

Fall 2014

# The decline of cisco *Coregonus artedii* at its southern range extent: Stock biology and management implications

Andrew E. Honsey  
*Purdue University*

Follow this and additional works at: [https://docs.lib.purdue.edu/open\\_access\\_theses](https://docs.lib.purdue.edu/open_access_theses)



Part of the [Terrestrial and Aquatic Ecology Commons](#)

---

## Recommended Citation

Honsey, Andrew E., "The decline of cisco *Coregonus artedii* at its southern range extent: Stock biology and management implications" (2014). *Open Access Theses*. 337.  
[https://docs.lib.purdue.edu/open\\_access\\_theses/337](https://docs.lib.purdue.edu/open_access_theses/337)

This document has been made available through Purdue e-Pubs, a service of the Purdue University Libraries. Please contact [epubs@purdue.edu](mailto:epubs@purdue.edu) for additional information.

**PURDUE UNIVERSITY  
GRADUATE SCHOOL  
Thesis/Dissertation Acceptance**

This is to certify that the thesis/dissertation prepared

By Andrew E Honsey

Entitled

The decline of cisco Coregonus artedi at its southern range extent: Stock biology and management implications

For the degree of Master of Science



Is approved by the final examining committee:

Tomas O. Hook

Steven B. Donabauer

J. Andrew DeWoody

To the best of my knowledge and as understood by the student in the Thesis/Dissertation Agreement, Publication Delay, and Certification/Disclaimer (Graduate School Form 32), this thesis/dissertation adheres to the provisions of Purdue University's "Policy on Integrity in Research" and the use of copyrighted material.

Tomas O. Hook

Approved by Major Professor(s): \_\_\_\_\_

Approved by: Robert K. Swihart

08/13/2013

Head of the Department Graduate Program

Date

THE DECLINE OF CISCO *COREGONUS ARTEDI* AT ITS SOUTHERN RANGE  
EXTENT: STOCK BIOLOGY AND MANAGEMENT IMPLICATIONS

A Thesis

Submitted to the Faculty

of

Purdue University

by

Andrew Edgar Honsey

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

December 2014

Purdue University

West Lafayette, Indiana

## ACKNOWLEDGEMENTS

I am greatly indebted to the following people, without any of which I wouldn't be who or where I am today.

To my advisor, Dr. Tomas Höök: Your constant advice, guidance, and support have provided a firm foundation for my future as a fisheries ecologist. Thank you for sharing your knowledge with me and for injecting the sometimes-discouraging life of a graduate student with a little humor now and again.

To my committee members, Dr. Andrew DeWoody and Mr. Steven Donabauer: Your expertise, encouragement, and willingness to dedicate large portions of your time to helping me in my efforts have proven invaluable. I thank you and I hope that we will continue to work together in the future.

To Scott Hanshue, Mike Porto, Tyler Delauder, and all members of the MI-DNR and IN-DNR crews which sampled ciscoes: Your hard work in the field and the lab, your insight, and your willingness to work with me were absolutely instrumental to this project. I've greatly enjoyed working with you all, and I thank you for your efforts.

To the past and current members of the Höök lab: Thank you for putting up with me despite my antics, and for always reminding me of how little I know. Most of all, thank you for being my friends.

To my family and friends: Thank you for your unending support as I pursue my goals and for always reminding me of the important things in life. I am truly lucky to have been blessed with you all in my life.

Finally, to my beautiful fiancée, Diana: Thank you for encouraging me, for supporting me, for going along with me as I continue to study fish and stuff. Thank you for sticking with me despite my flaws, and for giving me a reason to better myself every day. I can't wait to spend the rest of my life catching speckled bass with you.

## TABLE OF CONTENTS

	Page
ABSTRACT.....	vi
CHAPTER 1. STOCK BIOLOGY OF THE DECLINING CISCO ( <i>COREGONUS</i> <i>ARTEDI</i> ) AT THE SOUTHERN EXTENT OF ITS RANGE.....	1
1.1 Introduction.....	1
1.2 Methods.....	4
1.2.1 Field Collection.....	4
1.2.2 Processing and Analysis.....	6
1.2.3 Genetic Analysis.....	9
1.2.3.1 Tissue Digestion and DNA Extraction.....	9
1.2.3.2 Mitochondrial DNA Amplification and Sequencing.....	10
1.2.3.3 Microsatellite DNA Amplification, Genotyping, and Analysis.....	11
1.3 Results.....	12
1.3.1 Stock Characteristics.....	12
1.3.2 Genetic Analysis.....	14
1.4 Discussion.....	15
1.5 References.....	26
1.6 Tables.....	35
1.7 List of Figure Captions.....	42
1.8 Figures.....	44
1.9 Supplementary Material.....	50
CHAPTER 2. AN ANALYSIS OF LAKE MORPHOMETRIC AND LAND-USE CHARACTERISTICS THAT PROMOTE THE SURVIVAL OF CISCO ( <i>COREGONUS</i> <i>ARTEDI</i> ) IN INDIANA.....	53
2.1 Introduction.....	53

	Page
2.2	Methods..... 55
2.2.1	Data Collection.....55
2.2.2	Data Analysis .....56
2.2.2.1	Overview ..... 56
2.2.2.2	Model Descriptions..... 57
2.2.2.3	Synthesis..... 58
2.3	Results and Discussion..... 60
2.4	References ..... 66
2.5	Tables ..... 70
2.6	List of Figure Captions..... 73
2.7	Figures..... 75
2.8	Supplementary Material ..... 79
VITA.....	88

## ABSTRACT

Honsey, Andrew E. M.S., Purdue University, December 2014. The decline of cisco *Coregonus artedi* at its southern range extent: Stock biology and management implications. Major Professor: Tomas O. Höök.

The cisco *Coregonus artedi* is distributed throughout northern North America and is relegated to coldwater, oligotrophic systems. Populations of cisco located at the species' southern range extent, including northern Indiana and southern Michigan, have drastically declined over the past century, seemingly due to a combination of climate warming and exacerbation of hypolimnetic hypoxic conditions *via* intensive land-use and resulting increases in nutrient loading. Apart from their decline, information on southern ciscoes is lacking, including basic stock demography and genetic variability. Such information may shed light on the likely sustainability (or lack thereof) of remaining populations. The first portion of this study aimed to (1) establish a baseline understanding of the stock biology of southern cisco populations, (2) assess the potential risk of extirpation among populations via assessments of stock biology and an analysis of intra-population genetic variation, and (3) explore the population history of southern ciscoes and assess their viability for conservation usage by examining inter-population genetic variation. Results indicate that southern cisco populations exhibit relatively consistent recruitment success and generally balanced sex ratios, indicating relatively healthy populations. However, the narrow size distributions exhibited in most lakes and the

skewed sex ratios seen in some lakes may indicate sampling biases or the potential vulnerability of larger ciscoes and females to mortality events. An analysis of mitochondrial DNA sequences suggested that variation both within and among cisco populations is low; furthermore, this low variation may be exacerbated by selective mortality events. In contrast, microsatellite genetic analyses showed higher intra-population variation and suggest that all southern populations are genetically distinct. Taken in concert, these results indicate that the Crooked/Little Crooked and Indiana lakes populations are among the most sustainable, while the population in Eve Lake may be among the most likely to become extirpated.

While biotic factors influence population sustainability, the viability of southern ciscoes may depend heavily on abiotic factors due to their strict environmental (e.g., oxythermal) tolerances. The second portion of this study focused on analyzing lake morphometric and land-use characteristics in Indiana lakes which support cisco, versus lakes where cisco have been extirpated or never existed. In general, larger, deeper lakes were found to be more likely to have contained cisco (either currently or in the past). However, smaller lakes with larger ratios of lake area to total catchment area (i.e., headwater lakes) were more likely to contain current cisco populations than larger lakes. These results highlight the importance of minimizing nutrient loading, particularly from land-use practices, in preserving cisco populations.

## CHAPTER 1. STOCK BIOLOGY OF THE DECLINING CISCO (*COREGONUS ARTEDI*) AT THE SOUTHERN EXTENT OF ITS RANGE

### 1.1 Introduction

Ciscoes or lake herring *Coregonus artedi* are widely distributed throughout northern North America (Dymond 1933; Latta 1995; Scott and Crossman 1998), where they are considered sensitive environmental indicators (Latta 1995; Jacobson et al. 2008; Sharma et al. 2011). Due to their strict requirements for cold water and high dissolved oxygen (DO) concentrations (Frey 1955; Jacobson et al. 2008), at the southern extent of their natural range (e.g., northern Indiana and southern Michigan; Colby and Brooke 1969; Turgeon and Bernatchez 2001, 2003) ciscoes are relegated to the most oligotrophic lakes (Latta 1995; Pearson 2001).

Across the southern range extent of cisco, intensive land-use within glacial lake catchments and resulting nutrient loading have exacerbated hypolimnetic hypoxic (low DO) conditions within many lakes. In turn, the interactive effects of warm water temperatures and hypolimnetic hypoxia have contributed to numerous mortality events and even local extirpations of ciscoes over the past century (Colby and Brooke 1969; Crisman 1993; Koza 1994; Pearson 2001; Steven Donabauer, IN-DNR, personal communication). For example, the number of lakes containing ciscoes in Indiana has precipitously declined from 45 in the 1900s to 42 in the 1950s, 24 in 1975, 15 in 1994, 13

in 2001, and 7 in 2012-3 (Fig. 1.1, inset; Table S1.2). The potential for additional warming (IPCC 2014) and water quality degradation places southern cisco populations at risk of continued decline and regional extinction.

In addition to risk owing to their strict environmental tolerances, the extinction risk of southern ciscoes may be elevated due to inconsistent annual recruitment (population-level reproductive success) patterns. Ciscoes have been shown to recruit in a “boom-and-bust” fashion, with a narrow range of age classes comprising large proportions of the population (Selgeby 1985; Cox and Kitchell 2004; Rook et al. 2012). These “boom-and-bust” patterns in cisco recruitment can be synchronized over broad spatial scales (~260 km in Lake Superior; Rook et al. 2012) presumably due to climatic factors driving interannual variation of recruitment success (i.e., the Moran effect; Moran 1953). The presence of few age classes, some of which may be more environmentally sensitive than others (i.e., as temperature and oxygen tolerances of cisco vary with size and age; Fry 1937; Kennedy 1941; Edsall and Colby 1970), may limit the potential for southern cisco populations to survive frequent periods of oxythermal stress. In addition, the potential for similar age class representation among populations (i.e., recruitment synchrony) may increase the risk of multiple population extirpations over a short period of time (e.g., given an environmentally extreme scenario).

Low genetic variation within populations may exacerbate extinction risk due to limited variation among individuals, thus increasing the risk of population declines given changes in biotic or abiotic conditions (*i.e.*, low evolutionary potential; Frankham 2005). Conversely, population persistence is generally positively related to genetic variation (Allendorf and Leary 1986; Milligan et al. 1994). A previous study (St. John-Pikel, IPFW

thesis, 1999) examined genetic variation within one southern cisco population (Crooked Lake, IN) and concluded that the population displayed a level of variation similar to those seen in other North American coregonid populations. However, intra-population genetic variation has yet to be evaluated for most southern cisco populations.

Although the threats of warming and habitat degradation paint a bleak picture for the future of southern ciscoes, efforts to preserve these populations are critical not only because cisco presence indicates pristine coldwater habitat and water quality, but also because southern ciscoes may be locally adapted to live in warmer, more productive systems compared to those inhabited by more northern populations. Thus, these populations may be of interest for conservation purposes, particularly given the threat of climate change to more northern populations (i.e., southern cisco stocking may augment more northern populations as climate warming continues). However, a thorough knowledge of among-population genetic variation is critical when considering peripheral populations for conservation purposes (Volis et al. 2014). Furthermore, by examining patterns of genetic variation across watersheds, knowledge of genetic variation among populations may help to elucidate the origin of southern ciscoes (i.e., whether they are likely native or stocked, which, at present, remains unknown for cisco in Indiana; Steven Donabauer, IN-DNR, personal communication), and may therefore augment the understanding of their utility in the context of conservation.

Very little is known about southern cisco populations, apart from their rapid decline. In order to preserve their existence, thereby preserving biodiversity and a potentially unique conservation resource, we must first understand the biology and origin of these populations. The objectives of this study, therefore, are to (1) establish a baseline

understanding of the stock biology of southern ciscoes by examining length and age distributions, sex ratios, condition, and diets among populations, (2) assess the potential risk of extirpation among populations *via* assessments of stock biology and an analysis of intra-population genetic variation, and (3) investigate the population history of southern ciscoes and assess their viability for conservation usage by examining inter-population genetic variation.

## 1.2 Methods

### 1.2.1 Field Collection

Ciscoes were collected in September, 2012 from six lakes (Crooked, Eve, Failing, Gage, Indiana, South Twin) in northern Indiana by the Indiana Department of Natural Resources (IN-DNR; Fig. 1.1) using experimental gill nets (76.2 m long  $\times$  1.8 m deep; 1.9, 2.5, 3.2, and 3.8 cm bar mesh panels) set overnight targeting the “cisco layer” (i.e., the depth layer with overlap of suitable thermal [ $\leq 20^{\circ}\text{C}$ ] and DO [ $\geq 3$  ppm  $\text{O}_2$ ] conditions, Frey 1955; Steven Donabauer, IN-DNR, personal communication). Spatial locations and depths of each net were recorded using a handheld global positioning system (GPS) device (Garmin GPSmap 76Cx) and a portable depthfinder (Eagle Fish Mark 320), respectively (Table 1.1). Sampling was conducted with the goal of catching 50-100 ciscoes per lake. To this end, a minimum of three gill nets were set per study lake per sampling day, with a limit of 10 total net lifts per lake (to limit excess by-catch mortality). The vast majority of ciscoes were dead when collected; however, three fish from Failing Lake and 22 fish from Indiana Lake were alive when sampled and

subsequently released, given the sample size goal had already been met (Table 1.2). All collected ciscoes were placed on ice in the field and taken to the nearest IN-DNR facility, where they were frozen at  $-20^{\circ}\text{C}$  until they could be transported on ice to Purdue University for processing and analysis.

Due to inadequate sample sizes ( $\ll 50$  ciscoes) from Crooked Lake during September, 2012, additional sampling was conducted on Crooked Lake during November, 2012. Two experimental gill nets (described above) were set on the afternoon of 26 November 2012 in the shallow northwest bay, targeted at spawning ciscoes (Tables 1.1, 1.2). These nets were lifted hourly for 4 hours in anticipation of catching large numbers of ciscoes. In addition, one experimental gill net was set overnight from 26-27 November 2012 in an attempt to meet the sample size goal.

An oxythermal mortality event that occurred on Little Crooked Lake (Whitley Co., connected to Crooked Lake and considered the same cisco population) in July, 2012 afforded an opportunity for cisco collection without increased mortality. A total of 104 dead and dying ciscoes were collected along the shoreline using dip nets by IN-DNR field technicians (Table 1.2).

In addition to collections in Indiana, cisco were sampled on 10-11 December 2012 from Howard Lake (Kalamazoo Co.) by the Michigan Department of Natural Resources (MI-DNR) using three experimental gill nets (38.1 m long  $\times$  1.8 m deep; 3.8, 5.1, 6.4, 7.6, and 10.2 cm mesh panels) set overnight and targeted at the “cisco layer” (Frey 1955; Tables 1.1, 1.2, Fig. 1.1; Scott Hanshue, MI-DNR, personal communication). Ciscoes were placed on ice in the field and transported to the MI-DNR Plainwell Operations Service Center for processing, which included recording measurements of

total length (TL; mm) and wet weight (g), inspecting gonads to determine sex, removing scales from the region between the dorsal fin and lateral line for ageing, and removing pectoral fins (stored in ~30 ml 95% EtOH) for genetic analysis. Scales and fins were kept at room temperature until they were transported to Purdue University for analysis.

### 1.2.2 Processing and Analysis

In the laboratory, measurements of TL (mm), standard length (SL; mm), and wet weight (g) were recorded for ciscoes collected by IN-DNR. Separate regressions of SL vs. TL were constructed for each sampling location in order to estimate TL for individuals with damaged caudal fins. In addition, gonads were inspected to determine sex, digestive tracts were removed and frozen at -20 °C for diet analysis, scales were removed from the region between the dorsal fin and lateral line for ageing, and adipose fins from 20 randomly-selected fish from each sampling location were removed and stored in ~25 ml 95% EtOH for genetic analysis.

Data from a total of 611 ciscoes (including those processed by MI-DNR) were included in the analysis (Tables 1.1, 1.2); however, in some cases, lack of specimen quality (i.e., due to degradation, net damage, decomposition, etc.) prevented complete data collection (Figs. 1.2-1.3). Despite occasionally poor specimen quality, genetic samples (i.e., fin clips) were successfully collected from 20 randomly-selected fish from each sampling location.

In order to characterize population age structures and explore the potential for infrequent recruitment success and recruitment synchrony among southern cisco

populations, all ciscoes collected were aged *via* scales. Approximately 4-10 scales from each individual were pressed between two acetate slides at 82-93 °C using 5-8 t of pressure for 6-10 s (Carver Laboratory Press, Model C, Series 27000-190). The impressed acetate slides were then placed in a slide projector (Bell and Howell MT-612), and images of the projected slide were taken using a digital camera (Canon PowerShot SD1200 IS). In an attempt to reduce bias in age estimation, three readers (1) convened to establish criteria for identifying annuli (using a random sample of scales for reference), (2) estimated ages for each individual independently, and (3) re-convened to resolve discrepancies in age estimates. Annuli were identified based on the presence of “cross-over” patterns among circuli throughout the scale. Although scale ages can be less accurate than ages estimated using other structures (e.g., otoliths; Schreiner and Schram 2000), inaccuracies are typically most pronounced in old (i.e., approximately  $\geq 10$  years old) ciscoes (Fig. 15 in Ebener et al. 2008). Given the prominence of younger ciscoes and the relatively high agreement in age estimates among readers in the present study, the scale ageing methodology used is likely adequate for characterizing age structures within and exploring the potential for recruitment synchrony among southern cisco populations. Moreover, age estimations were in majority agreement (i.e., at least two out of the three readers agreed on the age of a given individual) for 91% of individuals after independent estimation. Additionally, in 77% of the cases in which all three readers disagreed, estimates differed by  $\leq 2$  years across readers. After consensus ages were reached, pairwise chi-squared tests for homogeneity were used to assess differences in age distributions among populations. This and all subsequent statistical analyses were performed using R version 3.0.2 (R Core Team, 2013).

Sex ratios, which can affect recruitment success (Bunnell et al. 2006), inbreeding (Maynard Smith and Stenseth 1978), and ultimately population sustainability, were compared among populations using pairwise chi-squared tests for homogeneity. In addition, two-tailed, one sample t-tests were used to examine the potential skew of sex ratios within populations using sex data from identifiable, mature fish (i.e., identified as male or female) and compared to a hypothetical mean sex ratio of 50% male and 50% female. Specimens which were too damaged to determine sex were classified as “unknown” and were not included in either analysis.

Individual relative weight ( $W_r$ ), an index of body condition which is correlated with growth (Murphy et al. 1991), was calculated and compared within and among populations using the equation

$$(2) \quad W_r = \left(\frac{W}{W_s}\right) * 100$$

where  $W$  is individual fish weight and  $W_s$  is the length-specific standard weight predicted by a length-weight regression constructed to represent the species as a whole. The standard weight equation ( $\log_{10}W_s = -5.517 + 3.224\log_{10}TL$ ) was taken from Fisher and Fielder (1998).

In order to assess differences in  $W_r$  among populations, an analysis of variance (ANOVA) was conducted in a Bayesian framework (Markov chain Monte Carlo settings: 4 chains, 10,000 total iterations, 2,000 burn-in iterations, thinning rate of 10). Derived parameters were used to estimate significant differences among groups (i.e., using 95% credible intervals; Kruschke 2011).

Analyses of diet contents may help to describe niche occupancy, explain differences in stock characteristics (e.g., condition, length distributions, etc.) among populations, and establish a basic understanding of the trophic interactions of southern ciscoes. To quantify diets of Indiana ciscoes, digestive tracts were selected at random from 20 individuals taken from each of four lakes (Crooked, Eve, Failing, Indiana). Diet contents from the esophagus to the end of the stomach were removed and weighed. If necessary, diets were subsampled by diluting the diet to a total volume of 10 ml, mixing, and collecting 2 ml (i.e., 20%) of the diluted diet for analysis. Diet items were identified and enumerated using a dissecting microscope (Unitron Z850). Photos of up to 20 specimens of each prey type were taken with a scope-mounted camera (MicroMetrics 318 CU), and prey items were measured using ImageJ software (Schneider 2012). Diet contents were dried in a 70°C oven for 48-72 hours and weighed to determine diet dry mass. Relative prey-specific biomass was calculated using published length-mass relationships (Dumont *et al.* 1975; Dumont and Balvay 1979; Culver *et al.* 1985; Benke *et al.* 1999) and accounting for relative prey abundance.

### 1.2.3 Genetic Analysis

#### 1.2.3.1 Tissue Digestion and DNA Extraction

Small tissue samples (approximately 1-2 mm in diameter) were clipped from each of the 20 randomly-selected fins per lake (stored in 95% EtOH; see above) and digested in a solution of 440 µl SNET (20 mM Tris·Cl, 5 mM EDTA, 400 mM NaCl, 1% (w/v) SDS) and 60 µg proteinase K at 55 °C for 12-15 hours, with agitation. DNA was

extracted using the classic phenol-chloroform protocol and precipitated with ethanol (Sambrook et al. 1989).

