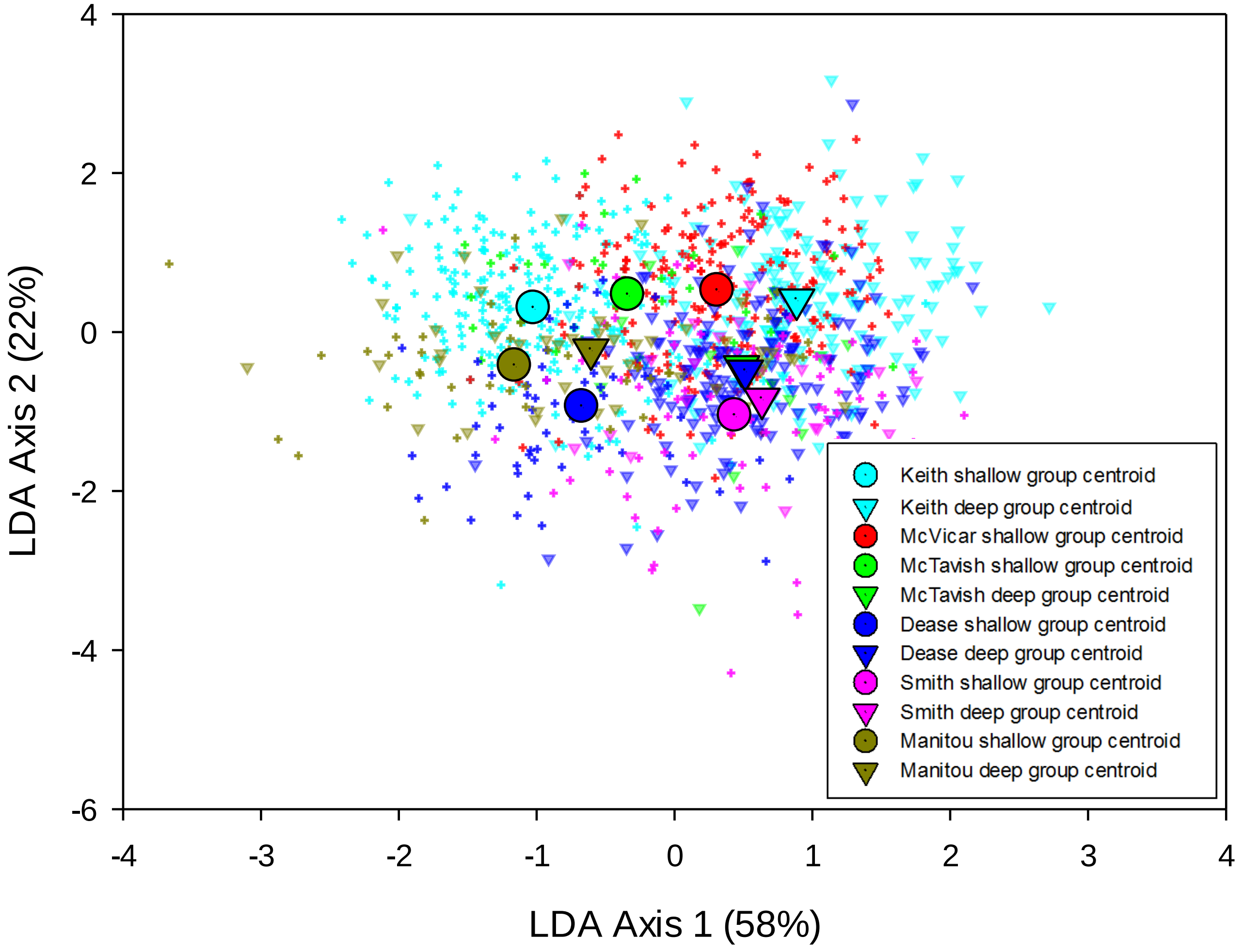
Univariate statistics (ANOVA) showed that all variables were different between depth and arm of capture locations (all P-value <0.001).

Similar to morphometric results, the predetermined groups were well supported by the LDA. The first two axes together accounted for 80% (LD1 58%, LD2 22%) of the variance in meristic counts between all predetermined groups (Wilks' Lambda = 0.233 and Chi-squared P-value < 0.001) (Figure 2-8). Axis one clearly divided groups between depths of capture while axis two loosely separated groups by arm. Axis one had high positive loadings for anal ray counts and lateral line scales and high negative loadings for dorsal ray counts, pectoral ray counts and total gillraker counts (Table 2-4). Axis two had high positive loadings for dorsal ray counts and lateral line scales (Table 2-4). Meristic variables on axis two with high negative loadings included pectoral ray counts, anal ray counts and total gillraker counts. Small trends were noticeable between groups based on depth of capture. Generally, shallow water groups had more lateral line scales, dorsal rays, pectoral rays and gillrakers in comparison to the deep water groups.

Table 2-4. Discriminant function loadings for the meristic analysis of Cisco in Great Bear Lake.

Loadings		
Meristic Code	Axis 1	Axis 2
LLS	0.5232	0.70455
DRC	0.2918	0.30099
ARC	0.009933	0.259339
PRC	0.16461	0.361513
VRC	0.05888	0.027467
TGR	0.45284	0.683777

Figure 2-8. Graphical results of the discriminant function analysis on Meristic variables of Cisco caught in Great Bear Lake, Northwest Territories, Canada.



Although the first two axes explained a relatively high proportion of the variance, the reclassification success to predetermined groups of Cisco based on meristics was not as strong as with morphometric measures (Table 2-1). High variability in classification success was seen among groups, with the Keith shallow and deep, and McVicar shallow groups having the highest proportion of individuals reclassifying properly at 80%, 59% and 70% respectively followed by the Dease shallow and deep groups at 36% and 44% respectively (Table 2-1). The remaining groups (McTavish, Smith and Manitou shallow and deep) all had ≤ 25% classification success. Misclassified individuals within these groups tended to reclassify into the groups with the larger sample sizes and in some cases the same depth category. For example, the McTavish shallow group mainly reclassified into the Keith and McVicar shallow groups whereas the McTavish deep group mainly reclassified into the Dease deep group. The Smith shallow and deep groups both had high percentages of their groups reclassify into the Dease deep group. The Smith deep group also had a relatively high percentage of individuals reclassify into the Smith shallow group. The Manitou groups (shallow and deep) also both showed strong reclassification to the Keith shallow group. Moreover, the Manitou deep group also had an equal number of its individuals reclassify into the Manitou shallow and the Dease deep groups similar to the patterns observed with the morphometric data.

Table 2-5. Reclassification success of the 11 Cisco groups from Great Bear Lake based on seven meristic variables using a discriminant function analysis.

	Keith shallow	**Keith deep**	**McVicar shallow**	**McTavish shallow**	**McTavish deep**	**Dease shallow**	**Dease deep**	**Smith shallow**	**Smith deep**	**Manitou shallow**	**Manitou deep**
Keith shallow	**185** **80%**	5 2%	14 6%	3 1%	0	7 3%	11 4%	2 <1%	0	2 <1%	2 <1%
Keith deep	4 2%	**116** **59%**	33 16%	1 <1%	0	1 <1%	21 10%	3 1%	0	1 <1%	3 1%
McVicar shallow	22 8%	36 14%	**117** **70%**	2 <1%	1 <1%	4 1%	30 12%	1 <1%	0	0	0
McTavish shallow	16 41%	2 5%	12 30%	**5** **12%**	0	0	3 7%	0	0	0	0
McTavish deep	1 6%	2 13%	3 20%	1 6%	**0**	0	7 46%	1 6%	0	0	0
Dease shallow	18 25%	0	7 9%	0	0	**26** **36%**	4 5%	4 5%	0	5 6%	2 2%
Dease deep	3 1%	25 14%	30 16%	2 1%	0	3 1%	**79** **44%**	15 8%	0	2 1%	1 <1%
Smith shallow	8 9%	12 14%	5 5%	0	0	5 5%	29 34%	**17** **20%**	1 1%	0	1 1%
Smith deep	0	3 13%	3 13%	1 4%	0	1 4%	6 27%	5 22%	**1** **4%**	1 4%	1 4%
Manitou shallow	18 45%	2 5%	1 2%	0	0	2 5%	1 2%	3 7%	0	**10** **25%**	3 7%
Manitou deep	17 37%	5 11%	2 4%	0	0	2 4%	7 15%	0	0	7 15%	**5** **11%**

2.4 DISCUSSION

The current study clearly shows that there is considerable variability among Cisco of Great Bear Lake, both at the local scale (within arms) and at a global scale (lake wide). Moreover, results indicate a strong distinction between shallow and deep water habitats. The variability seen among Cisco with respect to morphology is most likely a consequence of niche partitioning in habitat use (depth) given that variability in morphology is frequently associated with either locomotion or feeding mechanisms and therefore strongly associated with depth of capture (Praebel et al. 2013).

The initial analysis of mean gillraker counts showed a general separation between Cisco captured in different habitats, with shallow water populations typically having more gillrakers than those from deep water habitats. However, this was not always clear as there were varying degrees of overlap between some shallow and deep water groups including Dease and Smith Arms as well as the Manitou area within Keith Arm. Cisco from the shallow habitat in Smith Arm, differed from all other areas by having the lowest number of gillrakers, and more closely resembling deep water Cisco. These results could be a function of sampling bias; Smith Arm was sampled in one specific area of the arm where the shallow water and deep water habitats are in close proximity which could have lead to mixing of the two groups or possibly movement of shallow and deep water adapted individuals into alternate habitats based on seasonal food availability. In addition, deep water Cisco are known to migrate vertically through the water column in pursuit of prey (Hrabik et al. 2006) and thus could have been caught in shallow water even though they originated in the deep water. Furthermore, the time (summer months) of capture for most of the samples as it relates to seasonally abundant foods such as emergent and/or terrestrial insects may have influenced the depths utilized by different morphotypes of the Cisco in all areas of the lake.