### 1.2.3.2 Mitochondrial DNA Amplification and Sequencing

A ~1.2 kb fragment within the mitochondrial control (D-loop) region was amplified using the HN20/LN20 primers described by Bernatchez and Danzmann (1993). Amplifications and all subsequent thermal cycling reactions were performed using Eppendorf Mastercycler EP Gradient instruments (Eppendorf AG). Reactions (total volume = 20  $\mu$ l) consisted of approximately 20-100 ng of template DNA, 1  $\mu$ M of each primer, 2  $\mu$ l of 10x buffer (100 mM Tris, 500 mM KCl, 0.5 mg/ml BSA; pH = 8.9), 200 nM of each dNTP, 1.5  $\mu$ M of MgCl<sub>2</sub>, and 0.4 units of NEB *Taq* polymerase. Polymerase chain reaction (PCR) cycles were as follows: an initial denaturation for 2 min at 95 °C followed by 35 cycles of denaturation (30 s at 95 °C), (annealing) 1 min at 55 °C, and (extension) 1 min at 72 °C with a final extension of 5 min at 72 °C. PCR products were purified using a low sodium acetate precipitation in preparation for sequencing reactions.

A 488 bp segment within the amplified region was sequenced using H2/LN20 primers (Bernatchez and Danzmann 1993). Samples were sequenced using BigDye Terminator v3.1 chemistry (Applied Biosystems; AB) in a total reaction volume of 10  $\mu$ l (2.5  $\mu$ l AB buffer, 1.5  $\mu$ l BigDye v3.1, 5  $\mu$ l cleaned PCR product, 1  $\mu$ M primer). Cycle settings were as follows: an initial denaturation of 1 min at 96 °C followed by 25 cycles of 10 s at 96 °C, 5 s at 50 °C, and 4 min at 60 °C. Sequencing reactions were purified using a low sodium acetate precipitation before electrophoresis using a Prism 3730XL

sequencer (AB). Sequences were aligned and edited using Sequencher 5.0 (Gene Codes Co.) and a haplotype network diagram was constructed using TCS 1.21 (Clement et al. 2000).

### 1.2.3.3 Microsatellite DNA Amplification, Genotyping, and Analysis

In addition to mtDNA sequencing, individuals were genotyped at three nuclear microsatellite loci (Cisco-157, Cisco-181, and Cisco-200) developed by Turgeon et al. (1999). Cisco-157 and Cisco-181 reactions required 0.975  $\mu\text{M}$   $\text{MgCl}_2$ , whereas Cisco-200 reactions used 1.5  $\mu\text{M}$   $\text{MgCl}_2$ . Remaining reactants were equivalent among reactions and consisted of approximately 20-100 ng of template DNA, 0.5  $\mu\text{M}$  of each primer, 2.5  $\mu\text{l}$  of 10x buffer, 200 nM of dNTPs, and 0.4 units of NEB *Taq* polymerase. Thermal cycler settings for all microsatellite reactions were as follows: an initial denaturation of 3 min at 95 °C followed by 5 3-step cycles of 45 s at 95°C, 40 s at 59°C, and 40 s at 72°C, 25 3-step cycles of 30 s at 95°C, 40 s at 59 °C, and 40 s at 72 °C, and a final extension for 2 min at 72°C. Fluorescence was determined with a Prism 3730XL instrument (AB) and alleles were scored using GeneMapper 5.0 (AB).

To assess genetic variation of ciscoes within and among sampling locations,  $F_{IS}$  and  $F_{ST}$  values were calculated and AMOVA tests were conducted using GenAlEx 6.5 (Peakall and Smouse 2006, 2012). In addition, *STRUCTURE* 2.3.4 (Pritchard et al. 2000; Falush et al. 2003, 2007; Hubisz et al. 2009) was used to estimate the number of genetically distinct populations among sampling locations. Model parameters were conservative (200,000 total iterations; 100,000 burn-in iterations assuming admixture and

correlated allele frequencies), and five independent models were run at  $k = 1-10$  ( $n = 50$  model runs).

### 1.3 Results

#### 1.3.1 Stock Characteristics

Total lengths (TL) of cisco ranged from 175 to 443 mm and median TL ranged from 219 to 412 mm among lakes, with the smallest and largest fish occurring in South Twin and Gage lakes, respectively (Fig. 1.2). Ages were estimated for 606 individual ciscoes [mean = 76 per lake, minimum = 49 (Eve Lake), maximum = 123 (Failing Lake)] among all study lakes, with estimated ages ranging from 1 to 10 years. A minimum of four and a maximum of eight age classes were represented within lakes. The following age classes were most prevalent in each lake: ages 3 (18%) and 4 (62%) in Crooked, ages 5 (63%) and 6 (21%) in Little Crooked, ages 6 (20%) and 7 (41%) in Eve, ages 1 (15%), 3 (21%), and 4 (44%) in Failing, ages 7 (35%) and 8 (31%) in Gage, ages 3 (16%), 4 (38%), and 5 (34%) in Howard, ages 1 (33%), 3 (22%), and 6 (15%) in Indiana, and ages 2 (59%) and 3 (33%) in South Twin. All age distributions differed significantly among populations (based upon pairwise chi-squared tests, all  $p \leq 0.001$ ), suggesting a lack of recruitment synchrony across the region.

Captured ciscoes from several individual lakes displayed a sex ratio which deviated significantly from the 50% male and 50% female null hypothesis (Crooked Lake,  $p < 0.001$ ; Little Crooked Lake,  $p \leq 0.001$ ; Howard Lake,  $p = 0.003$ ; South Twin Lake,  $p$

= 0.004; all other lakes,  $p > 0.05$ ). However, the directions of these deviations were inconsistent, with some populations biased towards males and some populations biased towards females. As a most extreme example, females comprised 89% of the samples collected after the mortality event on Little Crooked Lake, suggesting that, during this event, females may have been more susceptible to mortality than males. Pairwise chi-squared test results suggest that sex ratios from the following pairs of lakes were not significantly different ( $p > 0.05$ ): Crooked and Howard; Eve and Failing; Gage and Indiana; and Gage and South Twin lakes (Fig. 1.3a). All other pairwise comparisons significantly differed ( $p < 0.05$ ).

Relative weights ( $W_r$ ) were highly variable, with individual values ranging from 52% to 117% across all lakes (Fig. 1.3b). Median  $W_r$  ranged from 74% (Howard Lake) to 93% (Lake Gage). Bayesian ANOVA results suggest that  $W_r$  values in Lake Gage are significantly greater than in all other lakes (all 95% credible intervals from pairwise comparisons  $> 0$ ), and that Crooked and Howard Lakes (i.e., the lakes sampled during the spawning period) displayed significantly lower  $W_r$  compared to other lakes (all 95% credible intervals from pairwise comparisons  $< 0$ ). There were no significant differences in  $W_r$  among the remaining lakes.

Diets among the 80 individuals examined (20 per lake for each of 4 lakes) were numerically dominated by Cyclopoida, Calanoida, and Daphniidae (Table 1.3, Fig. 1.4). Bosminidae were found only in Crooked and Indiana lakes and were a dominant prey item in Crooked Lake. Average total diet dry mass within lakes ranged from 33 to 58 mg but did not differ significantly among lakes ( $F_{3,76} = 0.947$ ,  $p = 0.422$ ). When present,

larger bodied prey such as Chaoboridae and Chironomidae represented large proportions of prey biomass despite low numerical abundance in diets.

### 1.3.2 Genetic Analysis

In general, mitochondrial genetic variation among ciscoes from the study populations was low. A total of six haplotypes were identified among the 159 individuals successfully sequenced (Table 1.4, Fig. 1.5). The dominant haplotype (denoted “Csc”) was found in 145 (91%) of individuals, and all other haplotypes differed from the dominant haplotype by only one nucleotide each. Three of the five variable sites found in the present study correspond with variable sites found in the same region among other coregonids; additionally, one of the two variable sites discovered fell outside of the regions previously sequenced (Turgeon and Bernatchez 2001, 2003).

Genetic polymorphism at the three microsatellite loci ranged from 11 to 49 alleles per locus (Table 1.5). Observed heterozygosity was variable, ranging from 0.30 (Cisco-157) to 1.0 (Cisco-181), and fell below expected heterozygosity in 18 of 24 cases (locus  $\times$  sampling location) and for all global averages.  $F_{IS}$  values were highest at the Cisco-157 locus ( $F_{IS} = 0.17$ ). Pairwise  $F_{ST}$  values were generally high, and AMOVA results suggest that ciscoes from all sampling locations are genetically distinct (all  $p \leq 0.001$ ; Table 1.6).

Results from the *STRUCTURE* analysis indicate the presence of four genetically distinct populations (Fig. 1.6). Ciscoes from five of the eight sampling locations (Crooked, Gage, Indiana, Little Crooked, and South Twin lakes), while they were statistically distinct according to AMOVA results, displayed similar genetic patterns. In

contrast, ciscoes from the three remaining locations (Eve, Failing, and Howard lakes) were heavily dominated by one genetic population each (Populations 4, 3, and 1, respectively; Fig. 1.6). No apparent trends in genetic assemblages were found across space or watersheds (Figure S1.1).

#### 1.4 Discussion

Over the past century, several cisco populations towards the southern extent of the species' range have become locally extirpated, and several other populations are at risk of extirpation in the near future (Colby and Brooke 1969; Crisman 1993; Koza 1994; Pearson 2001; Steven Donabauer, IN-DNR, personal communication). Our study aimed to describe stock biology and genetic variation to elucidate the extirpation risk of understudied cisco populations in Indiana. We documented higher than expected intra-population age variation, and results suggest that inter-annual recruitment success of these cisco populations is not synchronized across the region (unlike observations in other systems; Selgeby 1985; Cox and Kitchell 2004; Rook et al. 2012). However, the intra-population size distributions of captured cisco were often narrow and some sex distributions were skewed, which may be representative of population structure (i.e., perhaps reflective of selective mortality events) or simply suggest sampling biases (see discussion below). Results from the genetic analyses suggest that the populations in the region exhibit low mitochondrial variation but are genetically distinct based on microsatellite genotypes. Collectively, patterns of demography and genetic variation indicate that some cisco populations in Indiana and southern Michigan may be at high

risk of extirpation. In addition, based on these data, it is unclear whether southern cisco populations diverged from a single common ancestor or if their evolutionary history has been compromised by stocking and/or supplementation from other populations.

Indiana and Michigan cisco populations appear to have relatively consistent recruitment success, as many of the populations displayed relatively broad ranges of age classes, despite the often narrow size distributions (Fig. 1.2). These patterns represent a stark contrast to cisco recruitment patterns described by other studies (e.g., Selgeby 1985; Cox and Kitchell 2004; Rook et al. 2012), in which a small range of age classes (typically separated from one another by multiple years) comprise large proportions of the population. Some factors that may contribute to more consistent recruitment success include the relatively small lake size (which reduces the chance of larval advection to poor quality habitat; Rook et al. 2012), higher productivity (potentially resulting in increased prey abundance for larval and juvenile individuals), and warmer waters (possibly leading to increased growth potential for young individuals) of the study lakes relative to most other cisco lakes, particularly those which contain heavily-studied populations (e.g., Lake Superior). Irrespective of drivers, the relatively consistent recruitment success of southern cisco populations indicates that 1) these populations are not exclusively dependent on single, dominant age classes and 2) based on past recruitment success, it appears unlikely that several consecutive year-classes will exhibit recruitment failure.

Although the similarity of length distributions among certain lakes (e.g., the bimodal distributions of similar size classes displayed by Crooked and Indiana lakes; Fig. 1.2) appears to suggest the potential for regional recruitment synchrony, all age

distributions significantly differed from one another, indicating that cisco recruitment is not synchronized across the northern Indiana and southern Michigan region. This lack of synchrony may be indicative of the relative unimportance of broad-scale factors, such as annual climatic variation (i.e., the Moran effect; Moran 1953), and of the relative importance of local factors in determining recruitment success (see Myers et al. 1997). Moreover, the lack of recruitment synchrony, and thus the apparent lack of common, region-wide recruitment drivers, reduces the probability that all cisco populations within the region will crash simultaneously (e.g., due to extreme climatic conditions). That is, because southern cisco population dynamics do not appear to be driven by regional factors, it is relatively unlikely that a single intense climatic event would decimate all populations in the region.

Sex ratios significantly varied among many of the populations (Fig. 1.3). Locations which displayed the most similar patterns were Crooked and Howard lakes (heavily dominated by males), Eve and Failing lakes (slightly dominated by males, with the highest observed proportions of immature fish), Gage and Indiana lakes (dominated by females), and Gage and South Twin lakes (dominated by females). In addition, sex ratios significantly deviated from parity in four instances (Crooked, Little Crooked, Howard, and South Twin lakes). However, three of these instances may be indicative of sampling or processing biases. The skewed sex ratios found in Crooked and Howard lakes may be due to an unintentional sampling bias based primarily on sampling time. Skurdal et al. (1985) found that males were more numerically prominent than females during the spawning run in the congeneric *Coregonus lavaretus*. Sampling during the spawning period (during which most of the Crooked and all of the Howard fish were

collected) may therefore select for the more abundant males. Indeed, of the six sexed ciscoes collected in Crooked Lake in September, three (50%) were female, whereas only 13 of the 54 (24.1%) fish collected in November were female. The skewed sex ratio exhibited in South Twin Lake may be a function of poor sample quality. In this instance, highly-damaged samples led to a relatively high proportion of “unknown” sex classifications, and thus the true sex ratio may not have been skewed. Therefore, it is plausible that some of the observed skewed sex ratios (and, to an extent, the differences in sex ratios among populations) are due to unintentional sampling or processing biases. On the other hand, the genetic data (i.e., low mitochondrial genetic variability) are consistent with the idea that females are subject to demographic bottlenecks not seen in males. Such sex-specific demographic bottlenecks could be manifested not only by a relatively high proportion of males but also by a lack of mitochondrial genetic variability relative to nuclear genetic variability, a pattern seen across the study populations.

The most unbalanced sex ratio was found in Little Crooked Lake (89% female). Although this sex ratio may not be representative of the population, it may have biological significance. Given that these fish were collected after a mortality event, it is plausible that this mortality event selected for females. One possible explanation for this selection could be that females in Little Crooked Lake were, in general, larger than males (as they were in some of the study lakes; Table S1.1). Increased size can lead to increased oxythermal sensitivity (Pörnter 2004; Pörnter and Knust 2007), thus making females more susceptible to mortality during periods of oxythermal stress. Selection for females in mortality events may have biological implications, particularly regarding genetic diversity (discussed below).

While populations displayed unexpectedly high age variation and moderately skewed sex ratios, several cisco populations displayed relatively narrow unimodal or bimodal size distributions. As with the sex ratios, there is a possibility that these size patterns may be reflective of unintentional sampling bias due to assortative schooling behavior. Cisco schooling behavior, particularly during the daytime, is well-documented (e.g., Scott and Crossman 1985; Milne et al. 2005; Kaufman et al. 2006), and some fish species have been shown to school assortatively by size, e.g., three-spined stickleback *Gasterosteus aculeatus* (Ranta and Lindström 1990; Ranta et al. 1992; Peuhkuri et al. 1997; Barber 2003) and parrotfish *Chlorurus sordidus* (Crook 1999). It is plausible that southern ciscoes also school assortatively by size, and that gill net sampling may capture merely one or two schools of fish in each population. However, it is important to note that the Crooked Lake cisco population has displayed narrow size distributions of similar size classes across many years (Steven Donabauer, IN-DNR, personal communication), thus reducing the probability that gill net sampling bias is the sole cause of the narrow distributions observed. If the observed data are indeed representative of population patterns, cisco extinction risk may be elevated due to relatively low size variability. Size is often related to DO (Robb and Abrahams 2003) and temperature (Pörnter and Knust 2007) tolerance ranges, with smaller individuals being more tolerant of extreme (low DO, high temperature) conditions. A lack of size diversity, and particularly a skew toward larger individuals (e.g., Eve, Gage, and Howard lakes; Fig. 1.2), may increase the risk of population extirpation given extreme oxythermal conditions.

Fish condition was similar among most populations, with median  $W_r$  typically falling near 85% (Fig. 1.3). According to the Bayesian ANOVA results, Lake Gage

displayed significantly higher condition, while lakes Crooked and Howard displayed significantly lower condition. It is plausible that the lower  $W_r$  values seen in Crooked and Howard Lakes are due to sampling time. Sampling during the spawning period likely leads to the collection of fish which have already spawned and have therefore lost mass, leading to lower condition values. Indeed, all of the females sampled from Howard Lake were void of eggs when sampled (Scott Hanshew, MI-DNR, personal communication). The high condition, as well as the abnormally large sizes and old ages, found in Lake Gage fish could be due to numerous factors, including high prey abundance, low predation, and favorable oxythermal conditions. The results appear to indicate that Lake Gage supports a very healthy cisco population. However, if the size distributions of the sample are representative, due to the lack of small individuals this population may be at high risk of extirpation given extreme oxythermal conditions.

Southern cisco diets were composed mostly of zooplankton, as expected (Higgins 1966; Aku and Tonn 1999; Pearson 2001) and were generally similar to cisco diets from other systems (e.g., Lake Superior; Link et al. 1995; Johnson et al. 2004). Where present, Chaoboridae and Chironomidae comprised large proportions of prey biomass despite low numerical abundance in diets. Ciscoes may take advantage of these prey items when available; however, foraging on such prey items may be limited to periods of prey suspension or emergence due to potentially low oxygen conditions near the benthos, particularly during hypoxic periods in the late summer when these benthic prey may be largely unavailable to ciscoes.

Mitochondrial DNA sequencing revealed very low amounts of genetic variation among individuals (Table 1.4, Fig. 1.5). Although six haplotypes were identified, one

haplotype dominated (“Csc”; 91% of individuals). Additional haplotypes were most prevalent in ciscoes taken from Indiana and Failing lakes, followed by those taken from Crooked and South Twin lakes (Fig. 1.5). These additional haplotypes differed from the dominant haplotype by only one nucleotide each. In previous studies, the variable sites associated with these nucleotide substitutions were documented not only in cisco *Coregonus artedi*, but also in the congeneric least cisco *C. sardinella* and bloater *C. hoyi* (Turgeon and Bernatchez 2001, 2003). Across the mitochondrial region sequenced, southern ciscoes were identical or very similar to many ciscoes from across North America and fell into Clade A (Mississippian lineage, “*Coregonus artedi* complex”) as described by Turgeon and Bernatchez (2003). It is useful to note that previous studies have found similarly low population genetic divergence in coregonids compared to other fishes (Bermingham and Avise 1986; Kornfield and Bodganowicz 1987), and that mitochondrial sequence divergence of North American ciscoes in general is comparable to that of salmonid hatchery populations (Gyllensten and Wilson 1987). Still, the lack of variation may be indicative of the history of southern cisco populations. One potential explanation is that ciscoes in the region were stocked relatively recently from a population (or populations) containing individuals with similar haplotypes. A second, non-mutually exclusive cause is only plausible if females are more susceptible to mortality events (as documented in Little Crooked Lake; Fig. 1.3). If so, selective mortality events may have led to a bottleneck in haplotype diversity across the region, especially if they occurred in the past when the populations were more closely connected to one another. A third potential explanation for the lack of mitochondrial variation is differential provisioning of resources; perhaps female mortality rates do not differ from

male mortality rates, but females are more prone to reabsorb their gametes and forego reproduction in a given year. This could result in demographic disparities between the sexes that could lead to reproductive bottlenecks in females. Irrespective of causes, the low mitochondrial variation observed in southern ciscoes could increase their vulnerability to extinction (St. John-Pikel 1999).

In contrast to the observed mitochondrial sequence variation, genotypic variation was relatively high both within and among populations (Tables 1.5, 1.6; Fig. 1.6). Southern ciscoes often displayed high numbers of alleles and, at times, high heterozygosity values. This may be characteristic of the species as a whole and/or of the particular microsatellite loci examined, as Turgeon et al. (1999) found similar results among Lake Nipigon ciscoes at the same loci. Fixation indices were highest across loci in Gage and Little Crooked lakes (mean  $F = 0.252$  and  $0.251$ , respectively), suggesting that these populations may be the most inbred (although data from additional loci are needed to evaluate this hypothesis). Allelic richness was typically lowest in Eve, Failing, and Howard lakes, whereas it was generally higher in Crooked, Indiana, South Twin, and Gage lakes. Overall, these results suggest that populations such as those in Crooked, Indiana, and South Twin may be among the most sustainable, whereas the population in Eve Lake may be the most likely to become extirpated (based solely on intra-population genetic variation).

In general, the results of the inter-population analyses of nuclear genetic variation reinforce those of the intra-population analyses. According to the AMOVA results, all populations were genetically distinct from one another (Table 1.6, Fig. 1.6). These results are in concert with the only other study which assessed genotypic variation among

populations in the region (St. John-Pikel 1999). Moreover, some populations were found to be more genetically differentiated than others, based on *STRUCTURE* and  $F_{ST}$  results. In particular, ciscoes from Eve, Failing, and Howard lakes displayed drastically different patterns in genetic population composition than individuals from the other lakes, with each of the three locations being dominated by one genetic population each. Although intra-population analyses showed that inbreeding at these locations is not alarming, each of the three populations contained relatively low numbers of alleles at each locus (Table 1.5). Furthermore, based on the *STRUCTURE* tree diagram of genetic differentiation (Fig. 1.6b), ciscoes from Eve Lake appear to be the most genetically distinct, followed by those from Failing and Howard lakes. Accordingly, Eve Lake consistently displayed the highest pairwise  $F_{ST}$  values, followed by Failing and Howard lakes (Table 1.6). These results suggest that the cisco population in Eve Lake may be at the highest risk of extirpation, followed by those in Failing and Howard lakes (based solely on inter-population genetic variation). Additionally, for the purposes of conservation and management, cisco populations from the five remaining lakes can be considered similar (in that they all contain relatively similar proportions of the four genetic populations and are not heavily dominated by one in particular) and may be useful as source populations for future stocking efforts.

The spatial patterns in inter-population genotypic variation were unclear (Fig. S1.1). Populations did not appear to differentiate based on location or across watersheds. That is, populations within watersheds were not more closely related to one another than populations across watersheds. Taken in concert with the lack of observed mitochondrial sequence variation, these results may suggest that southern cisco populations were

stocked across the region. However, the evidence is far from conclusive, and the observed patterns could be attributed to other causes. For example, the observed patterns may have resulted from supplemental stocking to native populations and/or from selective mortality events in specific lakes. Data describing genotypes at additional microsatellite loci may help to elucidate the relationships among populations and provide additional information to help explain the origin of southern ciscoes.

The decline of southern cisco populations over the past century has been drastic, and remaining populations may be at risk of extirpation. However, ciscoes from the study populations displayed many patterns characteristic of seemingly healthy populations. For instance, age distribution results suggest that southern cisco populations may exhibit relatively consistent recruitment success, and fish from some populations displayed high condition (particularly within Gage Lake). In addition, many populations displayed balanced sex ratios; the skewed sex ratios observed in some populations may be due to sampling or processing biases and, in the case of Little Crooked Lake, a selective mortality event. Microsatellite genetic variation both within and among populations was generally high, indicating that southern cisco populations as a whole are relatively genetically diverse. However, size distributions were generally narrow, which may place these populations at risk of extirpation given extreme environmental conditions (although these patterns may also be due, in part at least, to sampling biases). Furthermore, mitochondrial genetic variation was low, but this may be characteristic of the species and/or exacerbated by selective mortality events. Taken together, these results suggest that cisco populations in lakes such as Crooked Lake and Indiana Lake may be among the most sustainable, whereas the population in Eve Lake may be at the highest risk of

extirpation. Moreover, this study highlights the need for additional research related to cisco population ecology and management. Specifically, there is a need to thoroughly examine the potential for biases in cisco sampling methodologies, including the potential for differential distribution across sexes, ages, and sizes, all of which may lead to biased sampling. Furthermore, additional information should be collected regarding the potential causes, effects, and management implications of selective mortality events.

## 1.5 References

- Aku, P.M.K. and Tonn, W.M. (1999). Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Transactions of the American Fisheries Society* 128: 17-30.
- Allendorf, F.A., and Leary, R.F. (1986). Heterozygosity and fitness in natural populations of animals. *In Conservation Biology: The Science of Scarcity and Diversity*, ed. M.E. Soule. Sinauer and Assoc., Sunderland, MA, pp. 57-76.
- Barber, I. (2003). Parasites and size-assortative schooling in three-spined sticklebacks. *Oikos* 101: 331-337.
- Benke, A.C., Huryn, A.D., Smock, L.A., Wallace, J.B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18: 308-343.
- Bermingham, E. and Avise, J.C. (1986). Molecular zoogeography of freshwater fishes in the southern United States. *Genetics* 113: 939-966.
- Bernatchez, L, Danzmann, R.G. (1993). Congruence in control-region sequence and restriction-site variation in mitochondrial DNA of brook charr (*Salvelinus fontinalis* Mitchill). *Molecular Biology and Evolution* 10: 1002–1014.
- Bunnell, D.B., Madenjian, C.P., Croley II, T.E. (2006). Long-term trends of bloater (*Coregonus hoyi*) recruitment in Lake Michigan: evidence for the effect of sex ratio. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 832-844.

- Clement, M., Posada, D., Crandall, K.A. (2000). TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657-1660.
- Colby, P.T., and Brooke, L.T. (1969). Cisco (*Coregonus artedii*) mortalities in a southern Michigan lake, July 1968. *Limnology and Oceanography* 14: 958-960.
- Culver, D.A., Boucherle, M.M., Bean, D.J., and Fletcher, J.W. (1985). Biomass of freshwater crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1380-1390.
- Crisman, T.L. (1993). Assessment of watershed-lake interactions influencing the cultural eutrophication of Little Crooked and Crooked Lakes, Indiana. Report submitted to the Crooked Lake Property Owners Association, on behalf of the Indiana Lake Enhancement Program, Division of Soil Conservation, Indiana Department of Natural Resources. Indianapolis, IN.
- Crook, A.C. (1999). Quantitative evidence for assortative schooling in a coral reef fish. *Marine Ecology Progress Series* 176: 17-23.
- Dumont, H.J. and Balvay, G. (1979). The dry weight estimate of *Chaoborus flavicans* (Meigen) as a function of length and instars. *Hydrobiologia* 64: 139-145.
- Dumont, H.J., Van de Velde, I., Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75-97.
- Dymond, J.R. (1933). The coregonine fishes of Hudson and James bays. In Biological and Oceanographic conditions in Hudson Bay. *Contributions to Canadian Biology and Fisheries* 8: 1-12.

- Ebener, M.P, Stockwell, J.D., Yule, D.L., Gorman, O.T., Hrabik, T.R., Kinnunen, R.E., Mattes, W.P., Oyadomari, J.K., Schreiner, D.R., Geving, S., Scribner, K., Schram, S.T., Seider, M.J., Sitar, S.P. (2008). Status of cisco *Coregonus artedi* in Lake Superior during 1970-2006 and management and research considerations. Report 1 of the Lake Superior Technical Committee. 126 p.
- Edsall, T.A. and Colby, P.J. (1970). Temperature tolerance of young-of-the-year cisco, *Coregonus artedi*. *Transactions of the American Fisheries Society* 99: 526-531.
- Falush, D., Stephens, M., Pritchard, J.K. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* 164: 1567-1587.
- Falush, D., Stephens, M., Pritchard, J.K. (2007). Inference of population structure using multilocus genotype data: dominant markers and null alleles. *Molecular Ecology Notes* 7: 574-578.
- Fisher, S.J. and Fielder, D.G. (1998). A standard weight equation to assess the condition of North American lake herring (*Coregonus artedi*). *Journal of Freshwater Ecology* 13: 269-277.
- Frey, D.G. (1955). Distributional ecology of the cisco *Coregonus artedi* in Indiana. *Investigations of Indiana Lakes and Streams* 4: 177-228.
- Fry, F.E.J. (1937). The summer migration of the cisco, *Leucichthys artedii* (LeSeur), in Lake Nipissing, Ontario. University of Toronto Studies in Biology Series 44, Publication of the Ontario Fisheries Research Laboratory 55: 1-91.

- Gyllensten, U. and Wilson, A.C. (1987). Mitochondrial DNA of salmonids: Inter- and intraspecific variability detected with restriction enzymes. In: *Population genetics and fishery management* (eds. Ryman, N. and Utter, F.). University of Washington Press, Seattle, WA., pp. 301-314.
- Higgins, B.E. (1966). Food selection by the cisco, *Coregonus artedi*, in Crooked Lake (Noble-Whitley counties), Indiana. Ph.D. dissertation, Indiana University. 131 p.
- Hubisz, M.J., Falush, D., Stephens, M., Pritchard, J.K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources* 9: 1322-1332.
- IPCC, 2014. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., and White, L.L., (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jacobson, P.C., Jones, T.S., Rivers, P., Pereira, D.L. (2008). Field estimation of a lethal oxythermal niche boundary for adult ciscoes in Minnesota lakes. *Transactions of the American Fisheries Society* 137: 1464-1474.
- Johnson, T.B., Brown, W.P., Corry, T.D., Hoff, M.H., Scharold, J.V., Trebitz, A. (2004). Lake herring (*Coregonus artedi*) and rainbow smelt (*Osmerus mordax*) diets in western Lake Superior. *Journal of Great Lakes Research* 30: 407-413.

- Kaufman, S.D., Gunn, J.M., Morgan, G.E., Couture, P. (2006). Muscle enzymes reveal walleye (*Sander vitreus*) are less active when larger prey (cisco, *Coregonus artedi*) are present. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 970-979.
- Kennedy, W.A. (1941). The migration of fish from a shallow to a deep lake in spring and early summer. *Transactions of the American Fisheries Society* 70: 391-396.
- Kornfield, I. and Bodganowicz, S.M. (1987). Differentiation of mitochondrial DNA in Atlantic herring, *Clupea harengus*. *Fisheries Bulletin* 85: 561-568.
- Koza, L. (1994). Current status of cisco abundance, habitat and harvest at northern Indiana lakes. Indiana Department of Natural Resources, Division of Fish and Wildlife report. Indianapolis, IN.
- Kruschke, J.K. (2011). *Doing Bayesian Data Analysis: A tutorial with R and BUGS*. Academic Press, Burlington, MA, USA. 653 pp.
- Latta, W.C. (1995). Distribution and abundance of the lake herring (*Coregonus artedi*) in Michigan. Michigan Department of Natural Resources, Fisheries Division research report 2014.
- Link, J., Selgeby, J.H., Hoff, M.H., Haskell, C. (1995). Winter diet of lake herring (*Coregonus artedi*) in Western Lake Superior. *Journal of Great Lakes Research* 21: 395-399.
- Maynard Smith, J., and Stenseth, N.C. (1978). On the evolutionary stability of the female-biased sex ratio in the wood lemming (*Myopus schisticolor*): The effect of inbreeding. *Heredity* 41: 205-214.
- Milligan, B.G., Leebens-Mack, J., Strand, A.E. (1994). Conservation genetics: beyond the maintenance of marker diversity. *Molecular Ecology* 3: 423-435.

- Milne, S.W., Shuter, B.J., Sprules, W.G. (2005). The schooling and foraging ecology of lake herring (*Coregonus artedii*) in Lake Opeongo, Ontario, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1210-1218.
- Moran, P.A.P. (1953). The statistical analysis of the Canadian lynx cycle, II. Synchronization and meteorology. *Australian Journal of Zoology* 1, 291-298.
- Murphy, B.R., Willis, D.W., Springer, T.A. (1991). The relative weight index in fisheries management: Status and needs. *Fisheries* 16, 30-38.
- Myers, R.A., Mertz, G., Bridson, J., 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 1400-1407.
- Peakall, R. and Smouse, P.E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288-295.
- Peakall, R. and Smouse, P.E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* 28: 2537-2539.
- Pearson, J. (2001). Cisco population status and management in Indiana. Indiana Department of Natural Resources, Division of Fish and Wildlife report. Indianapolis, IN.
- Peuhkuri, N., Ranta, E., Seppä, P. (1997). Size-assortative schooling in free-ranging sticklebacks. *Ethology* 103: 318-324.

- Pörnter, H.O. (2004). Climate variability and the energetic pathways of evolution: the origin of endothermy in mammals and birds. *Physiological and Biochemical Zoology* 77: 959-981.
- Pörnter, H.O. and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315: 95-97.
- Pritchard, J.K., Stephens, M., Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ranta, E. and Lindström, K. (1990). Assortative schooling in three-spined sticklebacks? *Annales Zoologici Fennici* 27: 67-75.
- Ranta, E., Juvonen, S.-K., Peuhkuri, N. (1992). Further evidence for size-assortative schooling in sticklebacks. *Journal of Fish Biology* 41: 627-630.
- Robb, T. and Abrahams, M.V. (2003). Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? *Journal of Fish Biology* 62: 1067-1081.
- Rook, B.J., Hansen, M.J., Gorman, O.T. (2012). The spatial scale for cisco recruitment dynamics in Lake Superior during 1978-2007. *North American Journal of Fisheries Management* 32: 499-514.
- Sambrook, J., Fritsch, E.F., Maniatis, T. (1989). *Molecular Cloning: A Laboratory Manual*. 2nd ed. N.Y., Cold Spring Harbor Laboratory, Cold Spring Harbor Laboratory Press. 1659 p.

- Schneider, C.A., Rasband, W.S., Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675.
- Schreiner, D.R. and Schram, S.T. (2000). Lake Superior fish aging manual. Great Lakes Fish. Comm. Misc. Pub., Ann Arbor, Mich.
- Scott, W.B. and Crossman, E.J. (1985). *Freshwater fishes of Canada*. Fisheries Research Board of Canada, Ottawa Bulletin 184.
- Scott, W.B. and Crossman, E.J. (1998). *Freshwater fishes of Canada*. Galt House Publications Ltd., Oakville, ON.
- Selgeby, J.H. (1985). Population trends of lake herring (*Coregonus artedii*) and rainbow smelt (*Osmerus mordax*) in U.S. Waters of Lake Superior, 1968-84. In Presented Papers from the Council of Lake Committees: Plenary Session on Great Lakes Predator-Prey Issues, March 20, 1985, ed. R.L. Eschenroder. Great Lakes Fisheries Commission Special Publication 85-3, Ann Arbor, MI.
- Sharma, S. Vander Zanden, M.J., Magnuson, J.J., Lyons, J. (2011). Comparing climate change and species invasions as drivers of coldwater fish population extirpations. *pLoS ONE* 6: e22906.
- Skurdal, J., Bleken, E., Stenseth, N.C. (1985). Cannibalism in whitefish (*Coregonus lavaretus*). *Oecologia* 67: 566-571.
- St. John-Pikel, K.A. (1999). *Population differentiation and genetic variability in four allopatric Indiana cisco (Coregonus artedi) populations*. M.Sc. Thesis, Indiana University-Purdue University Fort Wayne, U.S.A.

- Turgeon, J., Estoup, A., Bernatchez, L. (1999). Species flock in the North American Great Lakes: molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). *Evolution* 53: 1857-1871.
- Turgeon, J., and Bernatchez, L. (2001). Mitochondrial DNA phylogeography of lake cisco (*Coregonus artedii*): evidence supporting extensive secondary contacts between two glacial races. *Molecular Ecology* 10: 987-1001.
- Turgeon, J. and Bernatchez, L. (2003). Reticulate evolution and phenotypic diversity in North American ciscoes, *Coregonus* spp. (Teleostei: Salmonidae): implications for the conservation of an evolutionary legacy. *Conservation Genetics* 4: 67-81.
- Volis, S., Ormanbekova, D., Yermekbayev, K., Song, M., Shulgina, I. (2014). Introduction beyond a species range: a relationship between population origin, adaptive potential, and plant performance. *Heredity* 1-9.

1.6 Tables

**Table 1.1.** Experimental gill net location, depth, date of sampling, and number of cisco caught in Indiana and Michigan during September-December, 2012 (Steven Donabauer, IN-DNR and Scott Hanshue, MI-DNR, personal communication).

Lake	County	Date	Net	# Cisco	Depth (m)	Start		End	
						Latitude	Longitude	Latitude	Longitude
Crooked	Whitley	9/26/2012	1	1	4.6-13.7	41.26599	-85.48083	41.26651	-85.48164
Crooked	Whitley	9/26/2012	2	2	7.6-9.1	41.26401	-85.48242	41.26326	-85.48221
Crooked	Whitley	9/26/2012	3	0	9.1-15.2	41.25868	-85.47902	41.25832	-85.47834
Crooked	Whitley	9/26/2012	4	0	4.6-9.1	41.26707	-85.48320	41.26643	-85.48365
Crooked	Whitley	9/27/2012	5	2	4.6-13.7	41.26599	-85.48083	41.26651	-85.48164
Crooked	Whitley	9/27/2012	6	1	10.1-10.1	41.26699	-85.48193	41.26731	-85.48277
Crooked	Whitley	9/27/2012	7	0	7.6-10.7	41.26495	-85.48326	41.26578	-85.48362
Crooked	Whitley	9/27/2012	8	0	9.8-12.2	41.25813	-85.47924	41.25793	-85.47826
Crooked	Whitley	9/27/2012	9	1	7.6-9.1	41.26401	-85.48242	41.26326	-85.48221
Eve	LaGrange	9/11/2012	1	6	5.8-6	41.56186	-85.32026	41.56227	-85.31958
Eve	LaGrange	9/11/2012	2	0	4.3-5.8	41.56168	-85.31891	41.56103	-85.31835
Eve	LaGrange	9/11/2012	3	4	6.4-8.2	41.55934	-85.31989	41.55957	-85.32070
Eve	LaGrange	9/12/2012	4	2	5.8-6.1	41.56186	-85.32026	41.56227	-85.31958
Eve	LaGrange	9/12/2012	5	3	4.9-6.4	41.56166	-85.31000	41.56102	-85.31842
Eve	LaGrange	9/12/2012	6	5	6.4-8.2	41.55934	-85.31989	41.55957	-85.32070
Eve	LaGrange	9/13/2012	7	2	5.8-6.1	41.56186	-85.32026	41.56227	-85.31958
Eve	LaGrange	9/13/2012	8	18	5.5-7	41.56163	-85.31912	41.56098	-85.31852
Eve	LaGrange	9/13/2012	9	7	6.4-8.2	41.55934	-85.31989	41.55957	-85.32070
Eve	LaGrange	9/13/2012	10	2	5.5-7	41.56033	-85.31789	41.56012	-85.31876
Failing	Steuben	9/5/2012	1	17	7.9-8.2	41.70406	-85.00040	41.70425	-85.00108
Failing	Steuben	9/5/2012	2	24	7.9-8.2	41.70594	-85.00064	41.70562	-85.00142
Failing	Steuben	9/5/2012	3	85	7.9-8.2	41.70579	-85.99834	41.70631	-84.99781
Gage	Steuben	9/25/2012	1	7	11.6-11.9	41.69982	-85.10617	41.69932	-85.10635
Gage	Steuben	9/25/2012	2	3	11.6-11.9	41.69961	-85.11606	41.69980	-85.11687
Gage	Steuben	9/25/2012	3	7	11.6-11.9	41.70435	-85.11085	41.70480	-85.11153
Gage	Steuben	9/26/2012	4	4	11.6-11.9	41.70488	-85.11160	41.70482	-85.11233

Table 1.1 continued.

Gage	Steuben	9/26/2012	5	13	11.6-11.9	41.70339	-85.12170	41.70353	-85.12080
Gage	Steuben	9/26/2012	6	2	11.6-11.9	41.69815	-85.10677	41.69875	-85.10642
Gage	Steuben	9/27/2012	7	1	11.6-11.9	41.70465	-85.11279	41.70454	-85.11359
Gage	Steuben	9/27/2012	8	11	11.6-11.9	41.70513	-85.12070	41.70548	-85.11996
Gage	Steuben	9/27/2012	9	3	11.6-11.9	41.70084	-85.10645	41.70143	-85.10632
Indiana	Elkhart	9/13/2012	1	15	12.8-13.1	41.75856	-85.83131	41.75803	-85.83204
Indiana	Elkhart	9/13/2012	2	39	12.8-13.1	41.76299	-85.83456	41.76355	-85.83445
Indiana	Elkhart	9/13/2012	3	47	12.8-13.1	41.76404	-85.83200	41.76430	-85.83120
S. Twin	LaGrange	9/25/2012	1	5	11.3-11.9	41.72822	-85.46461	41.72783	-85.46544
S. Twin	LaGrange	9/25/2012	2	11	11.3-11.9	41.72255	-85.46564	41.72322	-85.46495
S. Twin	LaGrange	9/25/2012	3	55	11.3-11.9	41.72404	-85.47009	41.72355	-85.46963
Crooked	Whitley	11/26/2012	1*	8	-	41.27019	-85.48776	-	-
Crooked	Whitley	11/27/2012	2	46	-	41.27019	-85.48776	-	-
Howard	Kalamazoo (MI)	12/11/2012	1	22	-	-	-	-	-
Howard	Kalamazoo (MI)	12/11/2012	2	46	-	-	-	-	-
Howard	Kalamazoo (MI)	12/11/2012	3	5	-	-	-	-	-

\*Set of eight one-hour daytime net lifts.

**Table 1.2.** Summary of sampling month, number of cisco caught, number of experimental gill net lifts (# Lifts), number of cisco caught per gill net lift (CPUE), number of ciscoes included in the analysis, lake area (km<sup>2</sup>), maximum depth (m), and shoreline development index (SDI) for each of the study lakes. Three fish from Failing Lake and 22 fish from Indiana Lake were alive when caught and subsequently released (Steven Donabauer, IN-DNR and Scott Hanshue, MI-DNR, personal communication).

Lake	Month	# Cisco	# Lifts	CPUE	# Analyzed	Area (km <sup>2</sup> )	Max. Depth (m)	SDI
Crooked	Sept	7	9	0.8	7	1.6	32.9	2.3
Little Crooked*	July	104	-	-	104	-	-	-
Eve	Sept	49	10	4.9	49	0.3	12.8	1.2
Failing	Sept	126	3	42	123	0.3	10.7	1.3
Gage	Sept	51	9	5.7	51	3.2	21.3	1.2
Indiana	Sept	101	3	33.7	79	1.2	8.8	1.4
South Twin	Sept	71	3	23.7	71	1.2	15.9	1.1
Crooked	Nov	54	1.3 <sup>†</sup>	41.5	54	1.6	32.9	2.3
Howard (MI)	Dec	73	3	24.3	73	-	-	-

\*Mortality event, after which dead and dying ciscoes were sampled using dip nets.

<sup>†</sup>Composite effort based on one overnight and eight one-hour daytime gill net lifts.

**Table 1.3.** Frequency of occurrence (%) of prey types (taxonomic family) among a random sample of 20 cisco diets in each of four study lakes.

Family	Sampling Location			
	Crooked Lake	Eve Lake	Failing Lake	Indiana Lake
Cyclopoida	85	35	95	50
Calanoida	90	50	80	20
Daphniidae	65	70	65	55
Bosminidae	85	0	0	10
Chaoboridae	0	25	0	20
Chironomidae	0	5	10	0

**Table 1.4.** Variable nucleotides found in the mitochondrial D-loop region (488 bp), location of individuals displaying each haplotype, number of individuals displaying each haplotype (N), and percent composition of each haplotype among all ciscoes (%). Positions denote the number of base pairs from the 3' end, with numbers in parentheses referring to positions from Turgeon and Bernatchez (2001, 2003; GenBank accession nos.: AF246932-34).