The multivariate analysis of morphometric traits for Cisco showed that the shallow water associated individuals generally had characteristics associated with a larger head, longer and more narrow snout and mouth parts (longer maxillary and pre-orbital length, greater head depth and smaller maxillary width) and more gillrakers. These morphological traits suggest specialization for feeding on smaller prey such as zooplankton as was shown by Amundsen et al. (2004) in European whitefish (*C.lavaretus*). The opposite set of traits was observed in the deep water associated morphs/populations. These attributes (smaller head, shorter snout, and reduced caudal peduncle) are most often associated with faster swimming (Blake 2004) and the utilization of faster more mobile prey as described by Zimmerman et al. (2006, 2007) with lake trout from Great Slave Lake and Lake Mistassini. Furthermore, a deeper body is characteristic of deep water Cisco which helps with vertical migration through the water as they chase prey.

The Smith Arm deep water Cisco were of special interest to the analysis, as they were morphologically distinct from all other morphs/populations found in Great Bear Lake. They showed very little overlap in any of the morphometric traits assessed and reclassified back to their group with 95% success thus indicating a novel Cisco form not seen before in the preliminary study of Cisco in Great Bear Lake. This morph/population differed from all other groups by having a greater body depth, longer maxillary length, and longer pre-orbital length than all other groups. However, the number of gillrakers was similar to what has been observed in other deep water associated morphs/species such as *C. zenithicus* from other large deep lakes (e.g. Mandrak et al. 2014). Given the limited sample sizes available for this population it is challenging to detect the exact nature of this deviation from the norm across the lake with respect to deep water Cisco, but some inferences can be made. This group may represent a different founding population in this area of the lake, or possibly the allochthonous inputs and associated food web in this arm may be driving these differences. Indeed, analyses show that Cisco from this arm of the lake have a unique diet (see Chapter 3).

A general set of traits was seen in all individuals regardless of depth of capture in the southern portion of the lake (McVicar Arm, McTavish Arm and Keith Arm excluding individuals from the Manitou area). These include greater lower arch length, increased pectoral and pelvic fin length, reduced orbital length and shorter dorsal length. Some of these common traits may not be directly associated with similarities in feeding or locomotion of these Cisco but rather may result from intermixing of stocks that are in closer geographical proximity to each other. Alternatively, these traits may be remnants from a founding population which have been retained by these individuals due to geographic isolation from other populations in the lake. Morphometric traits such as these can often be retained while more plastic meristic traits (e.g, gillraker numbers) may change more rapidly due to their functional significance (Amundsen et al. 2004). Chavarie et al. (2013) referred to morphological properties (phenotypic traits) that reflect ecological roles within a fish community. In particular, the phenotypic traits associated with ecological properties are most often head and mouth shape because these are in direct contact with the environment. Further genetic and diet studies would be required to better understand the mechanisms driving the differences in these traits for Cisco populations in Great Bear Lake.

The reclassification of individuals into their respective groups based on morphometric characteristics shows that most individuals are clearly well separated and that depth grouping of Cisco, in particular was an effective discriminator. Another important aspect of the reclassification success of each of the groups was that the majority of misclassifications continued to reclassify into the same depth grouping showing that in general the shallow water groups had a similar set of traits that were fairly easily distinguishable from the deep water groups. However, in cases where they did classify to a different depth grouping, it was usually within the same arm suggesting there may be movement/mixing of deep or shallow water adapted individuals between these habitats within a given location. The reclassification of individuals from the meristic characteristics was less effective at identifying the original group membership. This may in part have been due to skewed sample sizes as it appears that misclassified individuals were typically distributed across groups with large samples sizes that were from within the same depth class (e.g., Keith shallow and deep and McVicar shallow).

Four groups/morphs were established from the LDA on morphometric data and may be associated with some possible mixing of populations/groups between areas of the lake. The shallow water Cisco from Keith, McVicar and McTavish grouped together showing that these fish may have some level of movement between areas. Similarly the deep water groups of the same areas (with the exception of McVicar Arm which has very little deep water and does not appear to have an established deep water population) clustered together and may have similar mixing. Mixing may be facilitated by the lake morphometry where all three of the lake arms radiate from a central basin and are therefore in relatively close proximity allowing for the movement of Cisco from one arm to the next within their preferred habitat. A third group/morph of Cisco identified by the morphometric LDA encompassed those individuals from Manitou deep and shallow, Dease deep and shallow and Smith shallow. This group may have residual traits from another founding population and appears to be an intermediate/general form between shallow water and deep water Cisco where no specific traits suggest affinity to either group. The last group entirely made up of individuals from the Smith deep area may be a result of small sample size but may also represent a distinct group/population where very little intermixing has taken place.

Anal ray counts, lateral line scales, dorsal ray counts and pectoral ray counts were associated with depth of capture and location of capture throughout the lake (lake arm). Differences in these characteristics may be a function of phenotypic plasticity relating to differences in habitat and ecological niches associated with utilization of different depths zones. As mentioned above these characteristics may be more plastic and represent functional adaptations within a niche (Chavarie et al. 2013). Other mechanisms may also be playing an important role in the differing characteristics between groups. The first three groups identified above in the morphometric LDA are loosely identifiable in the meristic LDA indicating that both the meristics and morphomentrics are capable of distinguishing between larger groups at a lake wide scale and a local scale (within arm).

2.5 CONCLUSION

Many of the results provided here are complementary to those discovered by Howland et al. (2014) in the initial evaluation of the Cisco diversity of Great Bear Lake and others are novel to this evaluation. The division of morphs/populations by depth of capture is one of the key findings in the study. This depth related segregation of Cisco illustrates that there continues to be a strong presence of Cisco in the deeper areas of the lake which indicates that many of the critical functions of deep water nutrient cycling have remained intact in this system. These deep water ciscoes may reflect a distinct morph or form of *C. zenithicus* in Great Bear Lake which are filling the important niche of deep water nutrient cycling. Current research on Cisco genetics has shown that what was formerly considered shortjaw Cisco has had multiple origins (originating independently in many lakes regardless of ancestral inhabitation) as a consequence of species plasticity (Turgeon and Bourret 2013). The Shortjaw-like Cisco morph found in this study has most likely arisen *in situ* as the result of specific habitat availability rather than from a founding ancestral population at the lake wide scale. Novel results from the Smith Arm deep water morph/population warrant more research; this group (Smith Arm) coupled with others may shed light on new mechanisms operating in the lake and how the Cisco diversity has changed or may change in the future as change takes place at the local scale with increased anthropogenic disturbance (increased fishing pressure, or increased development on shore contributing to new inputs into the lake), or at the global scale as climate change continues to alter the northern landscape.

Finally, the new information provided above will help conservation efforts as managers move forward making critical decisions on how best to conserve this unique assemblage of Cisco in Great Bear Lake. Conservation managers now have a better understanding of the unique stocks of Cisco and other fish inhabiting the waters of Great Bear Lake such that they can now begin to apply the conservation strategies outlined by COSEWIC with respect to designatable units. Furthermore, Great Bear Lake epitomizes an intact deep water lake which continues to harbor a complete assemblage of Cisco; information from these populations can thus provide managers with the tools to understand the changes that have taken place in other large deep lakes as it relates to the Cisco group as a whole.

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ABSTRACT

Researchers have identified the importance of the trophic hierarchy as it relates to isolated food webs where nutrient cycling and nutrient flow are relatively constant from a stable nutrient input. In this study, stomach content analysis, stable isotope analysis, and fatty acid analysis were used to determine the trophic positioning of morphologically distinct groups of Cisco associated with different habitats (depths) and areas of Great Bear Lake.

Stomach content analysis showed that Cisco from shallow water habitats fed on a more diverse array of foods than those captured in deeper water, with terrestrial insects making up a greater proportion of the diet. The main prey item of the shallow water Cisco were copepods while deep water Cisco tended to feed mainly on mysids. The stable isotope analysis revealed that the deep water morphs were more enriched in δ^{15}N as was expected given that mysids are more trophically enriched than copepods. No clear trend was observed between morphs for the depletion of δ^{13}C, this may be in part due to the varying allochthonous inputs from around the lake that may be driving patterns. Fatty acid signatures showed unique biomarker patterns for feeding strategies within different morphs, with deep water Cisco exhibiting stronger signals of pelagic feeding and shallow water Cisco having stronger terrestrial and benthic biomarkers. It appears that the shallow water and deep water Cisco of Great Bear Lake each occupy different dietary niches and therefore strategic management methods should reflect these differences in order to preserve these two habitat distinct groups of Cisco.

CHAPTER 3:

EVALUATION OF THE TROPHIC ECOLOGY OF THE CISCO OF GREAT BEAR LAKE

3.0 INTRODUCTION

A new emphasis on trophic structuring of ecosystems has been emerging in recent years (Thompson et al. 2005). Researchers have identified the importance of the trophic hierarchy as it relates to isolated food webs where nutrient cycling and nutrient flow are relatively constant from a stable nutrient input (Thompson et al. 2005). These criteria are central to most lake systems and possibly exemplified by northern water bodies due to their low anthropogenic inputs (nutrient loading from outside sources) and steady natural environmental inputs from the relatively homogeneous surroundings (Post et al. 2000). These conditions create a situation where the trophic ecology can be explained and understood in great detail. However, Great Bear Lake is unique because it is at the intersection of three different ecozones (Johnson 1975, Chavarie et al. 2014) that possibly contribute different environmental inputs which in turn could lead to differences in trophic ecology in different arms of the lake. This information can help researchers understand how and why changes to the ecosystem are or will be taking place.