Haplotype	Lake	Position					N	%
		76 (75)	273 (272)	286 (285)	361	412		
Csc	Multiple	C	T	A	A	G	145	91.2
Fa2	Failing	T	.	.	.	.	6	3.8
In3	Indiana	.	C	.	.	.	5	3.2
St2	S. Twin	.	.	G	.	.	1	0.6
In2	Indiana	.	.	.	T	.	1	0.6
Cr2	Crooked	.	.	.	.	T	1	0.6

**Table 1.5.** Number of alleles ( $A$ ), range of allele sizes (bp), observed heterozygosity( $H_o$ ), expected heterozygosity ( $H_e$ ), fixation index ( $F = 1 - \frac{H_o}{H_e}$ ), and number of scoredindividuals ( $n$ ) for each cisco sampling location. Global  $F = F_{IS}$ .

Locus	Sampling Location								Global
	Crooked	Little Crooked	Eve	Failing	Gage	Howard (MI)	Indiana	S. Twin	
<b><u>Cisco-157</u></b>									
<b>A</b>	6	7	5	4	6	5	7	6	11
<b>Range</b>	143-157	141-157	143-157	143-159	139-157	143-159	143-159	145-159	139-159
<b><math>H_o</math></b>	0.30	0.55	0.55	0.60	0.45	0.50	0.60	0.35	0.49
<b><math>H_e</math></b>	0.54	0.72	0.51	0.63	0.73	0.42	0.76	0.42	0.59
<b><math>F</math></b>	0.44	0.23	-0.08	0.05	0.38	-0.19	0.21	0.17	0.17
<b><math>n</math></b>	20	20	20	20	20	20	20	20	160
<b><u>Cisco-181</u></b>									
<b>A</b>	23	10	11	17	16	11	19	22	49
<b>Range</b>	174-350	178-338	206-392	178-384	190-354	198-342	206-370	186-366	174-392
<b><math>H_o</math></b>	0.95	0.40	0.75	0.80	0.75	0.74	1.0	0.95	0.79
<b><math>H_e</math></b>	0.94	0.73	0.81	0.92	0.87	0.83	0.93	0.94	0.87
<b><math>F</math></b>	-0.01	0.45	0.07	0.13	0.13	0.11	-0.08	-0.02	0.09
<b><math>n</math></b>	20	20	20	20	20	19	20	20	159
<b><u>Cisco-200</u></b>									
<b>A</b>	13	11	4	6	12	9	12	11	25
<b>Range</b>	204-260	204-260	212-256	210-256	206-274	206-266	204-264	202-258	202-274
<b><math>H_o</math></b>	0.70	0.74	0.50	0.90	0.65	0.74	0.85	0.79	0.73
<b><math>H_e</math></b>	0.81	0.79	0.52	0.74	0.86	0.81	0.89	0.85	0.78
<b><math>F</math></b>	0.13	0.07	0.04	-0.21	0.24	0.09	0.04	0.07	0.07
<b><math>n</math></b>	20	19	20	19	20	19	20	19	156

**Table 1.6.** Pairwise  $F_{ST}$  values among cisco sampling locations. All comparisons differed significantly ( $p \leq 0.001$ , based on 9999 permutations).

Location	Location						
	Crooked	Eve	Failing	Gage	Howard (MI)	Indiana	Little Crooked
Eve	0.254						
Failing	0.176	0.259					
Gage	0.042	0.189	0.110				
Howard (MI)	0.083	0.315	0.209	0.101			
Indiana	0.073	0.182	0.090	0.062	0.147		
Little Crooked	0.052	0.209	0.155	0.043	0.103	0.097	
S. Twin	0.035	0.270	0.190	0.052	0.056	0.099	0.087

## 1.7 List of Figure Captions

**Figure 1.1.** Map depicting the locations of the study lakes in Indiana and Michigan (denoted by stars). Little Crooked Lake, where the mortality event took place, is directly connected to the southeastern end of Crooked Lake. *Inset:* The decline in the number of lakes containing cisco in Indiana since 1900, based on IN-DNR gill net surveys (Steven Donabauer, IN-DNR, personal communication).

**Figure 1.2.** Proportional compositions of total length classes (10 mm bins), separated by age, among the cisco populations studied: (a) Crooked Lake; (b) Little Crooked Lake; (c) Eve Lake; (d) Failing Lake; (e) Lake Gage; (f) Howard Lake; (g) Indiana Lake; (h) South Twin Lake. Sample sizes (N) denote the number of fish for which length and age data were successfully collected.

**Figure 1.3.** (a) Sex ratios and (b) relative weight (%) values among ciscoes collected from the study lakes. Fish which were too highly damaged to determine sex (e.g., gonads were missing) were classified as “unknown.” Numbers in parentheses denote sample sizes (i.e., fish from which adequate data could be collected). Asterisks indicate populations which significantly departed from the 50% male and 50% female null hypothesis, according to t-test results. Letters denote significant differences among groups, based on Bayesian ANOVA results. In (b), whiskers indicate 10<sup>th</sup> and 90<sup>th</sup> percentiles, boxes indicate, 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> percentiles, and points indicate values outside of the 10<sup>th</sup> and 90<sup>th</sup> percentiles.

**Figure 1.4.** (a) Count and (b) biomass ( $\mu\text{g}$ ) of identifiable prey items from 20 randomly selected diets from each of four study lakes.

**Figure 1.5.** Haplotype network diagram of Indiana and Michigan ciscoes across 488 bp. Oval size is proportional to the number of individuals represented by each haplotype. The dominant haplotype (Csc) represents 91.2% of individuals, and all other haplotypes differ by one nucleotide each.

**Figure 1.6.** (a) Proportional composition of the four genetic populations estimated by *STRUCTURE* among sampling locations. (b) Tree diagram depicting genetic differentiation among the four estimated populations.

1.8 Figures

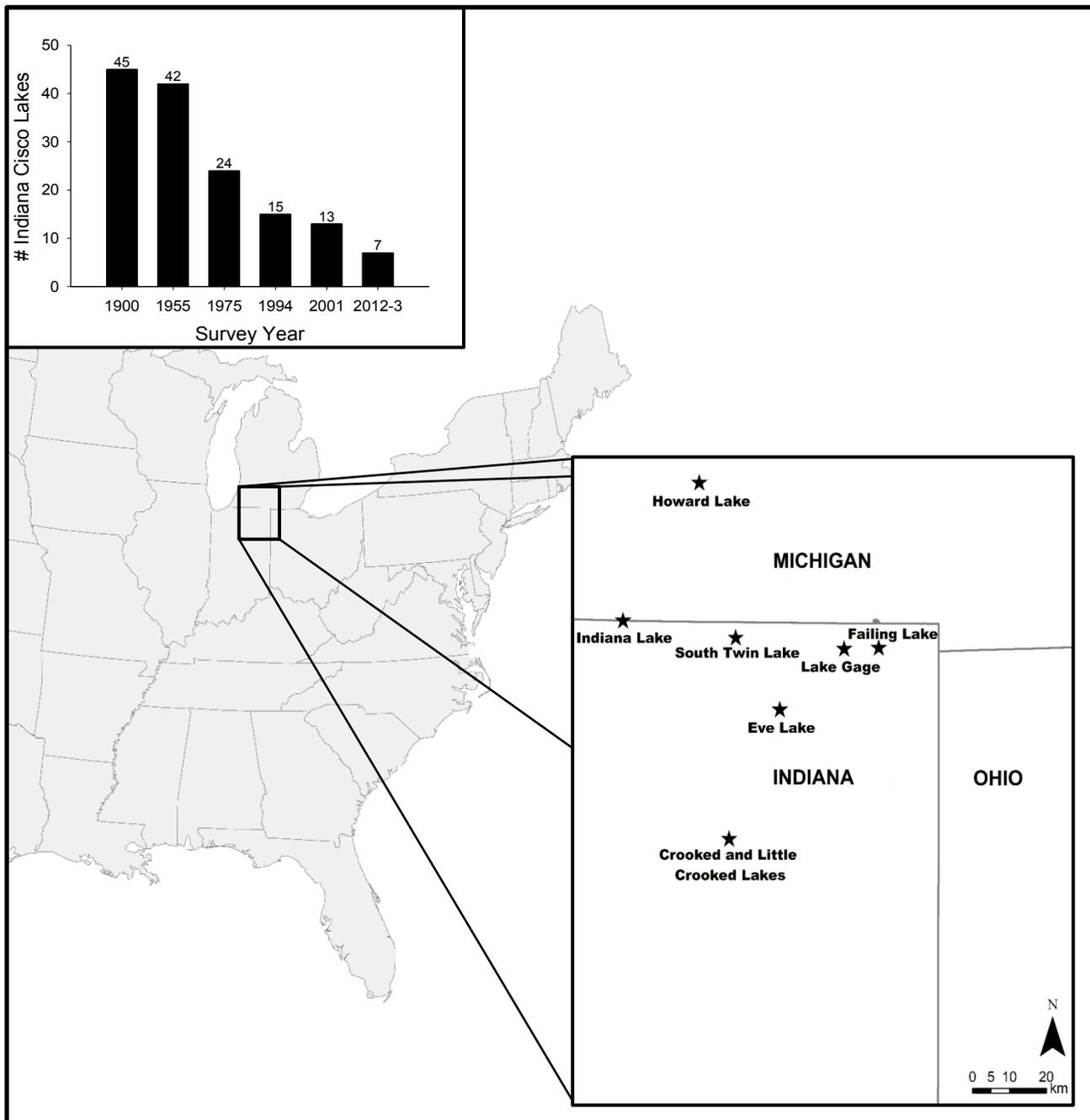


Figure 1.1

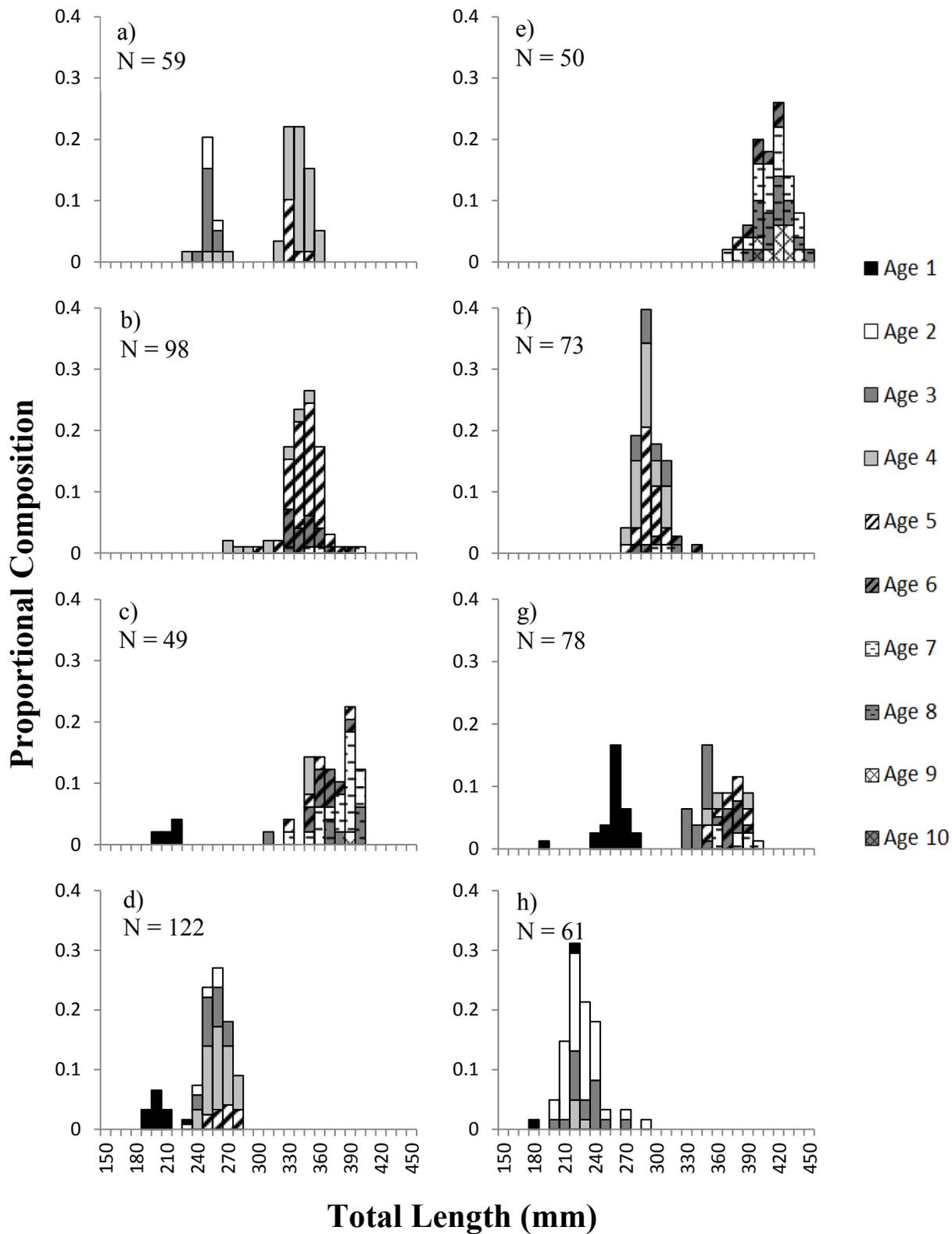


Figure 1.2

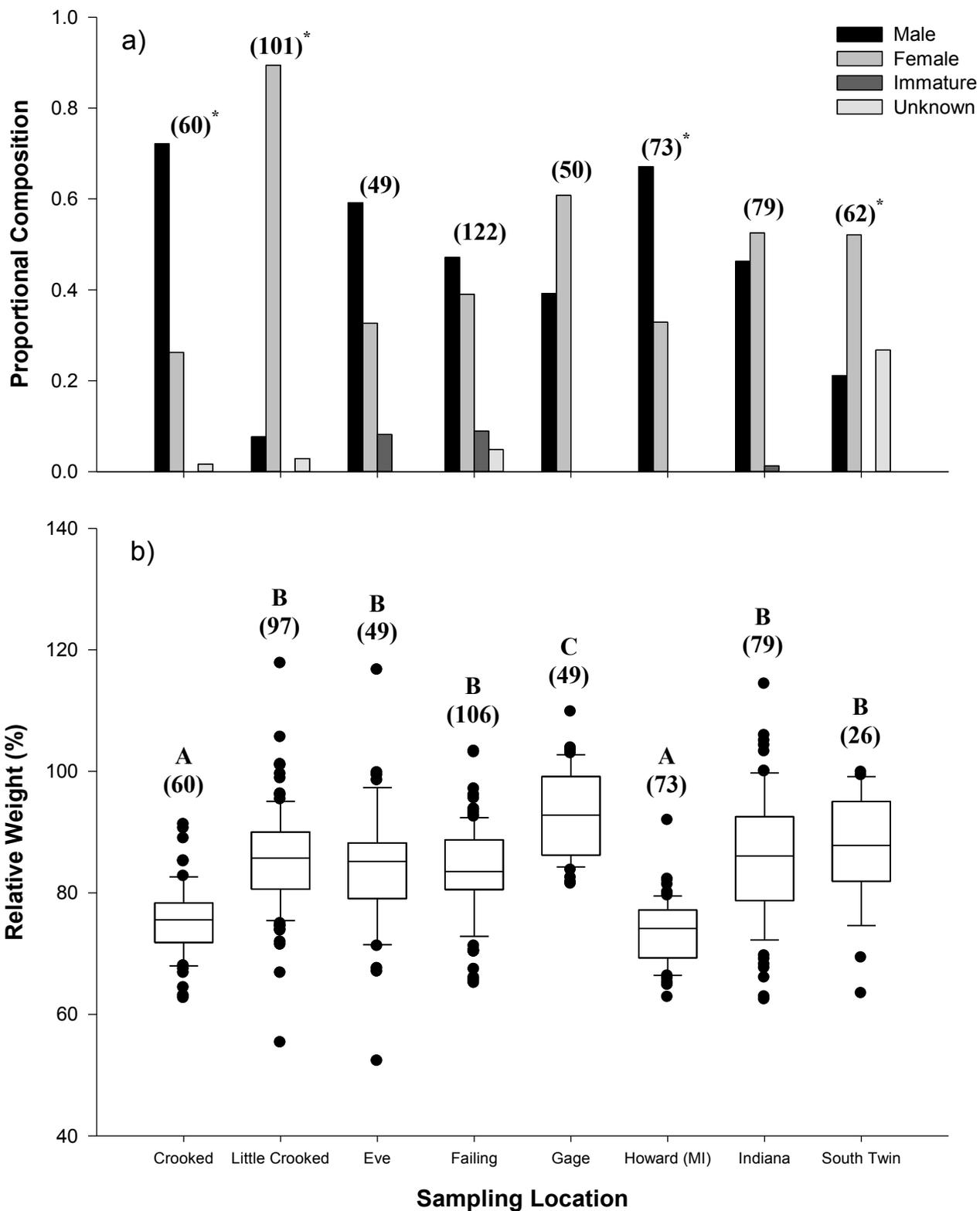


Figure 1.3

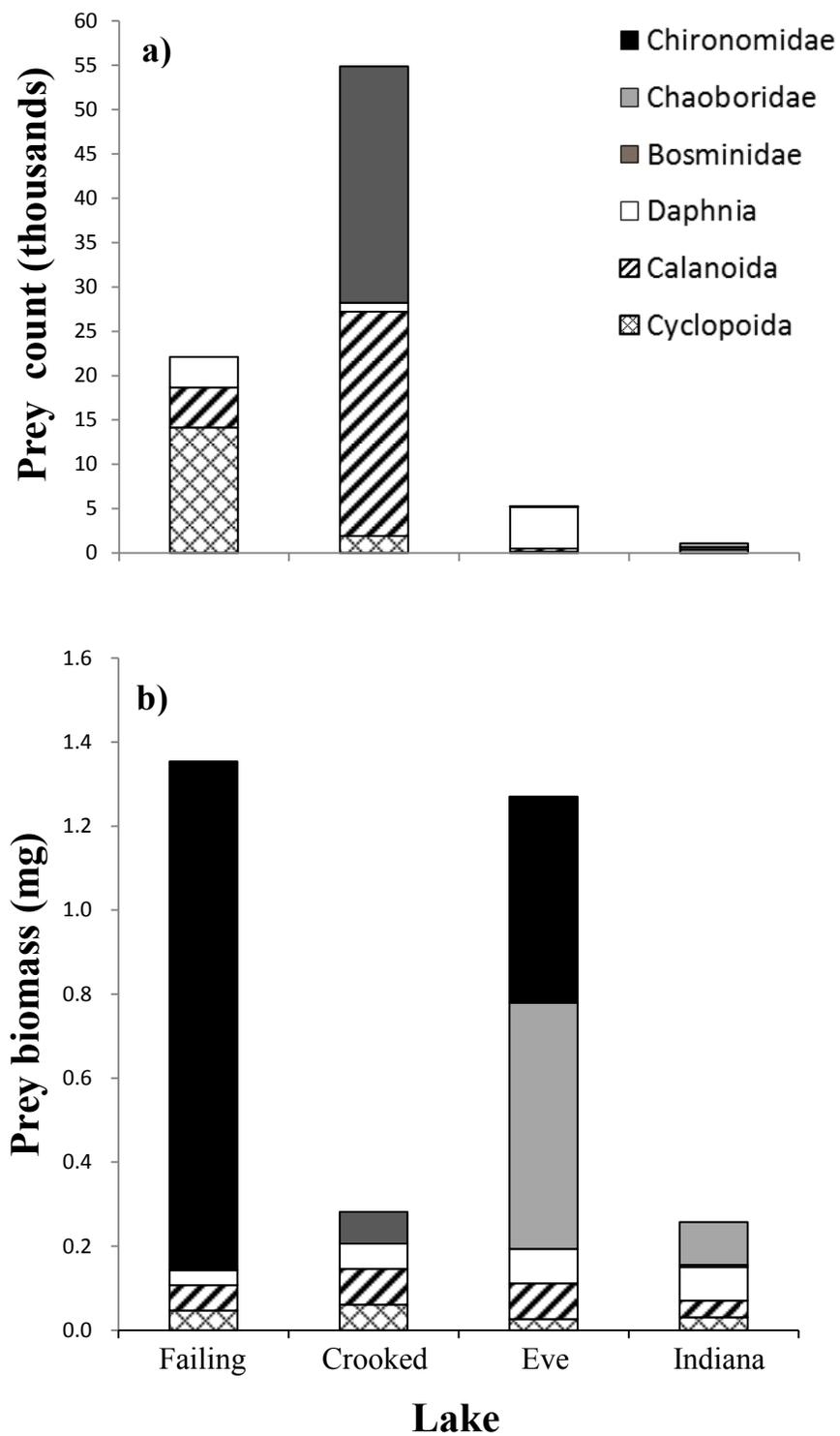
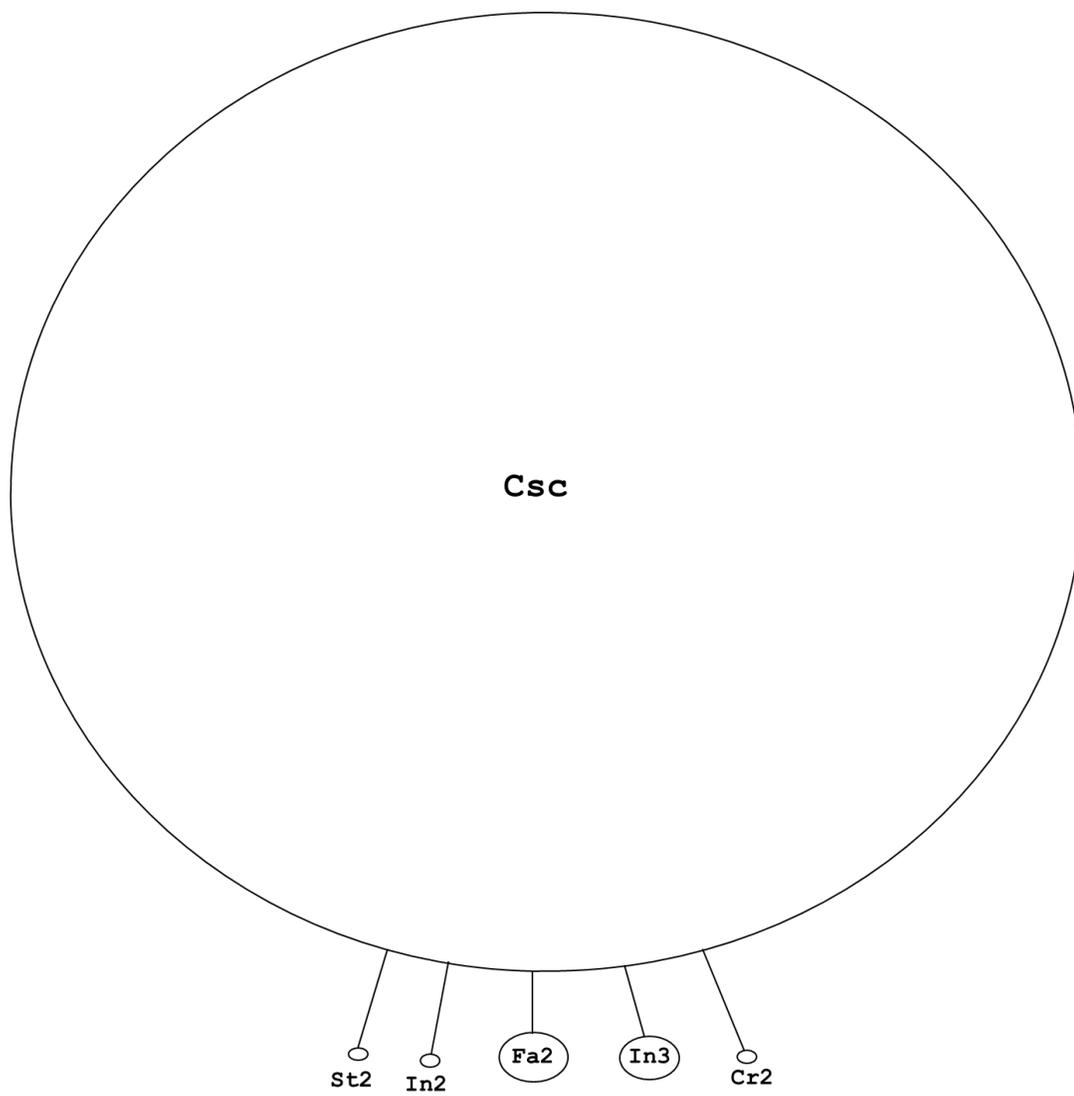