Previous studies have typically relied on stomach content analyses when determining trophic positioning or niche occupancy, however this only gives the researcher a snapshot in timeof what the organism in question has ingested. With newer methods, researchers are now able to determine what prey items were ingested over the last few weeks using stable isotope (Vander et al. 2015) analyses and what prey items were being ingested over the last months using fatty acid analyses (Tocher 2003). The use of stable isotopic signatures and a variety of fatty acids found in the different organisms within a given ecosystem can be informative in understanding food web linkages and placement within the ecosystem (Hobson and Wassenaar 1999, Thompson et al. 2005). Organisms at the primary production level contain proportions of both the fatty acids and isotopes which are then passed up the food web as they get consumed in larger quantities through the bioaccumulation of primary consumers and later secondary consumers until they arrive at the apex of the food web. Therefore, the total amounts and composition of isotopes or fatty acids can be linked to a given organism's placement within the food web (Hecky and Hesslein 1995, Hobson and Wassenaar 1999, Post et al. 2000, Post 2002, Thompson et al. 2005) which is the focus of this chapter for the different morphs/populations of Cisco in Great Bear Lake.

Cisco are at an intermediate point between predator and prey as they themselves are both predator and prey within the food web as was shown by Chavarie et al. (2014) in her analysis of trophic patterns in Great Bear Lake. Therefore, exploring the relationship between Cisco and their prey will help identify differences in niche occupancy between morphological groups within Great Bear Lake. In turn, identifying the differences in niche occupancy will help in determining the mechanisms driving these differences and aid in determining the consequences of this niche partitioning. This chapter aims to characterize the trophic ecology (trophic positioning) of the different morphs/populations of Cisco identified in Great Bear Lake to determine mechanisms driving differentiation and niche partitioning among morphs/populations and to shed light onto possible consequences of niche partitioning and differential habitat use. Based on chapter two we evaluated the trophic variation of two morphs: deep and shallow water.

3.1 STUDY AREA

Refer to Chapter One for detailed study area description.

3.2 METHODS

3.2.1 Diet and Trophic Analysis

A subsample of ciscoes from each predetermined morph/group, hereafter referred to as "morphological grouping," were randomly selected from all Cisco collected in Great Bear Lake from 2003 to 2014, with only those individuals containing food in their stomachs included for further analysis (Table 3-1). However, despite all efforts some individuals did not have any recognizable food items in their stomachs leading to a possible bias in some of the results. A small piece of muscle tissue was removed from the left posterior side of the fish for isotope and fatty acid analyses, while the gut (from esophagus to anus) was removed for stomach content analysis. Zooplankton captured near each net set location from vertical tows and depth stratified tows as part of a larger ecosystem study were made available for stable isotope analyses to help determine possible depletions and enrichments of δ^{13}C and δ^{15}N respectively in the morphological groupings.

Table 3-1. Sample sizes from each of the Cisco groups within Great Bear Lake that were used in all stomach content analyses, stable isotope analyses and fatty acid analyses.

Morphological Grouping	Sample Size
Keith shallow	30
Keith deep	20
McVicar shallow	10
McVicar deep*	4
McTavish shallow	20
McTavish deep	7
Dease shallow	21
Dease deep	20
Smith shallow	21
Smith deep	11

*no McVicar deep sample were used for the fatty acid analysis because the sample size was too small for the discriminant function analysis

3.2.2 Laboratory procedures

3.2.2.1 Stomach Contents

Stomachs were emptied and all dietary items were sorted, enumerated and identified to the lowest taxonomic level possible (species, genus, family, order) by use of a dissecting microscope. All samples were then preserved in 95% ethanol.

3.2.2.2 Stable Isotopes

Muscle samples to be analyzed for δ^{13}C and δ^{15}N at the Fresh Water Institute (Winnipeg Manitoba) were freeze dried, ground to a fine powder and 400 ug +/- 10 ug was weighed into 3.5x5 mm tin cups (Costech Analytical). Samples were analyzed using a continuous flow isotope ratio mass spectrometer (Thermo-Delta 5 Plus) equipped with a Costech elemental analyzer. Stable isotope results are expressed in delta (δ) notation defined as the deviation from a standard reference material in parts per thousand (‰). δ^{13}C results are relative to Vienna Pee Dee Belemnite (VPDB) while δ^{15}N results are relative to atmospheric air and are calculated using the following equation:

$$\delta X = [(Rsample/Rstandard) - 1] \times 1000$$

where X is δ^{13}C or δ^{15}N, Rsample is the ratio (δ^{13}C /^{12}C or δ^{15}N /^{14}N) in the sample while Rstandard is the ratio in the standard.

Every 10th sample was run in duplicate. Certified reference materials (USGS40 and 41) were analyzed repeatedly with each batch of samples. Standard deviations of 60 replicates of each reference material were <0.07‰ for δ13C and <0.12‰ for δ15N. The standard deviation of repeated (12) measurements of an in-house homogenized fish standard was <0.1‰ for δ13C and <0.1‰ for δ15N.

3.2.2.3 Fatty Acids

Lipids were extracted from 0.25 grams of freeze-dried muscle with 2:1 chloroform-methanol containing 0.01% butylated hydroxytoluene (BHT) (v/v/w) (Folch et al., 1957). The lipid phase was filtered, collected, and dried with anhydrous sodium sulphate and evaporated under nitrogen to obtain the total lipid weight. The extracted lipid was used to prepare the fatty acid methyl esters (FAME) by transesterification with Hilditch reagent (0.5 N H_2SO_4 in methanol) (Morrison et al, 1964). The samples were heated for 1 h at 100 °C. Gas chromatographic (GC) analysis was performed on an Agilent Technologies 7890N GC equipped with a 30 m J&W DB-23 column (0.25 mm I.D; 0.15 μm film thickness). The GC was coupled to a Flame Ionization Detector (FID) operating at 350 ^{o}C. Hydrogen was used as carrier gas flowing at 1.25 mLs/min for 14 minutes and ramped to 2.5 mLs/min for the reminder of the run.

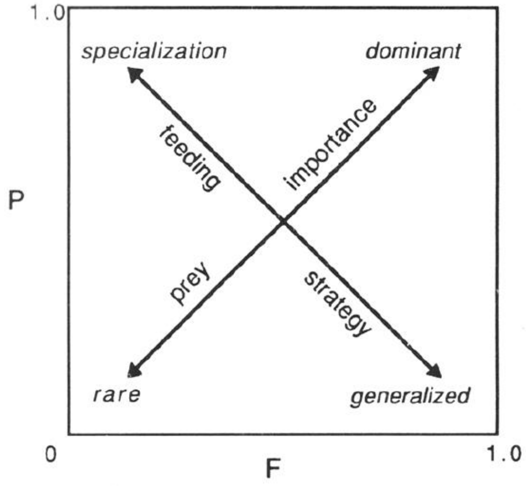
The split/splitless injector was heated to 260 ^{o}C and run in splitless mode. The oven program was as follows: 60 ^{o}C for 0.66 min; 22.8 ^{o}C/min to 165 ^{o}C with a 2.0 min hold; 4.7 ^{o}C/min to 174 ^{o}C and 7.6 ^{o}C/min to 200 ^{o}C with a 6 min hold. Peaks were quantified using Agilent Technologies ChemStation software. Fatty acid standards were obtained from Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463). Eighty FAME were identified via retention time and known standard mixtures and are reported as a percent of a particular fatty acid from all fatty acids within the sample. Each fatty acid is described using the shorthand nomenclature of A:Bn-X, where A represents the number of carbon atoms, B the number of double bonds and X the position of the double bond closest to the terminal methyl group. This raw analysis was completed at the Fresh Water Institute (Winnipeg Manitoba).

3.2.3 Data Analyses

3.2.3.1 Stomach Contents

Percent frequency of occurrence (%F, total number of fish in a given morphological grouping that had dietary item *i* present in the stomach) and percent total number (%N, proportion of dietary item *i* relative to all dietary items for that morph) for each group was calculated and graphically presented using side by side bar charts to identify important dietary items (i.e., those with high %F and high %N). In addition, a graphical analysis developed by Costello (1990) of the frequency of occurrence and total number was created to illustrate 1) the feeding strategy and 2) the dietary importance of each item identified for predetermined morphological groupings. Points on the graph represent individual prey items with those in the upper right quadrant indicating the dominant prey items and those in the lower left quadrant indicating rare prey items being consumed by few individuals within the group and in low numbers. Points in the upper left quadrant (low in frequency but high in abundance) indicate a specialization of an individual and clustering of points in the lower right quadrant indicates a generalized feeding strategy (many prey items in low quantities). These graphs are interpreted as shown in Figure 3-2, noting that information at the population level and individual level are included in the graphs.

Figure 3-1. Descriptive diagram of the graphical diet analysis. The X axis represents percent frequency of occurrence (%F) and the Y axis represents the percent abundance (%N) (taken from Costello 1990).



Diets of morphological groupings were compared mathematically and statistically using "R" (R Core Team 2013) with the RInSp package (Zaccarelli et al. 2013). Resource richness and Levins' D index of diversity (Levins 1968) were calculated by first determining the proportions q_j of prey category j in the morph's/population's niche; the formula is expressed as:

$$q_j = \frac{\sum_i n_{ij}}{\sum_{ji} n_{ij}}$$

where n_{ij} is the average proportion for each resource i. Next the degree of each morph's/population's specialization was calculated as:

$$D = 1 - \frac{1}{\sum q_j^2}$$

where q_j is defined as above. For this metric, low D values indicate a large degree of specialization and conversely large D values indicate a more generalized diet.

In addition to these diet metrics, The Total Niche Width (TNW) and both of its components; Within Individual Component and the Between Individual Component (WIC and BIC) were calculated first for the entire collection of ciscoes regardless of location, and then individually for each of the predetermined morphs/populations. Total Niche Width (TNW) was calculated from its two components, the WIC and BIC (Roughgarden 1974; Bolnick et al. 2002) as follows:

$$WIC = \sum_i p_i \left(-\sum_k p_{ik} ln(p_{ik})\right)$$

$$BIC = \sum_k p_i \, ln(p_i) - \sum_k q_k\left(-\sum_i t_{ik} ln(t_{ik})\right)$$

$$TNW = -\sum_k q_k ln(q_k)$$

where p_i is the proportion of all resources used by individual I; q_k is the proportion of the kth resource category in the morph's/population's niche, and t_{ik} is the proportion of the morph's/population's total use of resource k that was used by individual i.

3.2.3.2 Stable Isotopes

The range and mean for δ^{15}N and δ^{13}C was calculated for each morphological grouping and an ANOVA was used to determine if differences existed between the two groups. Next, an ANOVA was used to compare all shallow water groups and all deep water groups independently. Lastly a biplot of δ^{13}C and δ^{15}N values was created to compare the differences between all morphological groups; the two main prey items discovered in the stomach content analysis were included in these plots to help in explaining the depletion and enrichment between morphological groups.

3.2.3.3 Fatty Acids

Eighty fatty acids were identified among all Cisco and prey but only the 14 most informative were retained for further analysis. These 14 fatty acids were used in the analysis because they were the most abundant (>1%) for all groups of Cisco across all locations within Great Bear Lake. The average difference among replicates of fatty acids was 0.02, showing low variability and consistent measures. The 14 fatty acids used in the analysis were C14:0, C16:0, C16:1n7, C18:0, C18:1n9c, 18:1n7, C18:2n6c, C18:3n3, 18:4n3, C20:4n6, 20:4n3, C20:5n3, 22:5n6, C22:6n3. Table 3-3 list the fatty acids used in the analysis and both their unique code for the statistical testing and corresponding biomarker which were taken from various sources in the literature compiled by Chavarie et al. (2014).

Table 3-2. List of fatty acids and their corresponding biomarkers (modified from Chavarie et al. 2014)

Fatty Acid	**Unique code for statistical testing**	**Fatty Acid biomarkers**
C14:0	X1	Pelagic (zooplankton) + diatom
C16:0	X2	Cannibalism or / and carnivorous
C16:1n7	X3	Benthic (bacterial synthesis + diatoms) Cannibalism or/and carnivorous
C18:0	X4	Cannibalism or/and carnivorous
C18:1n9c	X5	Pelagic (Zooplankton)
18:1n7	X6	Benthic (bacterial synthesis + algal)
C18:2n6c	X7	Terrestrial
C18:3n3	X8	Terrestrial
18:4n3	X9	Pelagic (Zooplankton)
C20:4n6	X10	Benthic (diatom)
20:4n3	X11	
C20:5n3	X12	Cannibalism or/and carnivorous
22:5n6	X13	Pelagic (Calanoid copepods diet based)
C22:6n3	X14	Benthic (Pennate diatoms + dinoflagellates + bivalves) Cannibalism

Note: FA biomarker information taken from: Sargent et al. 1995; Brett & M€uller-Navarra 1997; Kattner et al. 1998; Virtue et al. 2000; Budge et al. 2002; Dalsgaard et al. 2003; Iverson et al. 2004; Kakela et al. 2005; Alfaro et al. 2006; Tucker et al. 2008; Ahlgren et al. 2009; Gladyshev et al. 2009; Loseto et al. 2009; Stowasser et al. 2006; Pich_e et al. 2010; Mariash et al. 2011. Compiled by Chavarie et al. 2014.

A discriminant function analysis of the 14 fatty acids biomarkers was run on the complete data set with depth of capture as the factor then a discriminant function analysis was performed on the entire data set with lake arm and depth as a factor using the same 14 biomarkers.

3.3 RESULTS

3.3.1 Stomach Contents

The analysis of the two individual component (%F and %N) indices (Figs. 3-3 and 3-4) generally showed that the shallow water Cisco were predominantly feeding on copepods while the deep water Cisco were more focused on mysids and in some cases daphnia (McTavish and Dease Arm groups). Exceptions to this trend were seen in the Smith shallow group which mainly fed on daphnia (Fig 3-3 panel E) and the McVicar deep group that had a diet more consistent with the other shallow water Cisco, with a predominance of copepods (Fig 3-4 panel B). For the latter it should be noted that that sample size was very low and thus results may not be representative. The average number of prey items (± standard deviation) for the shallow water Cisco (14 ± 2.9) was about double that of those inhabiting deep water (6 ± 2.6). The shallow water Cisco tended to have a higher predominance of littoral and terrestrial organisms in their diets (e.g. adult trichoptera, adult diptera and copepods), whereas the deep water morphs tended to eat dietary items associated with offshore deep pelagic habitat (e.g., *Mysis diluviana*).

Costello's graphs (Fig 3-5) generally reflected the findings from the individual component indices and showed that the diets of the deep water morphological groups are more homogeneous with most individuals specializing on one or two dominant prey items which are being consumed in high abundance. Contrary to the deep water morphological groups, the shallow water morphological groups had a more generalized diet made up of a wider array of diet items which are being consumed in low numbers, however some individuals within each of the morphological groupings seemed to specialize on specific diet items as seen in the Keith, McTavish, and Dease shallow water groups.

Figure 3-2. Bar chart showing the percent frequency of occurrence and percent total number if diet items for the subsample of Cisco captured in the shallow water of each arm of Great Bear Lake

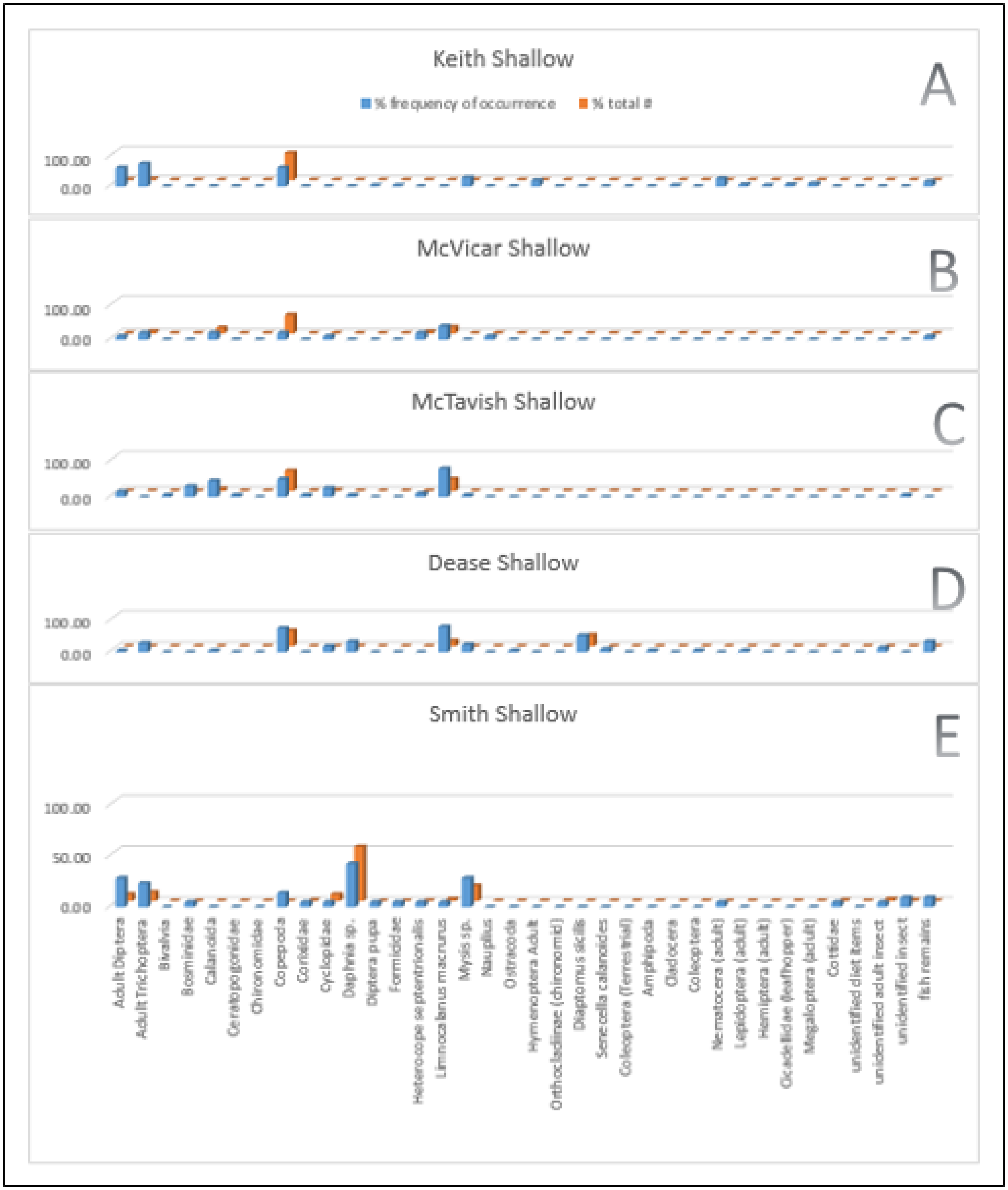


Figure 3-3. Bar chart showing the percent frequency of occurrence and percent total number if diet items for the subsample of Cisco captured in the deep water of each arm of Great Bear Lake