Figure 1.4



**Figure 1.5**

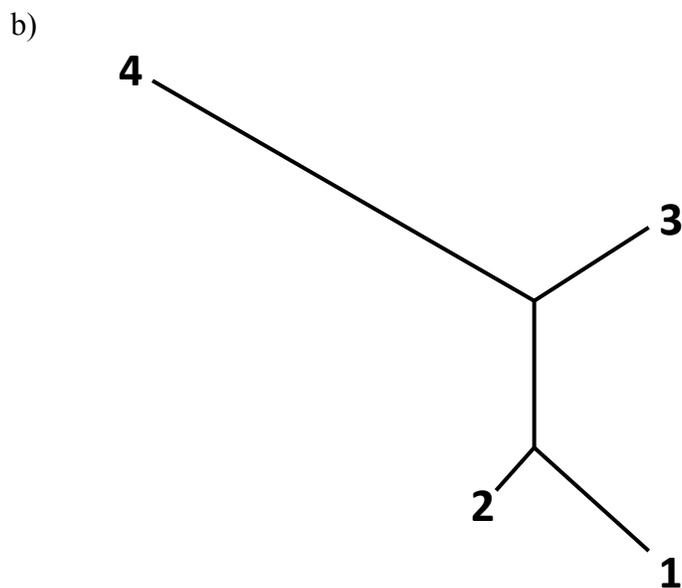
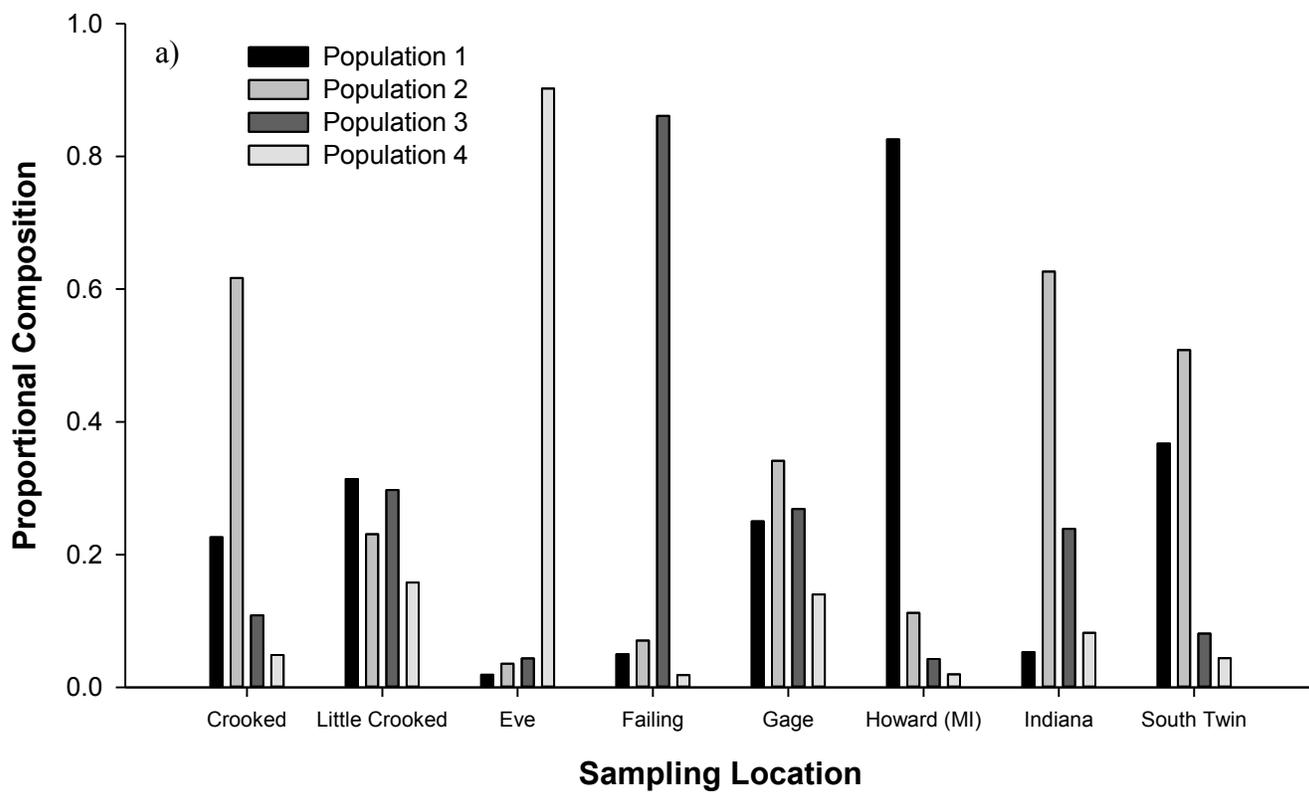


Figure 1.6

1.9 Supplementary Material

**Table S1.1** Mean total length (mm) and wet weight (g) of males versus females in the study lakes. Two-sample t-tests assuming unequal variances were used to assess significance of differences (two-tailed p-values are reported).

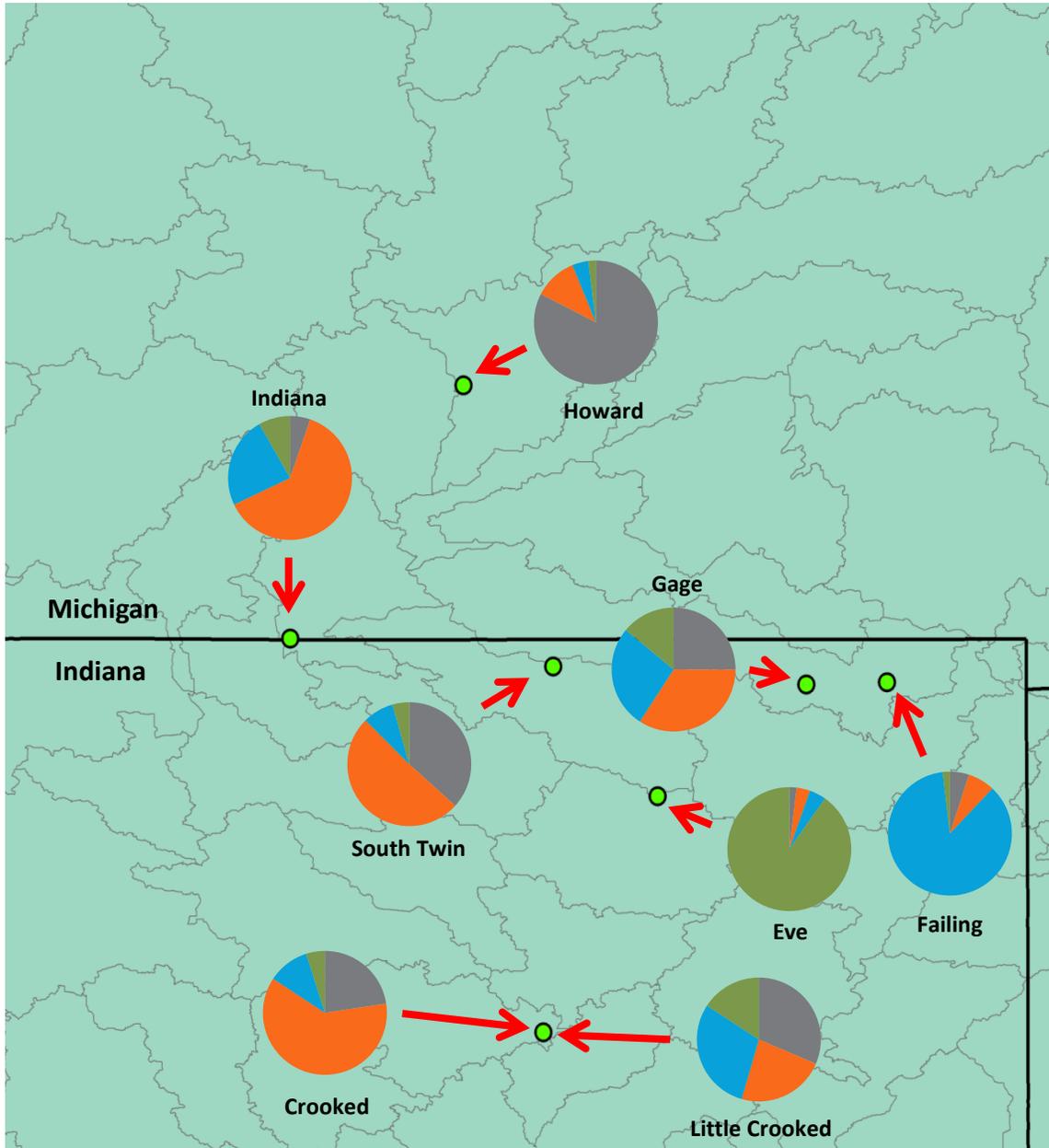
Lake	Mean Total Length (mm)			Mean Wet Weight (g)		
	Male	Female	p-value	Male	Female	p-value
Crooked <sup>†</sup>	312.7	281.7	0.036*	258.9	203.4	0.114
Little Crooked	339.6	338.5	0.918	340.1	381.3	0.108
Eve	362.9	370.4	0.273	466.8	482.9	0.563
Failing	252.7	255.5	0.286	141.7	156.1	0.006*
Gage	398.1	416.1	<0.001*	664.2	797.3	<0.001*
Howard (MI)	287.3	293.3	0.038*	194.4	189.3	0.388
Indiana	328.6	324.1	0.696	346.9	354.7	0.812
South Twin	221.8	220.9	0.870	98.0	105.5	0.408

\*Denotes  $p < 0.05$

<sup>†</sup> Only individuals collected during November sampling were included in calculations

**Table S1.2** Potential cisco lakes sampled by the Indiana Department of Natural Resources using experimental gill nets in 2012-2013. Although these lakes were thought to be the most likely remaining cisco lakes (based on recent surveys), ciscoes were found in only seven locations (Steven Donabauer, IN-DNR, personal communication). Y = yes, N = no.

<b>Lake</b>	<b>County</b>	<b>Year Sampled</b>	<b>Cisco Present</b>
Big Cedar	Whitley	2013	N
Clear	Steuben	2013	N
Crooked	Noble	2012	Y
Dillard's Pit	Kosciusko	2013	N
Eve	LaGrange	2012	Y
Failing	Steuben	2012	Y
Gage	Steuben	2012	Y
George	Steuben	2013	N
Gordy	Noble	2012	N
Green	Steuben	2013	N
Indiana	Elkhart	2012	Y
Knapp	Noble	2013	N
Lawrence	Marshall	2013	N
Little Lime	Steuben	2013	N
Martin	LaGrange	2013	N
Meserve	Steuben	2013	N
Myers	Marshall	2013	N
North Twin	LaGrange	2013	Y
Olin	LaGrange	2013	N
Oliver	LaGrange	2013	N
South Twin	LaGrange	2012	Y



**Figure S1.1** Proportional compositions of genetic populations estimated by *STRUCTURE* (based on microsatellite genotypes) across 10-digit watersheds in northeastern Indiana and southern Michigan cisco lakes. Purple = population 1, orange = population 2, blue = population 3, green = population 4 (see Fig. 1.6). There were no apparent patterns in genetic composition across watersheds. Trends across 8-digit (coarser) watersheds were also examined, with similar results.

CHAPTER 2. AN ANALYSIS OF LAKE MORPHOMETRIC AND LAND-USE  
CHARACTERISTICS THAT PROMOTE THE SURVIVAL OF CISCO  
(*COREGONUS ARTEDI*) IN INDIANA

2.1 Introduction

There is broad evidence that climate change is impacting distributions of plant and animal species worldwide (e.g., Parmesan and Yohe 2003; Hampe and Petit 2005). As climates continue to change, the response of species in the northern hemisphere to changing environments may depend heavily upon populations which exist at southern range margins (Thomas et al. 2001; Iverson et al. 2004; Travis and Dytham 2004). These southernmost populations may be disproportionately critical for the survival and evolution of a species, and they may require conservation strategies that are specifically designed to meet their individual needs (Hampe and Petit 2005).

The cisco, *Coregonus artedi*, occurs in many northern North American coldwater lacustrine systems, from the upper Mississippi River and Great Lakes basins to Labrador and the Mackenzie River drainage (Dymond 1933; Latta 1995; Scott and Crossman 1998; Aku and Tonn 1999). Their intolerance for warm water and low dissolved oxygen (DO) concentrations (Frey 1955) make cisco sensitive indicators of environmental change (Latta 1995; Jacobson et al. 2008; Sharma et al. 2012) and render the species susceptible to mortality events and local extirpations given warm water or hypoxic (low DO) conditions (Frey 1955; Colby and Brooke 1969; Crisman 1993; Koza 1994; Pearson

2001). In Indiana, the southern range limit for cisco (Koza 1994; Turgeon and Bernatchez 2001, 2003), pristine coldwater habitat is lacking (Clingerman et al. 2013) and ciscoes are limited to some of the most oligotrophic glacial lakes in the northern portion of the state (Latta 1995; Pearson 2001). However, climate warming and intensive land-use within glacial lake catchments have exacerbated high thermal and hypoxic conditions and led to a drastic decline in the number of cisco lakes in Indiana, from 45 in the 1900s to 42 in the 1950s, 24 in 1975, 15 in 1994, 13 in 2001, and 7 in 2012-3 (Koza 1994; Pearson 2001; Table S1.2).

The decline of cisco populations in Indiana has prompted the listing of cisco as a species of special concern within the state (Whitaker and Amlaner 2012). This listing, in turn, has led to an increased interest in cisco conservation and management within the Indiana Department of Natural Resources. The agency's course of action may include strategies such as, but not limited to, (1) identifying and preserving the healthiest, most sustainable cisco populations (which may be the most monetarily and logistically feasible method), (2) identifying and attempting to conserve the populations at the highest risk of extirpation (which may be the most biologically valuable conservation method, given the biological importance of southernmost populations; Hampe and Petit 2005), and (3) reintroducing ciscoes into lakes which have previously lost cisco populations (which may supplement either of the above methods).

The management of Indiana's ciscoes is currently limited by a paucity of knowledge regarding the sustainability of remaining populations. In particular, knowledge of the characteristics of glacial lakes and their catchments that promote the survival of the obligate coldwater fish is lacking. Therefore, in order to help to inform

cisco management and preservation efforts in Indiana, the objectives of this study were to analyze lake morphometric and land-use data to identify lakes which are most likely (1) to continue supporting a cisco population for the foreseeable future, (2) to lose cisco in the near future (i.e., due to population extirpation), and (3) to serve as candidates for cisco reintroduction.

## 2.2 Methods

### 2.2.1 Data Collection

This analysis aimed to characterize Indiana's glacial lake habitats using data that spanned multiple spatial scales while simultaneously preserving relatively large sample sizes. Specifically, the analysis aimed to include data which described measures of (1) lake, (2) catchment, and (3) land-use variables for each glacial lake in the dataset. To that end, data collected by the Indiana Department of Natural Resources (IN-DNR) which describe the morphometric characteristics of glacial lakes in Indiana were assembled (Steven Donabauer, IN-DNR, personal communication). Limited data availability for certain metrics across lakes (e.g., mean depth) necessitated the removal of those measures from the dataset. The final dataset included measures of lake area (km<sup>2</sup>), maximum depth (m), shoreline development index (SDI), and geographic location (latitude and longitude of the lake's centroid) for each of 359 glacial lakes in Indiana, including 44 of the 45 historically reported cisco lakes (excluding Waubee Lake, Kosciusko Co.). In addition, Perry (2011) conducted catchment delineations of all lakes included, thereby providing data describing both local (lake only) and total (lake plus tributary) catchment areas (km<sup>2</sup>)

for each lake. Using these data, ratios of lake area to both local and total catchment area (which serve as proxies for the amount of potential nutrient loading in a lake) were calculated for each lake. Finally, four variables describing the proportional composition of agricultural, developed, forested, and wetland land cover in the total catchment were calculated for each lake using data from the National Land Cover Database 2011 (Jin et al. 2013) and ArcGIS software (ESRI 2013). Thus, a total of 13 explanatory variables describing each lake across the three scales mentioned above (5 lake-level variables, 4 catchment-level variables, and 4 landscape-level variables) were incorporated in the analysis. Aside from the land cover calculations, all calculations and all subsequent statistical analyses were conducted in R version 3.0.2 (R Core Team 2013).

## 2.2.2 Data Analysis

### 2.2.2.1 Overview

Each of the three study objectives was evaluated in the context of two datasets: (1) a dataset including all 359 lakes (hereafter D1) and (2) a dataset which included only the past and present cisco lakes ( $n = 44$  lakes for which morphometric data were available; hereafter D2). To this end, three distinct modeling approaches were employed and applied to each dataset: multiple logistic regression (MLR), classification and regression tree modeling (CART), and principal components analysis (PCA). For the first two model types (MLR and CART), the response was cisco presence, defined as a binary variable (0 = absent, 1 = present). In the case of D1, cisco presence was given a value of 1 if the lakes currently or previously contained cisco populations. In the case of D2, only lakes

which currently contain cisco were assigned a presence value of 1. Therefore, analyses of D1 assess the lake morphometric and land-use characteristics which distinguish past and present cisco lakes from lakes which never contained cisco, whereas analyses of D2 assess the characteristics which distinguish current cisco lakes from lakes which are reported to have lost cisco populations within the last century. Although they differ, analyses of both datasets are able to address the three goals listed above, and agreement among results of the two analyses may serve to strengthen analytical inference.

#### 2.2.2.2 Model Descriptions

The MLR and CART modeling approaches were similarly constructed in order to increase comparability of results across modeling frameworks. Due to significant correlations ( $r \geq 0.7$ ) among explanatory variables, six of the 13 available metrics were removed from these models (SDI, longitude, local catchment area, the ratio of lake area to local catchment area, the proportion of wetland land cover in the total catchment, and the proportion of forested land cover in the total catchment). The final models were both additive and consisted of the remaining seven explanatory variables: lake area, maximum depth, latitude, total catchment area, the ratio of lake area to total catchment area, the proportion of agricultural land cover in the total catchment, and the proportion of developed land cover in the total catchment. Thus, the aim of assessing glacial lake habitats across multiple spatial scales was preserved in these univariate contexts, as 3 lake-level variables, 2 catchment-level variables, and 2 landscape-level variables were included. In addition, the proportions of land cover (agricultural and developed) were

arcsin-square root transformed for approximate normalization. Both models were applied to D1 and D2. The CART model only included splits which improved the overall fit of the model ( $R^2$ ) by 1% (i.e., the complexity parameter was set to 0.01). CART model trees were pruned by minimizing cross-validated error (Breiman et al. 1984). Given that this analysis does not aim to identify the most important explanatory factors driving cisco presence and in order to maintain comparability across analyses of D1 and D2, no model selection methods (e.g., AIC selection) were employed. MLR and CART models were coded using the `glm` (stats package) and `rpart` (rpart package) functions in R, respectively.