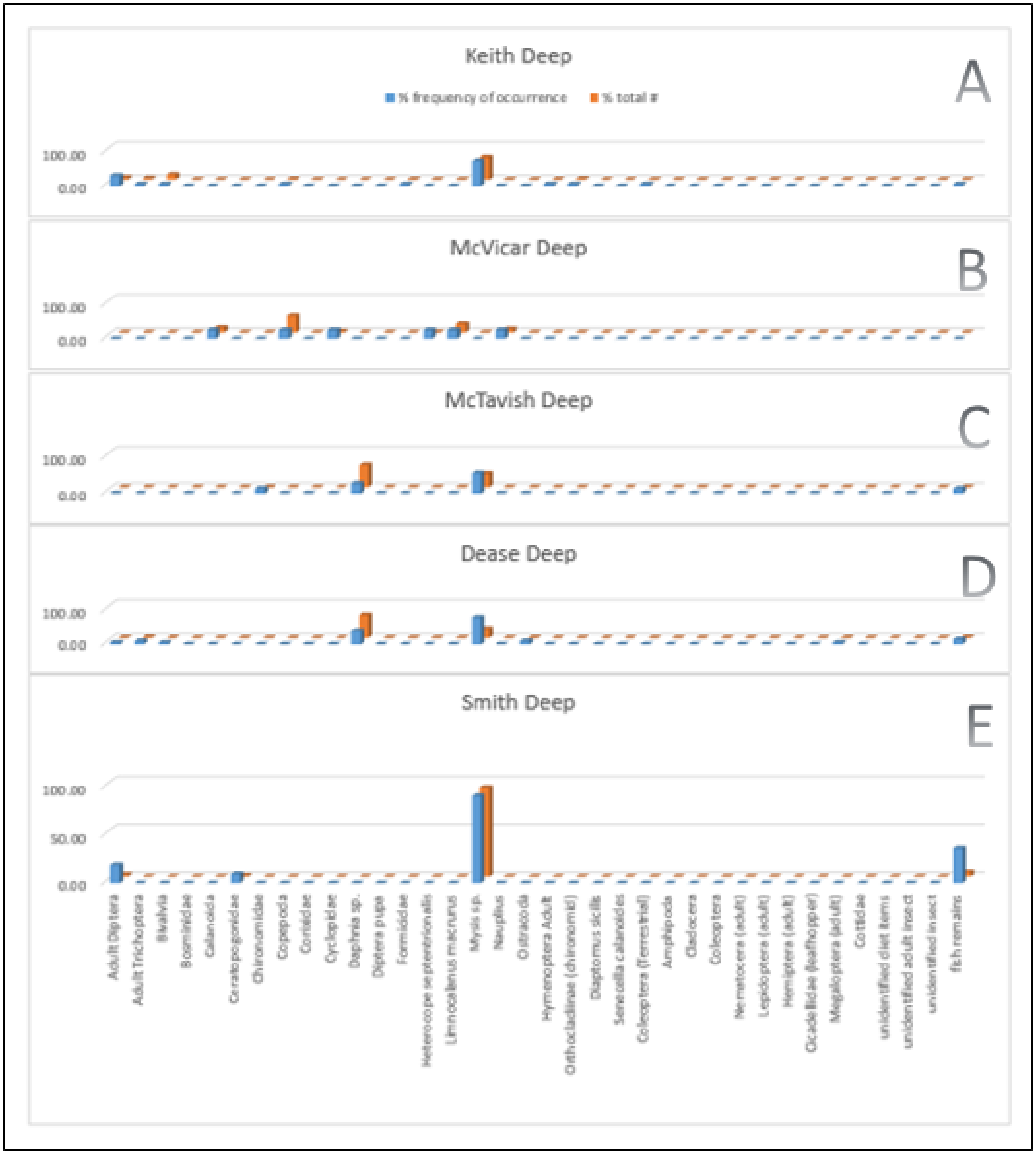
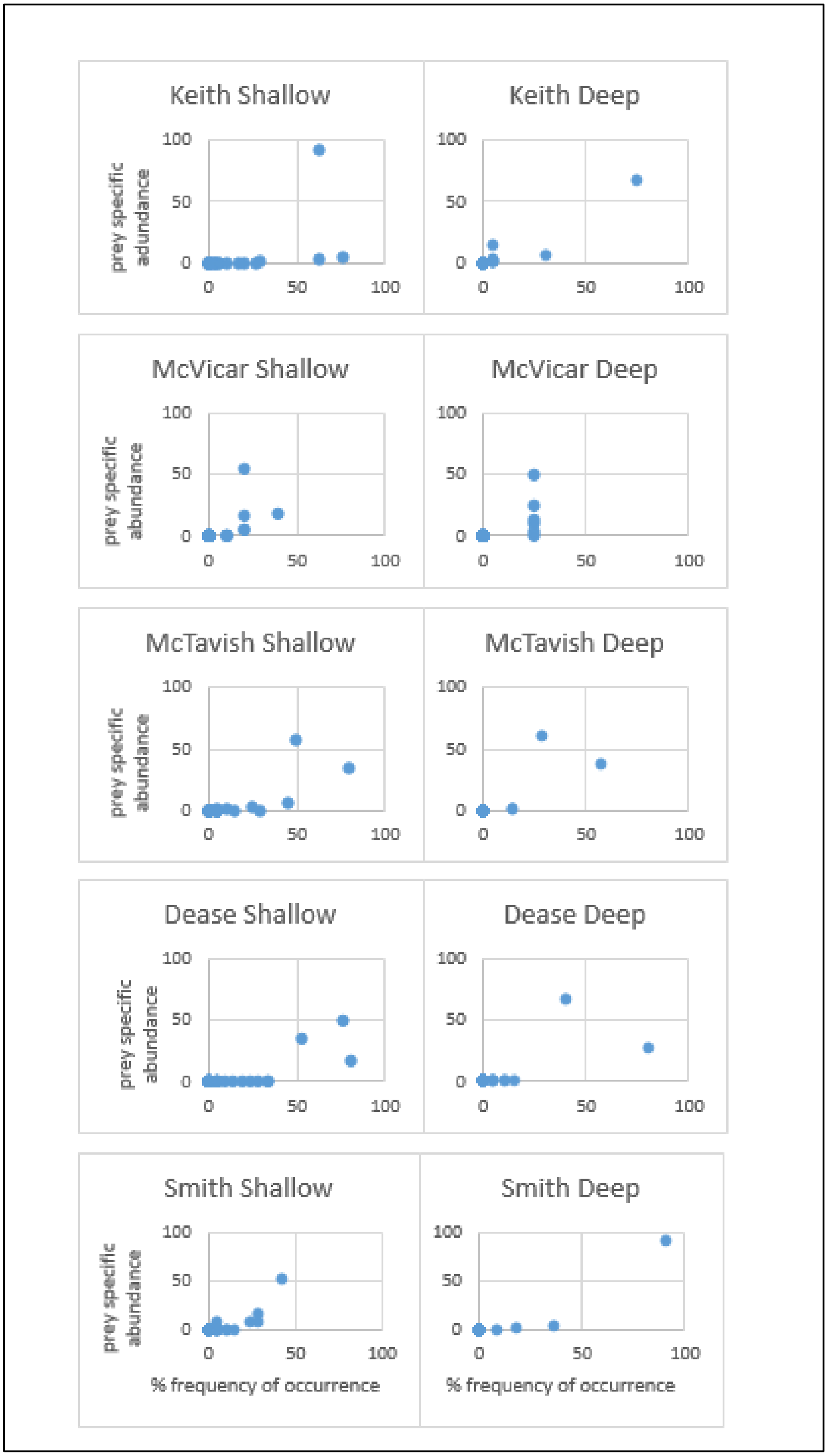


Figure 3-4: Costello graph showing the percent frequency of occurrence and prey specific abundance of diet items for the subsample of Cisco captured in all arms of Great Bear Lake



Results returned from the RInSp R package for population diet showed that resource richness and D values varied among populations (Table 3-3 and 3-4). When morphological groupings were separated by depth of capture shallow water groups were generally found to have higher resource richness and D values (ranging from 9-17 and 3.27-5.45) showing that they are more generalized feeders. An exception was the Dease Arm shallow group which despite the high resource richness (16) had a lower than expected resource D value (2.67) possibly indicating a specialized feeding strategy. Conversely the deep water groups all had lower resource richness and D values (range 4-11 and 1.46-3.01, respectively) showing that these groups have more specialized diets.

Table 3-3. Resource richness and resource D value of each of the shallow water morphological groups in Great Bear Lake.

Morphological Grouping	Resource Richness	Resource D Value
Keith shallow	16	3.37
McVicar shallow	9	4.1
McTavish shallow	13	3.27
Dease shallow	16	2.67
Smith shallow	17	5.45

Table 3-4. Resource richness and resource D value of each of the deep water morphological groups in Great Bear Lake.

Morphological Grouping	Resource Richness	Resource D Value
Keith deep	11	2.0
McVicar deep	6	3.01
McTavish deep	4	2.83
Dease deep	9	2.24
Smith deep	4	1.46

Based on the ratio of the average individual niche (WIC) width to the population niche width (TNW) (Table 3-1) Keith shallow was ranked as the most specialized feeding morphological grouping while the Dease shallow group was the most generalized feeding morphological group. Patterns among populations for this metric resembled those found in the Costello graphs where most of the shallow water groups tended to cluster together with higher ratios indicating more generalized feeding while most of the deep water groups clustered together and had lower ratios, indicating greater specialization. Exceptions are seen with the Keith shallow group which had a higher proportion of specialized individuals in the population and the Dease deep group which was the least specialized among the deep water populations. The overall ratio of WIC/TNW for the entire set of Cisco regardless of morphological grouping shows that Cisco in Great Bear Lake are rather specialized with regards to their feeding strategies.

Table 3-5. The ratio of the average individual niche (WIC) width to the population niche width (TNW) using Roughgarden's 1974 equations for all ciscoes simultaneously and each pre determined morphological grouping separately using the average population diet measure; respective rankings from low to high are also provided.

Location	WIC/TNW	Rank (low to high)	Location	WIC/TNW	Rank (low to high)
All combined	0.3692				
Keith Shallow	0.1582	1	Keith Deep	0.2805	4
McVicar Shallow	0.6681	8	McVicar Deep*	1	10
McTavish Shallow	0.3431	5	McTavish Deep	0.2393	2
Dease Shallow	0.8223	9	Dease Deep	0.3777	6
Smith Shallow	0.3910	7	Smith Deep	0.2530	3

*only one individual evaluated others had no stomach contents or unidentified diet items

3.3.2 Stable Isotopes

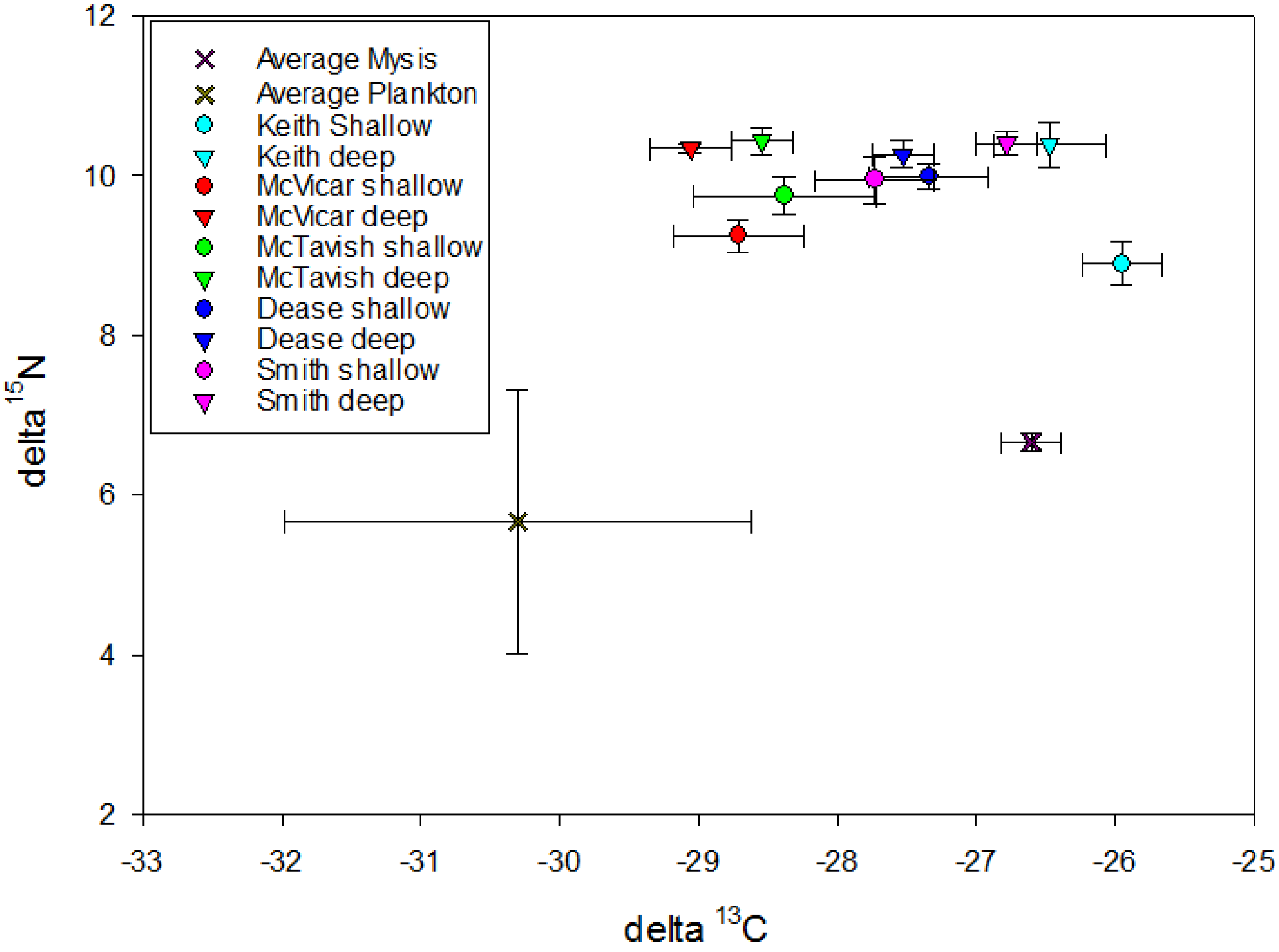
The ranges and mean of δ^{13}C and δ^{15}N for the ten morphological groups of Cisco showed a general trend of deep water Cisco being more enriched in δ^{15}N than their shallow water counterparts (Figure 3-5), suggesting that the deep water Cisco are feeding at a higher trophic level; all comparisons of δ^{15}N, between morphological groups from the same arm were significantly different (Table 3-7). Likewise, all but the Smith Arm groups followed a trend of δ^{13}C depletion in deep relative to shallow water groups within any given arm; however, a significant amount of overlap existed between the respective groups from the same arm (Figure 3-5) and differences were only significant in Keith and Smith Arm groups (Table 3-7). Smith Arm showed the opposite trend to other locations with the shallow water group being more depleted in δ^{13}C than the deep water group (Figure 3-6), but again a large degree of overlap was present. Mysids the main prey in deep water Cisco collected from Great Bear Lake were more enriched in δ^{15}N and less depleted in δ^{13}C than plankton (Figure 3-6).

Comparison between all shallow water groups showed statistical differences among lake arms in both δ^{13}C and δ^{15}N. However, the deep water groups only showed statistical differences in δ^{13}C but not in δ^{15}N (Table 3-7). Among shallow water Cisco, the McVicar group was most depleted of its' δ^{13}C followed by McTavish, Smith, Dease, and lastly the Keith Arm group which was the least depleted. Similar results were found for δ^{15}N of the same groups; the group most enriched in δ^{15}N was from Dease Arm, followed by Smith, McTavish, McVicar and finally the Keith Arm group which was the least enriched in δ^{15}N (Table 3-7). Among the deep water groups, McVicar Arm was most depleted of its' δ^{13}C followed by McTavish, Dease, Smith and lastly Keith Arm which was the least depleted.

Table 3-7. One-way ANOVA results (F statistic, degrees of freedom (df) and P-value) of the comparison between morphological groups found in Great Bear Lake; P-values ≤ 0.05 are considered significant.

	δ^{15}C		δ^{15}N	
Morphological groups	**ANOVA F Statistic**	**P-Value**	**ANOVA F Statistic**	**P-Value**
Keith shallow vs. Keith deep	F= 6.7 df = 1, 49	0.01	F = 84.9, df = 1, 49	<0.001
McVicar shallow vs. McVicar deep	F = 0.49 df = 1, 26	0.49	F = 25.28 df = 1, 26	<0.001
McTavish shallow vs. McTavish deep	F = 0.09 df = 1, 24	0.76	11.5 df = 1, 24	<0.001
Dease shallow vs. Dease deep	F = 0.71 df = 1, 39	0.41	F = 7.31 df = 1, 39	0.01
Smith shallow vs. Smith deep	F = 12.7 df = 1, 33	<0.001	F = 6.86 df = 1, 33	0.01
All shallow groups together	F = 35.62 df = 4, 111	<0.001	F = 23.78 df = 4, 111	<0.001
All deep groups together	F = 26.94 df = 4, 60	<0.001	F = 0.34 df = 4, 60	0.85

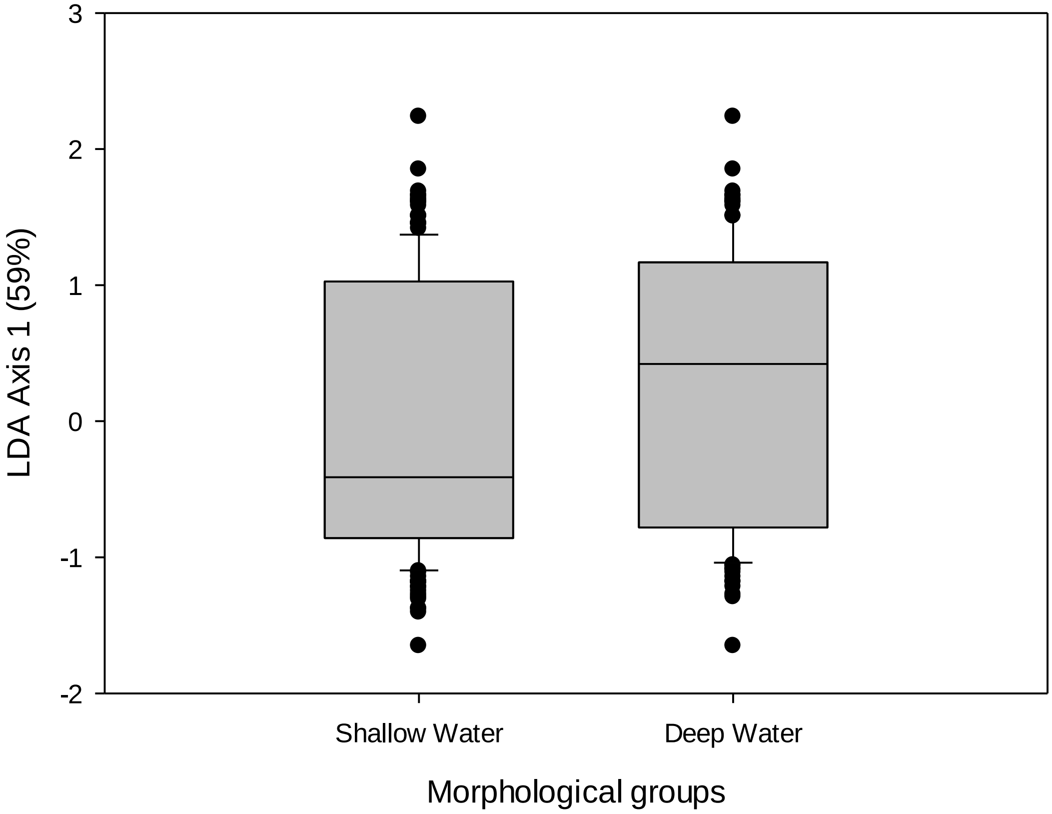
Figure 3-5. Mean and standard deviation of δ^{13}C and δ^{15}N of deep and shallow water groups of Cisco and their respective dominant prey from Great Bear Lake.