The PCA model construction differed from that of the MLR and CART. The PCA included all 13 explanatory variables, as it is robust to correlation among variables (Legendre and Legendre 2012) and it did not model a response. Rather, the PCA was used to visualize cisco presence/absence in ordination space based on the 13 explanatory variables. Prior to conducting the PCA, all four variables describing proportional land cover were arcsin-square root-transformed. Furthermore, all explanatory variables were scaled to a mean of 0 and standard deviation of 1, allowing for adequate relative comparisons among lakes in multivariate space.

#### 2.2.2.3 Synthesis

In order to evaluate the three objectives of the analysis, results from each of the modeling frameworks were combined. For the MLR and CART frameworks, this was accomplished *via* a comparison of residuals. Residual values were calculated for each lake within each framework and ranked from least to greatest. In the context of D1, the

most negative residuals (lowest rank) signify lakes which never contained cisco but are the most similar to cisco lakes, whereas the most positive residuals (highest rank) indicate cisco lakes which are most unlike other cisco lakes (i.e., more similar to non-cisco lakes). In addition, D1 residual values which are slightly positive are informative in that they indicate the “best” cisco lakes, i.e., those which are most likely to continue supporting cisco populations, based on land-use and morphometry. If, however, ciscoes have become extirpated from any of these lakes (which would not be indicated *a priori* in analyses of D1, as they treat both past and present cisco lakes in the same manner), they may serve as good candidates for cisco reintroduction. In the context of D2, the most negative residual values (lowest rank) indicate good candidates for cisco reintroduction, while the most positive values (highest rank) indicate those current cisco lakes which are most similar to lakes which have lost cisco (i.e., the current cisco lakes that are most likely to lose cisco). In this case, residuals that are slightly positive indicate the current cisco lakes which are most likely to continue supporting cisco populations. To synthesize results, residual ranks from both the MLR and CART frameworks were averaged, and lakes were sorted according to average rank.

Results from the PCA were used to graphically display and qualitatively compare the relationships among lakes as well as the results of the MLR and CART models. Lakes were plotted on the first two principal components for both dataset scenarios (D1 and D2) and labeled according to cisco presence or absence. In addition, lakes which may be of interest (“good” cisco lakes, “poor” cisco lakes, and potential reintroduction lakes) were labeled separately for comparison.

### 2.3 Results and Discussion

The results of the MLR for D1 show that maximum depth and latitude are significantly, positively related to cisco presence (Table 2.1). That is, deeper lakes that are further north within Indiana are more likely to be cisco lakes, either currently or in the past. Although the MLR for D2 explained more variance overall (32% versus 24% for D1), it did not contain any variables which significantly explained variation in cisco presence ( $\alpha = 0.05$ ; Table 2.1). The difference in the amount of variance explained between the MLRs of D1 and D2 may be due, in part, to the relatively low null deviance among lakes in D2, thereby resulting in a high proportion of variance explained despite poor explanatory variable performance. In addition, the poor performance of the explanatory variables in the MLR of D2 may indicate a high degree of similarity among past and current cisco lakes (i.e., past and current cisco lakes are, on the whole, morphometrically similar).

The pruned CART model tree for D1 retained a total of two splits, the first for maximum depth and the second for total catchment area (Fig. 2.2a). These results indicate that lakes which currently contain or previously contained cisco are often deeper lakes, and that they tend to occur at a higher frequency in larger catchments. Total catchment area may serve as a proxy for overall lake size given that it is often positively correlated with local catchment area, lake area, maximum depth, and shoreline development index (see Figs. 2.3a, 2.4a). The final CART model tree for D2 included only one split based on total catchment area (Fig. 2.2b). In this case, the model indicates that current cisco lakes tend to exist in smaller catchments than lakes that have lost cisco.

Again, catchment area may serve as a proxy for overall lake size; thus, results suggest that current cisco lakes are often smaller and shallower than former cisco lakes.

The synthesized residual rank results closely mirror the results from the MLR and CART models, as results from both model types were generally in agreement across lakes and datasets (Tables 2.2, 2.3, S2.1, S2.2). That is, residual rank orders were not drastically different between MLR and CART frameworks for either dataset. In general, analyses of D1 indicate that larger, deeper lakes are more likely to support cisco populations (Tables 2.2, S2.1). Thus, lakes such as Crooked (Noble Co.) and Gage (Steuben Co.), the largest of the current cisco lakes (1.6 km<sup>2</sup> and 3.2 km<sup>2</sup>, respectively) are considered to contain the most sustainable cisco populations (i.e., they have the lowest positive residual values). Analyses of D1 also point to North Twin (Lagrange Co.) and Failing (Steuben Co.) lakes as being the most likely to lose current cisco populations, as they are smaller and more morphometrically similar to non-cisco lakes. Moreover, analyses of D1 suggest that large, deep lakes which have lost cisco, e.g., Tippecanoe Lake (Kosciusko Co.), Dallas Lake (Lagrange Co.), Clear Lake (Steuben Co.), James Lake (Steuben Co.), and Snow Lake (Steuben Co.) are the most advisable lakes to consider for cisco reintroduction. These lakes are easy to distinguish on the plot of the first two principal components from the PCA of D1 (Fig. 2.3); they load heavily in the direction of large, deep lakes (i.e., large maximum depth, large lake area, etc.; Fig. 2.3a) and are among the largest former cisco lakes. Finally, analyses of D1 indicate that Adams (Lagrange Co.), Pretty (Lagrange Co.), Round (Whitley Co.), Loon (Noble Co.), and Diamond (Noble Co.) lakes are the non-cisco lakes that are most morphometrically

similar to cisco lakes; thus, they may plausibly serve as lakes in which cisco could be introduced (depending upon management aims).

As a whole, results from analyses of D2 provide a contrast to those of D1. D2 results suggest that the smaller and shallower of the cisco lakes are best suited for cisco persistence (Tables 2.3, S2.1). Thus, Gage and Crooked lakes, considered by D1 results to be among the most sustainable of the current cisco lakes, are considered among the least sustainable according to analyses of D2. South Twin (Lagrange Co.), Indiana (Elkhart Co.), and Failing lakes are considered the most sustainable of the D2 lakes, and Green (Steuben Co.), Atwood (Lagrange Co.), Seven Sisters (Steuben Co.), Clear (Steuben Co.) and Olin (Lagrange Co.) lakes are considered the lakes most suitable for cisco reintroduction (Table 2.3).

The differences between analyses of D1 and D2 are illustrated well by the PCA plot of D2 (Fig. 2.4). Many of the current cisco lakes fall in quadrants I and IV, away from the larger and deeper lakes that D1 analyses suggest would be suitable for cisco reintroduction. The suggested reintroduction lakes from D2 align well with the current cisco lakes. However, these patterns may, in part, be a function of probabilities (i.e., most of the cisco lakes are in quadrants I and IV) or represent the effects of factors not directly modeled in this analysis (e.g., predation, competition, water temperature, dissolved oxygen concentrations, etc.) on cisco survival.

In addition to displaying the contrasts between analyses, the D2 PCA plot sheds light on the notion that cisco may persist more effectively in lakes where the lake area to total catchment area ratio is high, i.e., headwater lakes (Fig. 2.4). Four of the seven current cisco lakes, along with three of the five most plausible reintroduction lakes

(according to analyses of D2), fall in quadrant I and have among the highest lake area to total catchment area ratios. A potential mechanism for the apparent success of ciscoes in headwater lakes is a relatively low amount of nutrient loading (likely positively related to catchment size), which may help to preserve water quality and restrict the duration and extent of hypoxia. Furthermore, this plot helps to display the morphometric “position” of Clear Lake (Steuben Co.), the only lake in the top five most likely reintroduction lakes for analyses of both D1 and D2. The lake is approximately centralized among the deep, large lakes and the small, shallow lakes that are favored by analyses of D1 and D2, respectively. Therefore, based on morphometry and land-use, Clear Lake may be the most plausible cisco reintroduction lake overall.

Taken together, the results of analyses of D1 and D2 highlight the importance of land-use practices as drivers of cisco extirpation. Larger lakes which are often deeper typically exist in larger catchments and are likely subject to higher levels of development, agriculture, and ultimately nutrient loading. Thus, land-use practices over the past century surrounding these larger lakes, which initially contained larger volumes of adequate cisco habitat, may have led to cisco extirpations. The smaller headwater lakes (which have a high lake area to total catchment area ratio) are more frequently spared of high nutrient loading due to intensive land-use. Therefore, given that these small lakes contain some level of adequate cisco habitat, they may better promote cisco survival compared to larger lakes. This is encouraging in that it suggests the potential for successful cisco reintroduction into larger lakes given reduced levels of nutrient loading. If, for instance, nutrient loading due to land-use practices around large, deep lakes (e.g., Tippecanoe,

Dallas) is reduced, then they may once again serve as suitable cisco lakes, thereby increasing the likelihood of cisco preservation in Indiana.

In addition to the apparent emphasis on the importance of land-use practices, the results emphasize the need for analyses such as these to be augmented by other salient information, such as knowledge of fish and prey community compositions, water quality, fishing pressure, and other factors. For instance, although Green Lake (Steuben Co.) is the most plausible cisco reintroduction lake according to D2 analyses, it is important to note that this lake is bisected by Interstate 69; thus, it may receive more chemical and nutrient loading than expected (given its catchment size) which may reduce water quality, thereby making the lake inappropriate for cisco reintroduction. Indeed, Green Lake served as a reintroduction site in the 1990s (Pearson 2001) but failed to sustain a cisco population based on the most recent survey (2013; Steven Donabauer, IN-DNR, personal communication), suggesting that this lake may be inadequate for future reintroduction efforts. Moreover, biotic conditions in some lakes may not be suitable for cisco persistence. For instance, several lakes which may be suitable for cisco based on lake morphometry and land-use contain high densities of native and introduced predators (e.g., northern pike *Esox lucius*, rainbow trout *Oncorhynchus mykiss*).

The preservation of Indiana's declining cisco populations may be important to the conservation of the species as a whole. This study highlights the importance of land-use practices, which often interact with lake- and catchment-level factors, in exacerbating cisco extirpations, and it points to Clear Lake as the most plausible lake for cisco reintroduction. As a whole, these results provide a quantitative foundation that, if considered in the context of other relevant (e.g., biotic) information, may be useful in

informing the management and preservation of this unique and potentially vital biological resource.

## 2.4 References

- Aku, P.M.K. and Tonn, W.M. (1999). Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Transactions of the American Fisheries Society* 128: 17-30.
- Breiman, L., Friedman, J., Olshen, R., Stone, C. (1984). *Classification and regression trees*. Wadsworth and Brooks: Pacific Grove, CA.
- Clingerman, J., Petty, T., Boettner, F., Letsinger, S., Strager, J., Hansen, E. (2013). Midwest Fish Habitat Partnership Fish Habitat Modeling Results: Regional Assessment. Report prepared by Downstream Strategies for the National Fish Habitat Partnership. 74 p.
- Colby, P.T., and Brooke, L.T. (1969). Cisco (*Coregonus artedii*) mortalities in a southern Michigan lake, July 1968. *Limnology and Oceanography* 14: 958-960.
- Crisman, T.L. (1993). Assessment of watershed-lake interactions influencing the cultural eutrophication of Little Crooked and Crooked Lakes, Indiana. Report submitted to the Crooked Lake Property Owners Association, on behalf of the Indiana Lake Enhancement Program, Division of Soil Conservation, Indiana Department of Natural Resources. Indianapolis, IN.
- Dymond, J.R. (1933). The coregonine fishes of Hudson and James bays. In Biological and Oceanographic conditions in Hudson Bay. *Contributions to Canadian Biology and Fisheries* 8: 1-12.
- ESRI. (2013). ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.

- Frey, D.G. (1955). Distributional ecology of the cisco *Coregonus artedi* in Indiana. *Investigations of Indiana Lakes and Streams* 4: 177-228.
- Gerking, S.D. (1945). Distribution of the fishes of Indiana. *Investigations of Indiana lakes and streams* vol. III: 1-137.
- Hampe, A. and Petit, R.J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461-467.
- Iverson, L.R., Schwartz, M.W., Prasad, A.M. (2004). How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13: 209-219.
- Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., Xian, G. (2013). A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of the Environment* 132: 159-175.
- Koza, L. (1994). Current status of cisco abundance, habitat and harvest at northern Indiana lakes. Indiana Department of Natural Resources, Division of Fish and Wildlife report. Indianapolis, IN.
- Latta, W.C. (1995). Distribution and abundance of the lake herring (*Coregonus artedi*) in Michigan. Michigan Department of Natural Resources, Fisheries Division research report 2014.
- Legendre, P. and Legendre, L. (2012). *Numerical Ecology, Third English Edition*. Elsevier: Amsterdam, the Netherlands.
- Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

- Pearson, J. (2001). Cisco population status and management in Indiana. Indiana Department of Natural Resources, Division of Fish and Wildlife report. Indianapolis, IN.
- Perry, P.C. (2011). *The role of compensatory dynamics and influence of environmental factors across multiple spatial scales in structuring fish populations*. M.Sc. Thesis, Purdue University, U.S.A.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Scott, W.B. and Crossman, E.J. (1998). *Freshwater fishes of Canada*. Galt House Publications Ltd., Oakville, ON.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E. (2004). Extinction risk from climate change. *Nature* 427: 145-148.
- Travis, J.M.J. and Dytham, C. (2004). A method for simulating patterns of habitat availability at static and dynamic range margins. *Oikos* 104: 410-416.
- Turgeon, J., and Bernatchez, L. (2001). Mitochondrial DNA phylogeography of lake cisco (*Coregonus artedii*): evidence supporting extensive secondary contacts between two glacial races. *Molecular Ecology* 10: 987-1001.
- Turgeon, J. and Bernatchez, L. (2003). Reticulate evolution and phenotypic diversity in North American ciscoes, *Coregonus* spp. (Teleostei: Salmonidae): implications for the conservation of an evolutionary legacy. *Conservation Genetics* 4: 67-81.

Whitaker, Jr., J. O. and C. J. Amlaner, Jr. 2012. Habitats and ecological communities of Indiana: presettlement to present. Indiana Department of Natural Resources and Indiana State University. Indiana University Press, Bloomington, Indiana. 491 pp.

2.5 Tables

**Table 2.1** MLR model results for D1 (all lakes) and D2 (cisco lakes only), including coefficient sign, z-value, and p-value for each explanatory variable included. The models for D1 and D2 explained 24% ( $D^2 = 0.241$ ) and 32% ( $D^2 = 0.316$ ) of the variance in the data, respectively. LA / TCA = ratio of lake area to total catchment area; Proportion Ag, Proportion Dev = arcsin-square root-transformed proportional composition of agricultural and developed land cover, respectively, in the total catchment. Asterisks indicate  $p < 0.05$ .

Factor	D1			D2		
	Sign	z-value	p-value	Sign	z-value	p-value
Intercept	-	-3.434	<0.001*	-	-1.608	0.108
Lake Area	-	-1.55	0.121	-	-0.895	0.371
Max. Depth	+	6.183	<0.001*	+	1.009	0.313
Total Catchment Area	+	0.734	0.463	-	-0.761	0.447
LA / TCA	+	0.277	0.782	+	1.156	0.248
Latitude	+	3.323	0.001*	+	1.611	0.107
Proportion Ag	+	1.095	0.274	-	-0.635	0.525
Proportion Dev	+	1.165	0.244	-	-0.332	0.740

**Table 2.2** Abridged results of MLR and CART models in the D1 (all 359 lakes) scenario, including lake name, MLR and CART residuals, residual ranks, and mean rank value.

Current cisco lakes are highlighted in bold. See Table S2.1 for complete results.

Lake Name	County	MLR Residual	MLR Rank	CART Residual	CART Rank	Mean Rank
Adams	Lagrange	-1.627	1	-0.308	1	1
Pretty	Lagrange	-1.492	2	-0.308	1	1.5
Round	Whitley	-1.369	3	-0.308	1	2
Loon	Noble	-1.226	4	-0.308	1	2.5
Diamond	Noble	-1.215	5	-0.308	1	3
--	--	--	--	--	--	--
Tippecanoe	Kosciusko	0.569	316	0	316	316
Dallas	Lagrange	0.717	318	0	316	317
Clear	Steuben	0.576	317	0.691	323	320
<b>Crooked</b>	Noble	0.777	319	0.691	323	321
James	Steuben	1.259	327	0	316	321.5
Snow	Steuben	0.807	320	0.691	323	321.5
--	--	--	--	--	--	--
<b>Gage</b>	Steuben	1.178	326	0.691	323	324.5
--	--	--	--	--	--	--
<b>South Twin</b>	Lagrange	1.411	328	0.691	323	325.5
--	--	--	--	--	--	--
<b>Eve</b>	Lagrange	1.959	346	0.943	344	345
<b>Indiana</b>	Elkhart	1.973	347	0.943	344	345.5
Hackenburg	Lagrange	2.041	349	0.943	344	346.5
<b>Failing</b>	Steuben	2.064	350	0.943	344	347
<b>North Twin</b>	Lagrange	2.067	351	0.943	344	347.5
Seven Sisters	Steuben	2.086	352	0.943	344	348
Gooseneck	Steuben	2.313	354	0.943	344	349
Atwood	Lagrange	2.352	355	0.943	344	349.5
Meserve	Steuben	2.402	356	0.943	344	350
Gordy	Noble	2.416	357	0.943	344	350.5
Village	Noble	2.708	358	0.943	344	351
Hindman	Noble	2.761	359	0.943	344	351.5

**Table 2.2.** Abridged results of MLR and CART models in the D2 (cisco lakes only) scenario, including lake name, MLR and CART residuals, residual ranks, and mean rank value. Current cisco lakes are highlighted in bold. See Table S2.2 for complete results.

Lake Name	County	MLR Residual	MLR Rank	CART Residual	CART Rank	Mean Rank
Green	Steuben	-1.349	1	-0.571	1	1
Atwood	Lagrange	-0.864	4	-0.571	1	2.5
Seven Sisters	Steuben	-1.041	2	-0.081	4	3
Clear	Steuben	-0.897	3	-0.081	4	3.5
Olin	Lagrange	-0.714	5	-0.081	4	4.5
--	--	--	--	--	--	--
<b>South Twin</b>	Lagrange	0.427	38	0.428	38	38
<b>Indiana</b>	Elkhart	0.686	39	0.428	38	38.5
<b>Failing</b>	Steuben	1.069	40	0.428	38	39
<b>Eve</b>	Lagrange	2.013	43	0.428	38	40.5
<b>Crooked</b>	Noble	1.723	41	0.918	42	41.5
<b>North Twin</b>	Lagrange	1.829	42	0.918	42	42
<b>Gage</b>	Steuben	2.127	44	0.918	42	43

## 2.6 List of Figure Captions

**Figure 2.1** Map depicting the location of Indiana's glacial lake catchments. Catchments are highlighted in dark gray.

**Figure 2.2** CART model trees for (a) D1 (all lakes) and (b) D2 (cisco lakes only).

**Figure 2.3** (a) Variable factor map for the PCA of D1 (all lakes) displaying the loading of each explanatory variable on the first two principal components. AG, WT, DV, FO = arcsin-square root transformed proportion of agricultural, wetland, developed, and forested land cover in the total catchment, respectively; LO = longitude; LA = latitude; TC = total catchment area ( $\text{km}^2$ ); LC = local catchment area ( $\text{km}^2$ ); MD = maximum depth (m); AR = lake area ( $\text{km}^2$ ); SD = shoreline development index; A/T, A/L = ratio of lake area to total and local catchment area, respectively. (b) Plot of lakes from D1 on the first two principal components. Dots = non-cisco lakes; square = five potential reintroduction lakes according to D1; triangles = all remaining former cisco lakes; circles = current cisco lakes.