3.3.3 Fatty Acids

The discriminant function analysis run on the complete data set with depth of capture as the factor explained 59% of the total variance among groups (Wilks' Lambda = 0.415 and P-value < 0.001), with an overall classification success of 89% (Figure 3-14). Approximately Eight percent of individuals misclassified from the shallow into the deep group and approximately 19 percent of individuals misclassified from the deep to shallow group.

Figure 3-6. Graphical representation of the discriminant function analysis of the fatty acids of the Cisco from Great Bear Lake separated by their depth of capture.

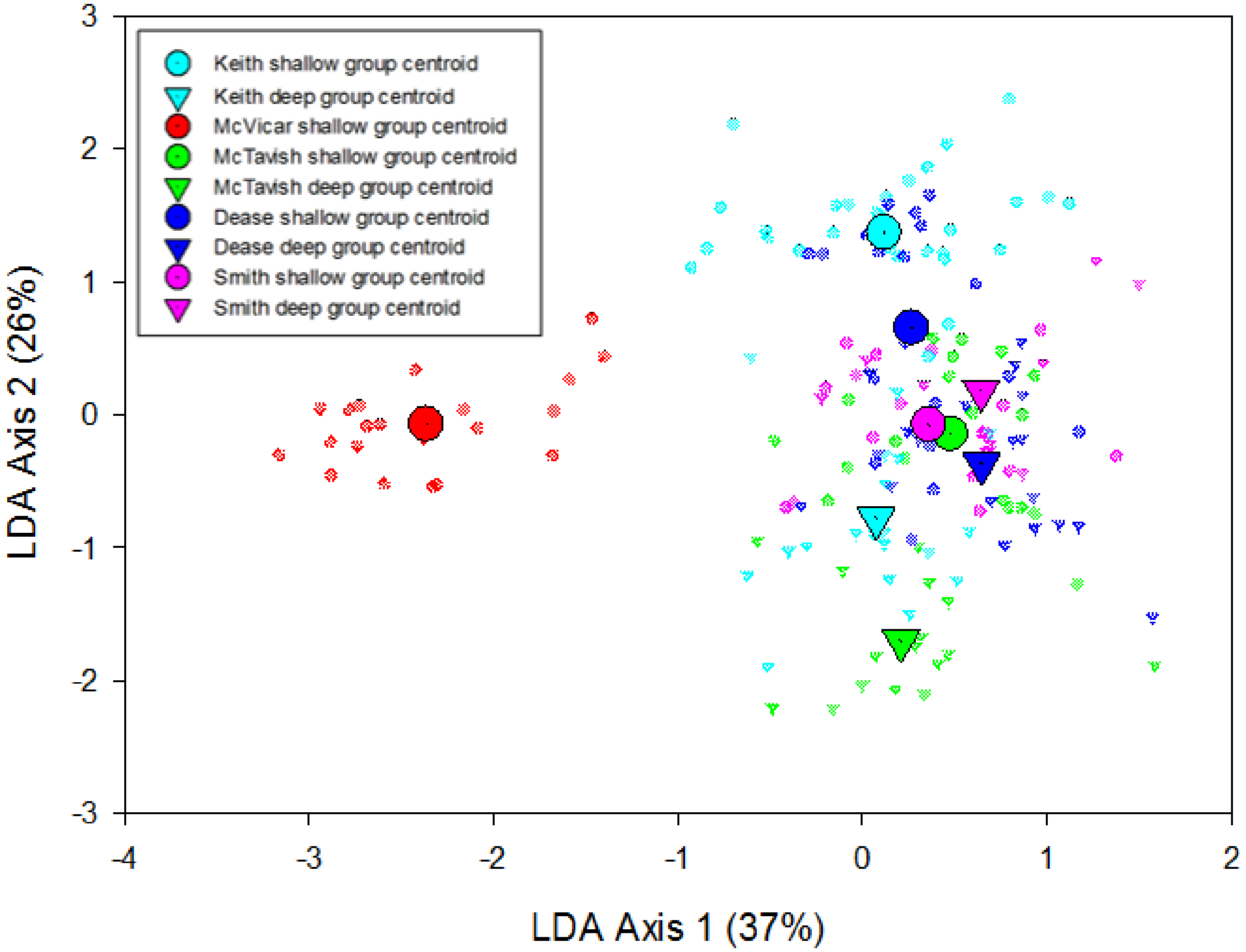


The discriminant function analysis run on the entire data set with lake arm and depth as a factor showed that the total variance explained by the first two axes was 63% (LD1 37%, LD2 26%) (Wilks' Lambda = 0.006 and P-value < 0.001), with an overall classification success of 74%. Axis one appears to divide groups based on feeding strategies (pelagic versus benthic), and axis two shows some separation based on depth of capture and thus again a descriptor of habitat use and associated feeding strategies. Axis one had high positive loadings for fatty acids associated with carnivorous (X2), terrestrial (X8), and benthic feeding (X14), and high negative loadings for fatty acids associated with pelagic (X1), terrestrial (X7), and benthic feeding (X10). Axis two had high positive loadings for fatty acids associated with benthic (X3), terrestrial feeding (X7), and pelagic feeding (X9), and high negative loadings for fatty acids associated with pelagic (X5) and terrestrial feeding (X8) (Table 3-8).

Table 3-8. Discriminant function loadings for the fatty acid analysis of the Cisco of Great Bear Lake

Loadings		
FA Code	Axis 1	Axis 2
X1	-0.35362	-0.3946
X2	1.020919	-0.52608
X3	0.063037	0.931708
X4	-0.13598	0.328688
X5	0.26082	-1.11532
X6	0.204249	-0.29732
X7	-0.34538	0.781265
X8	0.446889	-0.55553
X9	-0.15919	0.452062
X10	-0.30047	-0.25948
X11	0.340163	-0.52774
X12	-0.0586	-0.0422
X13	-0.0262	0.23236
X14	0.384613	-0.18096

Figure 3-7. Graphical representation of the discriminant function analysis of the fatty acids of the Cisco from Great Bear Lake separated by depth and arm of capture.



3.4 DISCUSSION

The results support that at least two different morphological groups, shallow and deep water adapted Cisco, occupy two different ecological niches in Great Bear Lake. The shallow water morphological group is a more generalized feeder taking advantage of all available food sources, as seen by the presence of terrestrial insects along with benthic invertebrates in the stomach content analysis. The deep water morphological group of Cisco appear to be selecting particular food sources such as *Mysis*, but also take advantage of seasonally abundant foods as seen by the presence of terrestrial insects in the stomachs of some of the individuals caught during the summer months.

3.4.1 Stomach Contents

The stomach content analysis revealed that the shallow water groups of Cisco regardless of arm have a more varied diet than the deep water groups, moreover the shallow water groups have a diet which is associated with near shore aquatic habitats. Interestingly, a higher number of terrestrial invertebrates were found in the stomachs of the shallow water groups, having been either blown in; living or dead, from the near shore environments or emerging at the time of consumption. These dietary preferences suggest that the shallow water group spend at least part of their time feeding at or near the surface. These shallow water groups with the exception of Smith Arm all a had a high number of copepods present in their stomachs showing that they are feeding closer to inshore areas of the lake as this is where the highest number of copepods was reported by Johnson (1975). The Smith Arm shallow water group had a higher number and greater frequency of occurrence of Daphnia in their diets which could be a product of capture bias with the majority of individuals (18) being caught in 2011. These fish may have been taking advantage of a temporally abundant food supply or this may be a reflection of actual prey availability in this arm of the lake. The latter hypothesis is supported by the lower gillraker numbers found in this group. This suggests an adaptation towards larger prey; copepods are smaller than Daphnia thus negating the need for smaller particulate filtering during feeding. Further information on zooplankton distribution and abundance in this area of the lake could help shed light on this question.

The deep water groups regardless of arm of capture had a less varied diet than the shallow water groups. The deep water groups all had high numbers of mysids present in their stomachs at the time of capture. These mysids are a vertically migrating prey species (Ahrenstorff et al. 2011) suggesting that the deep water groups are more closely associated with offshore pelagic feeding and is supported by previous studies of plankton distribution by Johnson (1975) who found the greatest *Mysis* density (number per square metre) between 22 and 75 metres. However, it should be noted that some terrestrial invertebrates such as true flies (Diptera) were found in the stomachs of deep water groups showing that ciscoes in general are opportunistic feeders (Janssen 2011). The inclusion of terrestrial prey items in the diet of the deep water groups is also a reflection of the time of year of capture (mid-July to mid-August) and may be an important feeding strategy which is only available during a short seasonal period of time on an annual basis.

These general findings were corroborated by the calculated TNW which was higher for the shallow water group than the deep water group. This is a direct reflection of the more varied diet found in shallow water groups as compared to the deep water groups. It is important to note however that a large degree of overlap does exist across all groups and therefore any further extrapolations should be made with caution.

3.4.2 Stable Isotopes

The findings from stable isotope analyses were consistent with the stomach content results; the shallow water morph's main prey item was copepods and the deep water morph's main prey item was mysids as previously described by Howland et al. (2013), and Trippel and Beamish (1993). The enrichment of δ^{15}N in all deep water groups regardless of lake arm reflects their dietary preference towards Mysids and vice versa for the plankton which is the preferred dietary items of the shallow water groups. Since mysids are higher in δ^{15}N than copepods it was not surprising that the deep water Cisco were more enriched in δ^{15}Ns. All of the deep water morphs had approximately the same enrichment of δ^{15}N regardless of arm of capture showing that the enrichment was in fact due to a dietary intake rather than other possible factors. Mysids were more enriched in δ^{15}N than copepods but were more depleted than Cisco thus accounting for the differences in δ^{15}N between the shallow and deep water groups. Therefore, the deep water groups are feeding at a higher trophic level than the shallow water groups as also noted by Muir et al. (2011) for Great Slave Lake.