**Figure 2.4** (a) Variable factor map for the PCA of D2 (cisco lakes only) displaying the loading of each explanatory variable on the first two principal components. AG, WT, DV, FO = arcsin-square root transformed proportion of agricultural, wetland, developed, and forested land cover in the total catchment, respectively; LO = longitude; LA = latitude; TC = total catchment area ( $\text{km}^2$ ); LC = local catchment area ( $\text{km}^2$ ); MD = maximum

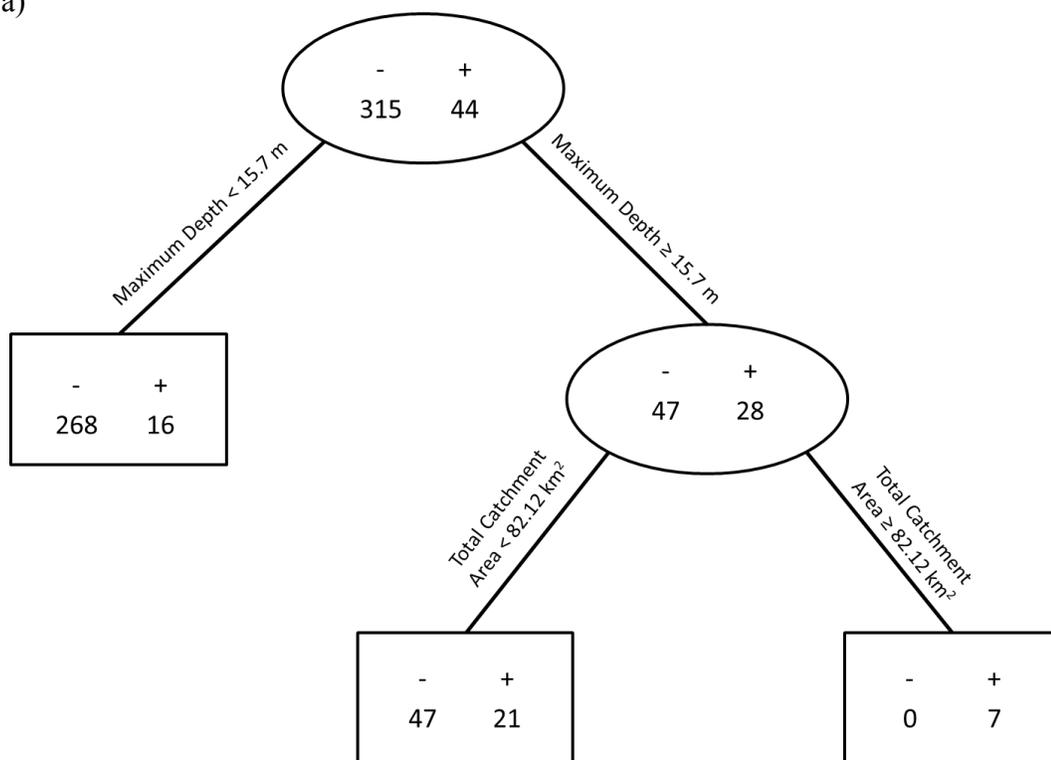
depth (m); AR = lake area ( $\text{km}^2$ ); SD = shoreline development index; A/T, A/L = ratio of lake area to total and local catchment area, respectively. (b) Plot of lakes from D2 on the first two principal components. Triangles = two lakes most likely to lose cisco according to univariate analyses of D2; closed circles = remaining current cisco lakes; crosshairs = five potential cisco reintroduction lakes according to univariate analyses of D2; squares = five potential cisco reintroduction lakes according to univariate analyses of D1; open circles = remaining former cisco lakes. Clear Lake (Steuben Co., labeled with crosshair and open square) was selected as a potential reintroduction lake by univariate analyses of both D1 and D2.

2.7 Figures



**Figure 2.1**

a)



b)

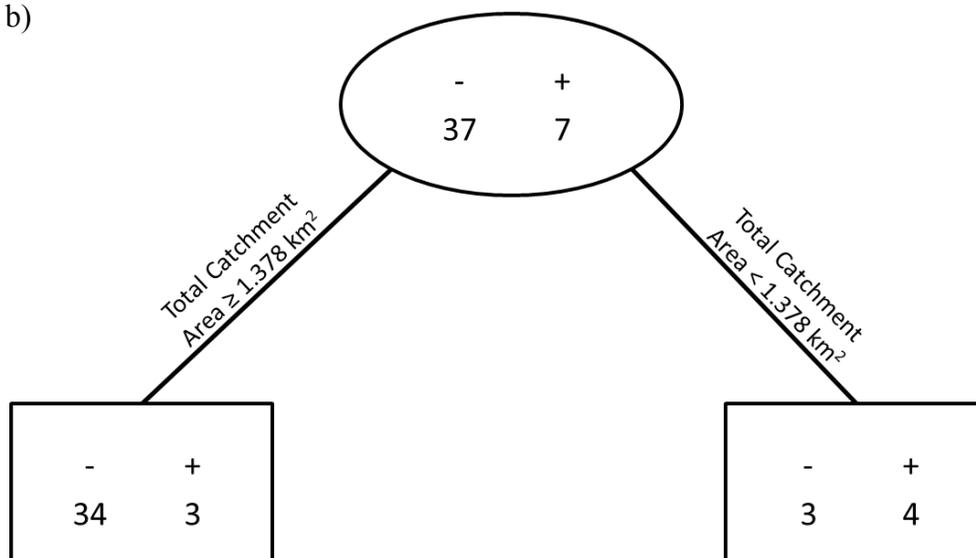


Figure 2.2

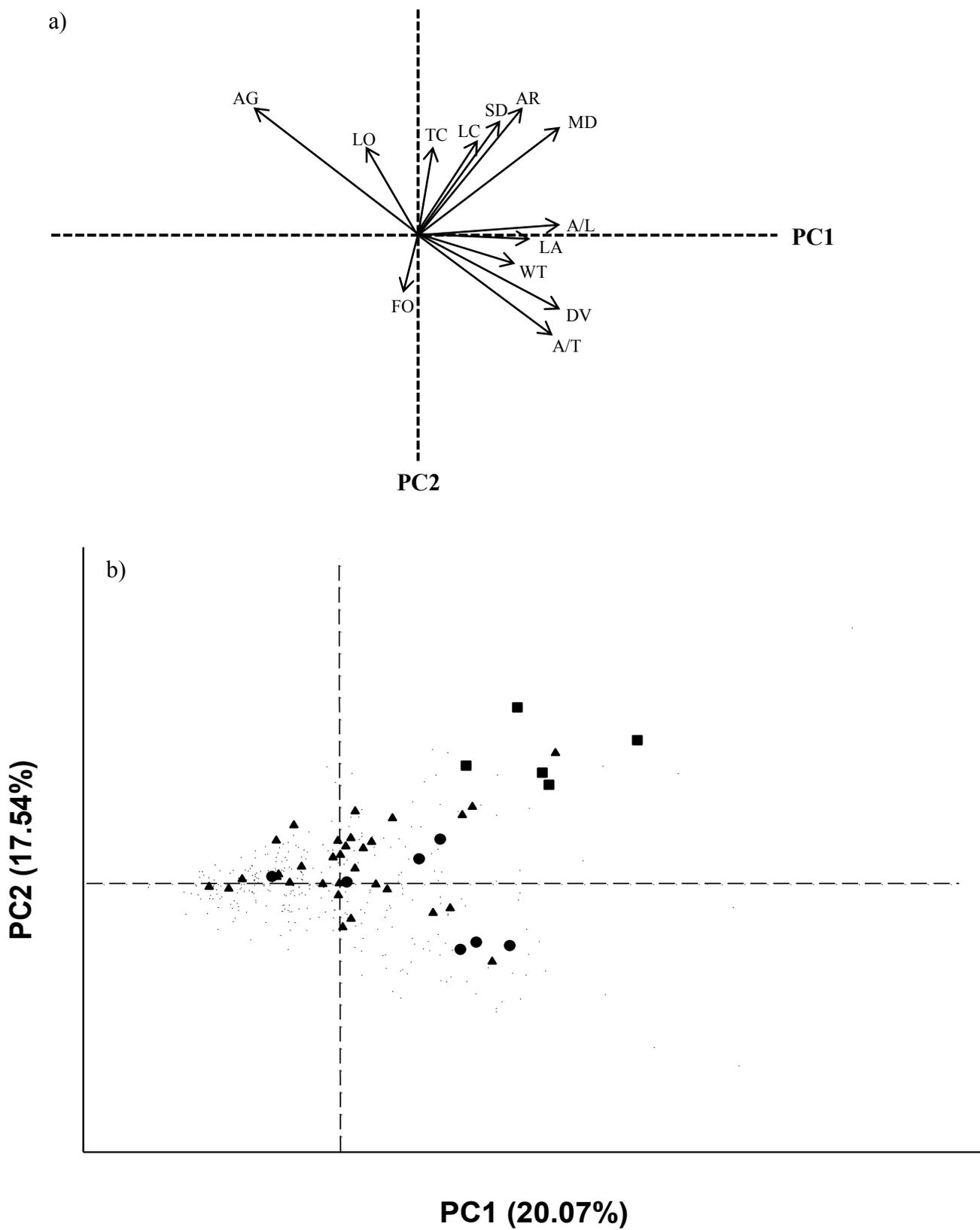


Figure 2.3

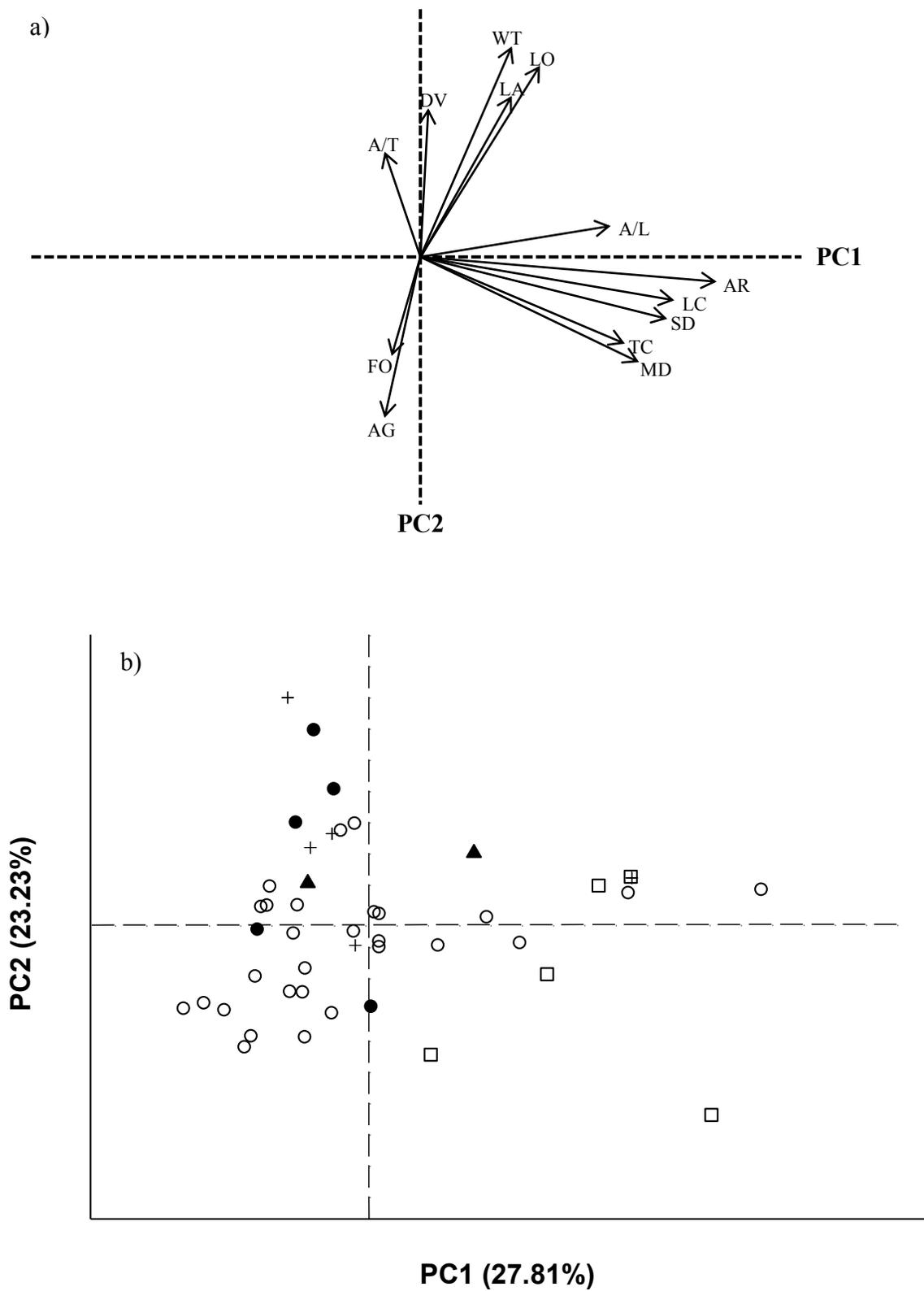


Figure 2.4

2.8 Supplementary Material**Table S2.1.** Complete results of MLR and CART models in the D1 (all 359 lakes)

scenario, including lake name, MLR and CART residuals, residual ranks, and mean rank value. Current cisco lakes are highlighted in bold.

Lake Name	County	GLM Residual	GLM Rank	CART Residual	CART Rank	Mean Rank
Adams	Lagrange	-1.627746224	1	-0.308823529	1	1
Pretty	Lagrange	-1.492516527	2	-0.308823529	1	1.5
Round	Whitley	-1.36936939	3	-0.308823529	1	2
Loon	Noble	-1.226466669	4	-0.308823529	1	2.5
Diamond	Noble	-1.215831854	5	-0.308823529	1	3
Saugany	LaPorte	-1.168571372	6	-0.308823529	1	3.5
Still	Lagrange	-1.166431333	7	-0.308823529	1	4
Troy-Cedar	Whitley	-1.157542199	8	-0.308823529	1	4.5
George	Steuben	-1.11483116	9	-0.308823529	1	5
Fish (n Scott)	Lagrange	-1.059337217	10	-0.308823529	1	5.5
Crooked	Steuben	-1.0318662	11	-0.308823529	1	6
Ball	Steuben	-0.993799646	12	-0.308823529	1	6.5
Little Long	Noble	-0.991750689	13	-0.308823529	1	7
Pine Canyon (Round)	Steuben	-0.990250493	14	-0.308823529	1	7.5
Pine (N&S)	LaPorte	-0.983248566	15	-0.308823529	1	8
Buck	Steuben	-0.960581112	16	-0.308823529	1	8.5
Blackman	Lagrange	-0.935171474	18	-0.308823529	1	9.5
Dewart	Kosciusko	-0.908583879	19	-0.308823529	1	10
Round	Noble	-0.904706588	20	-0.308823529	1	10.5
Pleasant	Noble	-0.904544364	21	-0.308823529	1	11
Big Turkey	Steuben	-0.895523521	22	-0.308823529	1	11.5
Stone	Lagrange	-0.884693996	23	-0.308823529	1	12
Hog	LaPorte	-0.86501871	24	-0.308823529	1	12.5
Holem	Marshall	-0.85377193	25	-0.308823529	1	13
Flint	Porter	-0.845061886	26	-0.308823529	1	13.5
Lake Pleasant	Steuben	-0.814762931	28	-0.308823529	1	14.5
Fox	Steuben	-0.752031878	30	-0.308823529	1	15.5
Sacarider	Noble	-0.741008255	31	-0.308823529	1	16
Goose	Whitley	-0.727207797	33	-0.308823529	1	17
Big	Noble	-0.722866192	35	-0.308823529	1	18
Hamilton	Steuben	-0.71261003	36	-0.308823529	1	18.5
Johnson	Noble	-0.672281772	40	-0.308823529	1	20.5
Cook	Marshall	-0.637888013	44	-0.308823529	1	22.5
Dollar	Whitley	-0.620827338	46	-0.308823529	1	23.5
Bristol	Noble	-0.603634082	50	-0.308823529	1	25.5
Lower Long	Noble	-0.600116716	51	-0.308823529	1	26
Winona	Kosciusko	-0.596608775	52	-0.308823529	1	26.5
Indian	Dekalb	-0.592490577	54	-0.308823529	1	27.5
Upper Long	Noble	-0.579949719	56	-0.308823529	1	28.5
Yellow Creek	Kosciusko	-0.574949875	57	-0.308823529	1	29
Bowen	Noble	-0.563186109	59	-0.308823529	1	30
Bear	Noble	-0.557094254	60	-0.308823529	1	30.5

Table S2.1 continued.

Pigeon North	Lagrange	-0.939311681	17	-0.056338028	48	32.5
Thomas	Marshall	-0.515341894	68	-0.308823529	1	34.5
Barton	Steuben	-0.830864697	27	-0.056338028	48	37.5
Fennel	Lagrange	-0.783060301	29	-0.056338028	48	38.5
St Mary's	St. Joseph	-0.733695352	32	-0.056338028	48	40
Simonton	Elkhart	-0.723693597	34	-0.056338028	48	41
Handy	Steuben	-0.696936295	37	-0.056338028	48	42.5
Rainbow	Lagrange	-0.688350622	38	-0.056338028	48	43
Pleasant	Steuben	-0.680966205	39	-0.056338028	48	43.5
Mud	Steuben	-0.67163465	41	-0.056338028	48	44.5
Booth	Steuben	-0.667373104	42	-0.056338028	48	45
Wall	Lagrange	-0.659215258	43	-0.056338028	48	45.5
Little Otter	Steuben	-0.636905882	45	-0.056338028	48	46.5
Beaver Dam	Kosciusko	-0.463082811	92	-0.308823529	1	46.5
Perch	Steuben	-0.617657463	47	-0.056338028	48	47.5
Fish	Steuben	-0.612416037	48	-0.056338028	48	48
Pigeon	Steuben	-0.604118415	49	-0.056338028	48	48.5
St Joseph	St. Joseph	-0.593685806	53	-0.056338028	48	50.5
Long (Little Long)	Steuben	-0.58942908	55	-0.056338028	48	51.5
Fancher	Lake	-0.565657233	58	-0.056338028	48	53
Little Bower	Steuben	-0.549509685	61	-0.056338028	48	54.5
Waubee	Kosciusko	-0.546289687	62	-0.056338028	48	55
Taylor	Lagrange	-0.543473561	63	-0.056338028	48	55.5
Eagle	Noble	-0.529776564	64	-0.056338028	48	56
Hudson	LaPorte	-0.528478864	65	-0.056338028	48	56.5
Brokesha	Lagrange	-0.518174941	66	-0.056338028	48	57
Bass(N Chain)	Pulaski	-0.516041394	67	-0.056338028	48	57.5
Emma	Lagrange	-0.510443018	69	-0.056338028	48	58.5
Long (Pigeon River)	Steuben	-0.492396142	70	-0.056338028	48	59
Hunter	Elkhart	-0.491845733	71	-0.056338028	48	59.5
Waldron	Noble	-0.490575219	72	-0.056338028	48	60
Mud	Steuben	-0.489135012	73	-0.056338028	48	60.5
Cedar	Lagrange	-0.488842102	74	-0.056338028	48	61
Golden	Steuben	-0.488297122	75	-0.056338028	48	61.5
Nauvoo	Lagrange	-0.487934105	76	-0.056338028	48	62
Johnson	Steuben	-0.486149898	77	-0.056338028	48	62.5
Dixon	Marshall	-0.485467363	78	-0.056338028	48	63
Pleasant	St. Joseph	-0.482597173	79	-0.056338028	48	63.5
Black	Steuben	-0.480860386	80	-0.056338028	48	64
Fish Trap	LaPorte	-0.478535361	81	-0.056338028	48	64.5
Bixler	Noble	-0.477103987	82	-0.056338028	48	65
Mud (Pigeon River)	Steuben	-0.47582221	83	-0.056338028	48	65.5
Hog (Michiana)	Steuben	-0.473168582	84	-0.056338028	48	66
Wauhob	Porter	-0.473093489	85	-0.056338028	48	66.5
Deep	Steuben	-0.472733621	86	-0.056338028	48	67
Steinbarger	Noble	-0.470403705	87	-0.056338028	48	67.5
Westler	Lagrange	-0.469648407	88	-0.056338028	48	68
Sally Owen	Steuben	-0.469319464	89	-0.056338028	48	68.5
Lime (near Gage)	Steuben	-0.464513768	90	-0.056338028	48	69
Smalley	Noble	-0.464009545	91	-0.056338028	48	69.5
Lake-of-the-Woods	Marshall	-0.45772714	93	-0.056338028	48	70.5
Walters	Steuben	-0.453214594	94	-0.056338028	48	71
Mud	Lagrange	-0.450683411	95	-0.056338028	48	71.5
Anne	Steuben	-0.448824601	96	-0.056338028	48	72
Cline	Lagrange	-0.442351024	97	-0.056338028	48	72.5

Table S2.1 continued.

West Otter	Steuben	-0.441327916	98	-0.056338028	48	73
Cotton	Lagrange	-0.439651438	99	-0.056338028	48	73.5
Stone	LaPorte	-0.438470516	100	-0.056338028	48	74
Heaton	Elkhart	-0.436177083	101	-0.056338028	48	74.5
Wolf	Elkhart	-0.435379033	102	-0.056338028	48	75
Tamarack	Noble	-0.435318032	103	-0.056338028	48	75.5
Norman	Noble	-0.433873424	104	-0.056338028	48	76
Fletcher	Fulton	-0.323101932	152	-0.308823529	1	76.5
Silver	Steuben	-0.430194076	105	-0.056338028	48	76.5
Sand	Noble	-0.42813583	106	-0.056338028	48	77
Chamberlain	St. Joseph	-0.425528161	107	-0.056338028	48	77.5
Warner	Steuben	-0.423949203	108	-0.056338028	48	78
Beaver Dam	Steuben	-0.423470208	109	-0.056338028	48	78.5
Hogback	Steuben	-0.423466827	110	-0.056338028	48	79
Little Turkey	Lagrange	-0.419611512	111	-0.056338028	48	79.5
Williams	Noble	-0.417700458	112	-0.056338028	48	80
Mud	Steuben	-0.413936113	113	-0.056338028	48	80.5
Yost	Lagrange	-0.411446067	114	-0.056338028	48	81
Little Turkey	Steuben	-0.409047738	115	-0.056338028	48	81.5
Robinson	Whitley	-0.409026471	116	-0.056338028	48	82
Appleman	Lagrange	-0.402686158	117	-0.056338028	48	82.5
Round (Clear)	Steuben	-0.401763097	118	-0.056338028	48	83
Bower	Steuben	-0.396474599	119	-0.056338028	48	83.5
Pretty	Marshall	-0.3952589	120	-0.056338028	48	84
Latta	Noble	-0.390504408	121	-0.056338028	48	84.5
East	Elkhart	-0.389962701	122	-0.056338028	48	85
Eddy	Marshall	-0.389768257	123	-0.056338028	48	85.5
Maxinkuckee	Marshall	-0.301827493	170	-0.308823529	1	85.5
Middle Center	Steuben	-0.383815741	124	-0.056338028	48	86
Story	Dekalb	-0.383613255	125	-0.056338028	48	86.5
New	Whitley	-0.370834804	126	-0.056338028	48	87
Round	Elkhart	-0.370346792	127	-0.056338028	48	87.5
Cass	Lagrange	-0.370330855	128	-0.056338028	48	88
Blue	Whitley	-0.370108349	129	-0.056338028	48	88.5
Gilbert	Marshall	-0.368467338	130	-0.056338028	48	89
Terry	Dekalb	-0.364948734	131	-0.056338028	48	89.5
Brown	Whitley	-0.361284213	132	-0.056338028	48	90
Bass	Noble	-0.360606491	133	-0.056338028	48	90.5
Bell	Steuben	-0.359474346	134	-0.056338028	48	91
Buck	Lagrange	-0.358673047	135	-0.056338028	48	91.5
George (Hammond)	Lake	-0.353618618	136	-0.056338028	48	92
Spectacle	Porter	-0.353348302	137	-0.056338028	48	92.5
Henry	Steuben	-0.352843738	138	-0.056338028	48	93
Fish	Elkhart	-0.346016582	139	-0.056338028	48	93.5
Summit	Noble	-0.342580501	140	-0.056338028	48	94
Bass	Steuben	-0.338823706	141	-0.056338028	48	94.5
Ridinger	Kosciusko	-0.338201988	142	-0.056338028	48	95
Goose	Kosciusko	-0.337423408	143	-0.056338028	48	95.5
Barr	Fulton	-0.335638223	144	-0.056338028	48	96
Jones	Noble	-0.333924019	145	-0.056338028	48	96.5
Meteer	Lagrange	-0.332835684	146	-0.056338028	48	97
Deep	Noble	-0.332634766	147	-0.056338028	48	97.5
Center	Kosciusko	-0.329352604	148	-0.056338028	48	98
Mud	Lagrange	-0.327412086	149	-0.056338028	48	98.5
Engle	Noble	-0.325178475	150	-0.056338028	48	99

Table S2.1 continued.