Carbon isotopes were more variable across all groups with a large amount of overlap possibly indicating that the depletion of δ^{13}C is a stronger reflection of the inputs from the surrounding terrestrial environments as suggested by Howland et al. (2013). Dease and Smith Arm groupings were closer together which may be related to the fact that they are both receiving inputs from the Southern arctic ecozone. McTavish and McVicar Arms receive inputs from the taiga plains ecozone which likely explains why their δ^{13}C signals were similar. Although Keith Arm also receives inputs from the same ecozone, it did not have similar δ^{13}C values; this could be due to the fact that Keith Arm has the largest inlet of the lake, the Great Bear River which receives inputs from further away and in greater quantity than all other arms and may confound the results of δ^{13}C.

3.4.3 Fatty Acids

The fatty acid results were consistent with other diet results showing that the shallow water morph had a diet with more terrestrial and benthic biomarkers and that the deep water morph had more pelagic and carnivorous biomarkers. The separation of the deep versus shallow morphs suggest that each morph is feeding in a different niche.

The linear discriminant function analysis with both depth and arm as factors mainly separated groups by depth of capture as seen in the high positive loadings on axis two for benthic, terrestrial and pelagic feeding biomarkers. All three of these biomarkers are associated with different feeding strategies of the two different morphological groups of ciscoes (shallow water and deep water) indicating that these groups are opportunistic feeders taking advantage of seasonally abundant prey such as terrestrial invertebrates (Janssen 2011). Similar to the results shown by Chavarie et al. (2014) on lake trout both the shallow and deep water groups of Cisco showed relatively dispersed fatty acid signatures possibly indicating that habitat use is the driver of biomarkers rather than actual prey preference. Axis one did not show any pattern for differentiating between depth of capture but it did show that the McVicar shallow group clustered separately from all others due to the presence of carnivorous and cannibalistic biomarkers; however it is not clear what the reasons are for this.

3.5 CONCLUSION

The results discussed above all show that there are differences between shallow and deep water habitats utilized by Cisco in Great Bear Lake. Moreover, the two distinct morphs occupy different dietary niches as was shown by the stomach content analysis which identified the main prey species of each morph (shallow-copepods and deep-mysids), the stable isotope analyses that showed differences in enrichment of δ^{15}N, and in some cases δ^{13}C (Smith deep water group), for each morph and lastly by the fatty acid analysis showing the different biomarkers from benthic and terrestrial, to pelagic in Cisco from both habitat types. Understanding the differences between these two groups of Cisco will help researchers identify the important links for the nutrient cycling from the deep water areas of the lake to the littoral areas by means of both Cisco morphs (deep water groups acting as vertical drivers of nutrients and shallow water groups acting as horizontal drivers of nutrients) along with key dietary items for this important forage species. Additionally, the new information regarding the distinctiveness of these two groups of Cisco with respect to dietary niches illustrates the flexibility of these fishes in regards to their habitat and associated resource use. These findings will help enable development of conservation strategies at the correct taxonomic level. Moreover, this new information will contribute to understanding diversifying processes that may have taken place in other large lake systems where the deep water community of Cisco has been altered and how this may have affected other biota in these systems.

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CHAPTER 4:

CONCLUSION AND RECOMMENDATIONS FOR THE EVALUATION OF THE CISCO DIVERSITY OF GREAT BEAR LAKE

4.0 DISCUSSION

Cisco in North America have long confused researchers with respect to their taxonomy and functioning in the systems where they are found (Scott and Crossman 1998). This is in part due to their highly plastic morphology and variable life histories (Scott and Crossman 1998). In addition, it has been shown that Cisco play an important role in nutrient cycling from pelagic environments to littoral environments (Muir et al. 2013 and Howland et al. 2013). The aim of this study was to evaluate Cisco diversity of Great Bear Lake using two complementary approaches to better understand their role in this aquatic system; first by analysing the specific morphology of the Cisco captured in Great Bear Lake (chapter 2), and secondly by evaluating their trophic ecology (chapter 3) based on the groups identified in chapter two.

The first goal of the study; analysing the morphology of the Cisco showed, that there are at least two distinct forms and possibly two others. The first morphological group found in Great Bear Lake is the common Cisco which was found in shallow waters (<50 metres) of the lake. The second morphological group, fished from deeper waters of the lake (>50 metres), is possibly a “shortjaw like” Cisco having fewer and shorter gillrakers (Pratt and Mandrak 2007) among other morphological differences. Additionally, a considerable amount of variability among both the shallow and deep water morphological groups was seen between arms of the lake illustrating the highly plastic nature of the Cisco taxonomic group as a whole (Todd and Smith 1980, Pratt 2008, Pratt and Chong 2012, Muir et al 2009, Muir et al. 2013). Moreover, that these two morphs appear to be segregated to some degree by habitation of different depth strata in the lake. A third group was seen in the morphometric analysis which was an intermediate sharing morphological traits from both the shallow and deep water groups. The fourth novel group discovered from the Smith Arm only, did not resemble any of the other morphs. Although found in shallow water, it had fewer gillrakers than its deep water counterparts and greater body depth than all other groups. These traits are typically associated with deep water Cisco (Mandrak et al. 2014).

The second goal of this study was to evaluate and describe the trophic ecology (niche) of the morphological groups determined from the first objective. The evaluation revealed that the two main morphological groups associated with deep and shallow water habitats were in fact occupying separate niches. The niches were separated by diet preference possibly as a consequence of habitat utilisation. Generally, the shallow water groups focused on littoral benthic organisms such as copepods with some seasonal use of terrestrial insects, whereas the deep water groups mainly consumed mysids with seasonal use of some terrestrial insects, indicating that seasonally abundant foods are an important food supply in northern lakes as was shown by Martin (1952), Zimmerman et al. (2007, 2009) and Chavarie (2014) with respect to lake trout. The evaluation of niche separation between the two morphological groups through stable isotope and fatty acid analyses supported the findings from the stomach content analysis. In addition, the variation in isotopic signatures between lake arms suggests that the different inputs around the lake likely have some affect on the signatures found in the Cisco in their respective arms.

The results of this thesis suggest that there is indeed more than a single morph of Cisco inhabiting Great Bear Lake, as suggested by Dymond (1943). Furthermore, the study describes at least two distinct forms, as was hypothesized and shown by Howland et al. (2013). This thesis complements and advances the work of Howland et al. (2013) by exploring the diversity of Cisco in all arms of Great Bear Lake. In particular, the results presented in chapter two demonstrate variability in morphology between arms of the lake. This variability may be the result of different founding populations, a single founding population and subsequent reproductive isolation between arms, phenotypic plasticity, or some combination of these. Although the basis for this variability is unclear, the notion that all Cisco from Great Bear Lake have the same ancestral origin is reinforced by genetic studies such as those from Turgeon and Bernatchez (2001, 2003), Turgeon et al. (2016) and Reed et al. (1998). These authors show evidence that the Parallel Origin Hypothesis (Turgeon et al. 2016) holds true for the Cisco taxonomic group, where different morphs of Cisco in the same lake are more closely related to each other than to their nearest counterpart from another lake. Regardless of the reasons for divergence, niche separation among Cisco populations in Great Bear Lake could be facilitated or maintained through competition for resources, as is explained by competition theory (Roughgarden 1983).

Chapter two of this thesis also showed novel results with respect to a Cisco group from Smith Arm not resembling the morphology of any other group in the analysis. Furthermore, both shallow and deep groups from this area of the lake showed differences from all other groups evaluated in the thesis. The shallow water group appeared to have a distinctive diet (mainly Daphnia) from all other groups in the study, and the morphology of the Smith Arm groups did not resemble any other group in the study (low gill raker counts). These two distinctive groups did, however, prove to be similar in some ways (shallow water group had similar morphology to other shallow water groups and the deep water group had similar feeding preferences). Further research will be required to better understand the nature of these unique characteristics..

4.1 RECOMMENDATIONS

Continued research on Cisco diversity of Great Bear Lake should attempt to determine if a Cisco presence is found in the centre area of the lake. Sampling at the deeper, more homogenous areas of the lake could shed light on the finer mechanisms of evolution at work in the evolution of the shortjaw-like form of Cisco within the lake. Moreover, future research on Cisco diversity of Great Bear Lake should include a more complete assessment (stable isotopes, and fatty acids) of the dietary items found in the stomachs of ciscoes across the lake. A more thorough evaluation of the food web could help to determine special linkages between predator and prey that are likely at the foundation of the Cisco diversity of Great Bear Lake. More investigative work at the terrestrial level around the lake could also help to determine the nutrient loading found within the lake, to aid in understanding of carbon isotopic signatures for which no real answers could be determined in this evaluation. Additionally, sampling at different times of year would potentially determine additional life history characteristics of Cisco (e.g. overall diet and habitat use). Special attention should be given to the Cisco in Smith Arm - more research is needed to determine why these Cisco are different from the rest of the Cisco in the lake. Lastly, a comprehensive genetic analysis to complement these morphological findings could also help shed light on the origin of diversity and mechanisms that are maintaining it in this complex group of Cisco

The work presented here expands on the knowledge base of the Cisco complex by identifying another ‘Shortjaw-like’ Cisco occupying the deeper areas of Great Bear Lake regardless of arm. This information will allow managers to apply the designatable unit strategy

(DFO 2013) to the conservation of this unique stock along with its other counterparts around the lake. Additionally, long term monitoring of Cisco diversity in Great Bear Lake would allow managers to make informed decisions about the full ecosystem from a bottom up perspective and help to better identify important linkages in possible rehabilitation efforts in other large deep lakes where Cisco diversity has been altered.

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