Baughner	Noble	-0.324153238	151	-0.056338028	48	99.5
Lime-Kiln	Steuben	-0.322444643	153	-0.056338028	48	100.5
Crystal	Kosciusko	-0.321773617	154	-0.056338028	48	101
Old	Whitley	-0.320780585	155	-0.056338028	48	101.5
Barrel & 1/2	Kosciusko	-0.319416329	156	-0.056338028	48	102
Grass	Steuben	-0.31901566	157	-0.056338028	48	102.5
Loomis	Porter	-0.31707757	158	-0.056338028	48	103
Shockopee	Noble	-0.313057335	159	-0.056338028	48	103.5
Center	Steuben	-0.312025833	160	-0.056338028	48	104
Tamarack	Noble	-0.311844614	161	-0.056338028	48	104.5
Port Mitchell	Noble	-0.311079531	162	-0.056338028	48	105
Skinner	Noble	-0.310906918	163	-0.056338028	48	105.5
Mud	Whitley	-0.309984162	164	-0.056338028	48	106
Everett	Allen	-0.308667787	165	-0.056338028	48	106.5
Gilbert	Noble	-0.30466926	166	-0.056338028	48	107
Crane	Noble	-0.30389842	167	-0.056338028	48	107.5
Tamarack	Steuben	-0.303068673	168	-0.056338028	48	108
Weir	Lagrange	-0.301851256	169	-0.056338028	48	108.5
Stanton	Kosciusko	-0.301518364	171	-0.056338028	48	109.5
Bushong	Noble	-0.301061475	172	-0.056338028	48	110
Lintz	Dekalb	-0.300466839	173	-0.056338028	48	110.5
Cree	Noble	-0.298124842	174	-0.056338028	48	111
Viberg	Allen	-0.296305957	175	-0.056338028	48	111.5
Yellow Creek	Elkhart	-0.293065349	176	-0.056338028	48	112
South Clear	St. Joseph	-0.292481111	177	-0.056338028	48	112.5
Millers	Noble	-0.286890412	178	-0.056338028	48	113
Wible	Noble	-0.286696076	179	-0.056338028	48	113.5
Irish	Kosciusko	-0.28653764	180	-0.056338028	48	114
Axel	Noble	-0.286029898	181	-0.056338028	48	114.5
Black	Whitley	-0.284901371	182	-0.056338028	48	115
Caldwell	Kosciusko	-0.279795684	183	-0.056338028	48	115.5
Shoe	Kosciusko	-0.277510566	184	-0.056338028	48	116
Mink	Porter	-0.276481419	185	-0.056338028	48	116.5
Marl	Noble	-0.273081309	186	-0.056338028	48	117
Webster	Kosciusko	-0.271919736	187	-0.056338028	48	117.5
Clear	LaPorte	-0.271179998	188	-0.056338028	48	118
Lily	LaPorte	-0.269974389	189	-0.056338028	48	118.5
Cheeseboro	Steuben	-0.269534966	190	-0.056338028	48	119
Shipshewana	Lagrange	-0.267766412	191	-0.056338028	48	119.5
Loon	Steuben	-0.266718968	192	-0.056338028	48	120
Rupel	St. Joseph	-0.265477562	193	-0.056338028	48	120.5
Morehead	Kosciusko	-0.265367818	194	-0.056338028	48	121
Green (Rawles)	Lagrange	-0.265219795	195	-0.056338028	48	121.5
Pike	Kosciusko	-0.264586	196	-0.056338028	48	122
Morgan	Porter	-0.264082131	197	-0.056338028	48	122.5
Deer	Noble	-0.261770263	198	-0.056338028	48	123
Long	Noble	-0.261395968	199	-0.056338028	48	123.5
Syracuse	Kosciusko	-0.261218062	200	-0.056338028	48	124
Sweet	Noble	-0.260890864	201	-0.056338028	48	124.5
Canada	Porter	-0.257692461	202	-0.056338028	48	125
Silver	LaPorte	-0.2569608	203	-0.056338028	48	125.5
Sously	St. Joseph	-0.256910232	204	-0.056338028	48	126
Mud	St. Joseph	-0.256725584	205	-0.056338028	48	126.5
Hoffman	Kosciusko	-0.255658172	206	-0.056338028	48	127
Koontz	Starke	-0.254945205	207	-0.056338028	48	127.5

Table S2.1 continued.

Rivir	Noble	-0.254646578	208	-0.056338028	48	128
Boner	Kosciusko	-0.254336481	209	-0.056338028	48	128.5
Harper	Noble	-0.251530207	210	-0.056338028	48	129
Shallow	Steuben	-0.251415006	211	-0.056338028	48	129.5
Riddles	St. Joseph	-0.249880555	212	-0.056338028	48	130
Horseshoe	LaPorte	-0.248673089	213	-0.056338028	48	130.5
Long	Porter	-0.246739898	214	-0.056338028	48	131
Hawk	Noble	-0.246655811	215	-0.056338028	48	131.5
Stafford	Kosciusko	-0.246229986	216	-0.056338028	48	132
Fites	St. Joseph	-0.24597851	217	-0.056338028	48	132.5
Clear	Porter	-0.244996384	218	-0.056338028	48	133
Heron	Kosciusko	-0.244797393	219	-0.056338028	48	133.5
Sawmill	Kosciusko	-0.244370502	220	-0.056338028	48	134
Spear	Kosciusko	-0.243787481	221	-0.056338028	48	134.5
Diamond	Kosciusko	-0.243785869	222	-0.056338028	48	135
Zink	Fulton	-0.242345425	223	-0.056338028	48	135.5
Henderson	Noble	-0.24196548	224	-0.056338028	48	136
Barr	Noble	-0.240565473	225	-0.056338028	48	136.5
Sherburn	Kosciusko	-0.239877953	226	-0.056338028	48	137
Upper/Lower Fish	LaPorte	-0.238700206	227	-0.056338028	48	137.5
Big Chapman	Kosciusko	-0.237381241	228	-0.056338028	48	138
Muncie	Noble	-0.237180958	229	-0.056338028	48	138.5
Loon	Kosciusko	-0.23567002	230	-0.056338028	48	139
Howard	Steuben	-0.235542056	231	-0.056338028	48	139.5
Little Barbee	Kosciusko	-0.2328075	232	-0.056338028	48	140
Dunton	Dekalb	-0.230550348	233	-0.056338028	48	140.5
Hill	Kosciusko	-0.230499078	234	-0.056338028	48	141
Pond Lil	Lagrange	-0.229847393	235	-0.056338028	48	141.5
Szmanda	St. Joseph	-0.229662962	236	-0.056338028	48	142
Kale	St. Joseph	-0.22961745	237	-0.056338028	48	142.5
Weber	Noble	-0.229147811	238	-0.056338028	48	143
Schauweker	Noble	-0.228153589	239	-0.056338028	48	143.5
Price	Kosciusko	-0.227135062	240	-0.056338028	48	144
Long	Wabash	-0.22565145	241	-0.056338028	48	144.5
High	Noble	-0.224509005	242	-0.056338028	48	145
Lindsey	Noble	-0.222841759	243	-0.056338028	48	145.5
Hartz	Starke	-0.222680145	244	-0.056338028	48	146
Bartley	Noble	-0.221859136	245	-0.056338028	48	146.5
Horseshoe	Noble	-0.220982966	246	-0.056338028	48	147
Hall	Noble	-0.22069673	247	-0.056338028	48	147.5
Carr	Kosciusko	-0.219659593	248	-0.056338028	48	148
Little Chapman	Kosciusko	-0.218715115	249	-0.056338028	48	148.5
Papakeechee	Kosciusko	-0.218387616	250	-0.056338028	48	149
Rhodes	Steuben	-0.218173263	251	-0.056338028	48	149.5
Duck	Noble	-0.217490609	252	-0.056338028	48	150
King	Fulton	-0.217175562	253	-0.056338028	48	150.5
Quog	Lagrange	-0.216648739	254	-0.056338028	48	151
Wolf	Lake	-0.215904132	255	-0.056338028	48	151.5
Silver	Noble	-0.21536769	256	-0.056338028	48	152
Big Barbee	Kosciusko	-0.214347193	257	-0.056338028	48	152.5
Wawasee	Kosciusko	-0.1149945	305	-0.308823529	1	153
Fish	Kosciusko	-0.214161147	258	-0.056338028	48	153
Moss	Porter	-0.211864002	259	-0.056338028	48	153.5
Miller	Noble	-0.211271716	260	-0.056338028	48	154
Moss	Noble	-0.208920244	261	-0.056338028	48	154.5

Table S2.1 continued.

Upper Summit	Fulton	-0.207644512	262	-0.056338028	48	155
Wilson	Whitley	-0.206961297	263	-0.056338028	48	155.5
Kuhn	Kosciusko	-0.206210632	264	-0.056338028	48	156
Duely	Noble	-0.203711333	265	-0.056338028	48	156.5
Cedar	Dekalb	-0.200527625	266	-0.056338028	48	157
Mill P (Kreighbaum)	Marshall	-0.198576485	267	-0.056338028	48	157.5
Grannis	Noble	-0.198052631	268	-0.056338028	48	158
Crane	LaPorte	-0.195350638	269	-0.056338028	48	158.5
Silver	Kosciusko	-0.194927369	270	-0.056338028	48	159
Beck	Noble	-0.194328138	271	-0.056338028	48	159.5
Flat	Marshall	-0.194042228	272	-0.056338028	48	160
Scott	Whitley	-0.193425751	273	-0.056338028	48	160.5
Dock	Noble	-0.192684968	274	-0.056338028	48	161
Lukens	Wabash	-0.190850675	275	-0.056338028	48	161.5
Beigh	Kosciusko	-0.189885931	276	-0.056338028	48	162
Goodman	St. Joseph	-0.189851766	277	-0.056338028	48	162.5
Cicott	Cass	-0.187503317	278	-0.056338028	48	163
McClure	Kosciusko	-0.182478671	279	-0.056338028	48	163.5
Lake 16	Fulton	-0.182279565	280	-0.056338028	48	164
Wolf	Noble	-0.181997238	281	-0.056338028	48	164.5
McColley	Wabash	-0.179274139	282	-0.056338028	48	165
Sparta	Noble	-0.178110504	283	-0.056338028	48	165.5
O'Blennis	Fulton	-0.176994003	284	-0.056338028	48	166
Pierceton	Kosciusko	-0.176646298	285	-0.056338028	48	166.5
Cub	Noble	-0.173994411	286	-0.056338028	48	167
North Little	Kosciusko	-0.168346618	287	-0.056338028	48	167.5
Sellers	Kosciusko	-0.166982691	288	-0.056338028	48	168
Swede	LaPorte	-0.166871897	289	-0.056338028	48	168.5
Muskellunge	Kosciusko	-0.160626257	290	-0.056338028	48	169
Banning	Kosciusko	-0.160446804	291	-0.056338028	48	169.5
Nyona	Fulton	-0.158680398	292	-0.056338028	48	170
Houghton	Marshall	-0.154333228	293	-0.056338028	48	170.5
Anderson	Fulton	-0.152414047	294	-0.056338028	48	171
Langenbaum	Starke	-0.150899384	295	-0.056338028	48	171.5
Rine	Whitley	-0.134497128	296	-0.056338028	48	172
Landis	Fulton	-0.134280102	297	-0.056338028	48	172.5
Lotz	Wabash	-0.132317845	298	-0.056338028	48	173
Eagle	Starke	-0.131880972	299	-0.056338028	48	173.5
Round	Wabash	-0.128766321	300	-0.056338028	48	174
Round	Starke	-0.127050694	301	-0.056338028	48	174.5
White	Allen	-0.124113687	302	-0.056338028	48	175
Bull	Wabash	-0.115672699	303	-0.056338028	48	175.5
Town	Fulton	-0.115587402	304	-0.056338028	48	176
Manitou	Fulton	-0.113872832	306	-0.056338028	48	177
Cedar	Lake	-0.10946214	307	-0.056338028	48	177.5
Bruce	Pulaski	-0.107546736	308	-0.056338028	48	178
South Mud	Fulton	-0.103067513	309	-0.056338028	48	178.5
Lost (Hawks)	Marshall	-0.099175226	310	-0.056338028	48	179
Twin	Wabash	-0.095047394	311	-0.056338028	48	179.5
Rock	Kosciusko	-0.082558344	312	-0.056338028	48	180
Bass	Starke	-0.06519565	313	-0.056338028	48	180.5
Mud	Fulton	-0.064650636	314	-0.056338028	48	181
Galacia	Grant	-0.034948554	315	-0.056338028	48	181.5
Tippecanoe	Kosciusko	0.569014006	316	0	316	316
Dallas	Lagrange	0.717690304	318	0	316	317

Table S2.1 continued.

Clear	Steuben	0.576322488	317	0.691176471	323	320
<b>Crooked</b>	Noble	0.777250805	319	0.691176471	323	321
James	Steuben	1.259813052	327	0	316	321.5
Snow	Steuben	0.806623477	320	0.691176471	323	321.5
Oliver	Lagrange	0.847063257	321	0.691176471	323	322
Lake-of-the-Woods	Steuben	0.892841093	322	0.691176471	323	322.5
Olin	Lagrange	0.903741006	323	0.691176471	323	323
Fish (n Plato)	Lagrange	0.966673013	324	0.691176471	323	323.5
Big Long	Lagrange	1.124879421	325	0.691176471	323	324
<b>Gage</b>	Steuben	1.178837287	326	0.691176471	323	324.5
Jimmerson	Steuben	1.586283184	334	0	316	325
Messick	Lagrange	1.592587897	335	0	316	325.5
<b>South Twin</b>	Lagrange	1.411825713	328	0.691176471	323	325.5
Royer	Lagrange	1.468230032	329	0.691176471	323	326
Shriner	Whitley	1.475275248	330	0.691176471	323	326.5
McClish	Steuben	1.513767218	331	0.691176471	323	327
Martin	Lagrange	1.518885768	332	0.691176471	323	327.5
Witmer	Lagrange	1.806272763	340	0	316	328
Cedar	Whitley	1.572621246	333	0.691176471	323	328
James	Kosciusko	1.855991774	343	0	316	329.5
Lawrence	Marshall	1.719048949	337	0.691176471	323	330
Sechrist	Kosciusko	1.747926402	338	0.691176471	323	330.5
Knapp	Noble	1.768407494	339	0.691176471	323	331
Round	Whitley	1.947854967	344	0.691176471	323	333.5
Myers	Marshall	1.975943124	348	0.691176471	323	335.5
Shock	Kosciusko	2.136110422	353	0.691176471	323	338
Lime (Orland)	Steuben	1.672622723	336	0.943661972	344	340
Marsh	Steuben	1.828000142	341	0.943661972	344	342.5
Big Otter	Steuben	1.830685169	342	0.943661972	344	343
Green	Steuben	1.958361821	345	0.943661972	344	344.5
<b>Eve</b>	Lagrange	1.959863879	346	0.943661972	344	345
<b>Indiana</b>	Elkhart	1.973519915	347	0.943661972	344	345.5
Hackenburg	Lagrange	2.04088791	349	0.943661972	344	346.5
<b>Failing</b>	Steuben	2.064201834	350	0.943661972	344	347
<b>North Twin</b>	Lagrange	2.067576034	351	0.943661972	344	347.5
Seven Sisters	Steuben	2.086395001	352	0.943661972	344	348
Gooseneck	Steuben	2.313117712	354	0.943661972	344	349
Atwood	Lagrange	2.351666768	355	0.943661972	344	349.5
Meserve	Steuben	2.401994773	356	0.943661972	344	350
Gordy	Noble	2.415942216	357	0.943661972	344	350.5
Village	Noble	2.70751716	358	0.943661972	344	351
Hindman	Noble	2.760514073	359	0.943661972	344	351.5

**Table S2.2.** Complete results of MLR and CART models in the D2 (cisco lakes only) scenario, including lake name, MLR and CART residuals, residual ranks, and mean rank value. Current cisco lakes are highlighted in bold.

Lake Name	County	GLM Residual	GLM Rank	CART Residual	CART Rank	Mean Rank
Green	Steuben	-1.349441048	1	-0.571428571	1	1
Atwood	Lagrange	-0.864527241	4	-0.571428571	1	2.5
Seven Sisters	Steuben	-1.041917613	2	-0.081081081	4	3
Clear	Steuben	-0.897883405	3	-0.081081081	4	3.5
Olin	Lagrange	-0.71456882	5	-0.081081081	4	4.5
Fish (n Plato)	Lagrange	-0.697809764	6	-0.081081081	4	5
Lake-of-the-Woods	Steuben	-0.654647742	7	-0.081081081	4	5.5
Lime (Orland)	Steuben	-0.650015773	8	-0.081081081	4	6
Royer	Lagrange	-0.61014165	9	-0.081081081	4	6.5
Sechrist	Kosciusko	-0.522903095	12	-0.571428571	1	6.5
Big Long	Lagrange	-0.594823807	10	-0.081081081	4	7
Shock	Kosciusko	-0.584162268	11	-0.081081081	4	7.5
McClish	Steuben	-0.521081593	13	-0.081081081	4	8.5
Martin	Lagrange	-0.494025341	14	-0.081081081	4	9
Marsh	Steuben	-0.453466264	15	-0.081081081	4	9.5
Oliver	Lagrange	-0.424229972	16	-0.081081081	4	10
Gooseneck	Steuben	-0.387944054	17	-0.081081081	4	10.5
Shriner	Whitley	-0.377901481	18	-0.081081081	4	11
Meserve	Steuben	-0.376977285	19	-0.081081081	4	11.5
Lawrence	Marshall	-0.36282148	20	-0.081081081	4	12
Big Otter	Steuben	-0.359739239	21	-0.081081081	4	12.5
Cedar	Whitley	-0.317438504	22	-0.081081081	4	13
Myers	Marshall	-0.30175443	23	-0.081081081	4	13.5
Snow	Steuben	-0.285691297	24	-0.081081081	4	14
Round	Whitley	-0.222790257	25	-0.081081081	4	14.5
Knapp	Noble	-0.189665311	26	-0.081081081	4	15
Dallas	Lagrange	-0.156341426	27	-0.081081081	4	15.5
Gordy	Noble	-0.124358342	28	-0.081081081	4	16
Jimmerson	Steuben	-0.097958833	29	-0.081081081	4	16.5
Hindman	Noble	-0.096513476	30	-0.081081081	4	17
Village	Noble	-0.095982473	31	-0.081081081	4	17.5
Witmer	Lagrange	-0.092619746	32	-0.081081081	4	18
Messick	Lagrange	-0.067493121	33	-0.081081081	4	18.5

**Table S2.2 continued.**

Hackenburg	Lagrange	-0.054256842	34	-0.081081081	4	19
James	Steuben	-0.044740551	35	-0.081081081	4	19.5
James	Kosciusko	-0.018338806	36	-0.081081081	4	20
Tippecanoe	Kosciusko	-0.002087923	37	-0.081081081	4	20.5
<b>South Twin</b>	Lagrange	0.427492598	38	0.428571429	38	38
<b>Indiana</b>	Elkhart	0.685876184	39	0.428571429	38	38.5
<b>Failing</b>	Steuben	1.069720255	40	0.428571429	38	39
<b>Eve</b>	Lagrange	2.01312756	43	0.428571429	38	40.5
<b>Crooked</b>	Noble	1.723144073	41	0.918918919	42	41.5
<b>North Twin</b>	Lagrange	1.829358372	42	0.918918919	42	42
<b>Gage</b>	Steuben	2.127133445	44	0.918918919	42	43

VITA

## VITA

**ANDREW E. HONSEY****CAREER INTERESTS**

Fisheries Management, Fisheries Ecology, Limnology, Resource Management, Ecology

**RESEARCH INTERESTS**

Great Lakes region fisheries ecology, recruitment dynamics, stock assessment, population ecology, population genetics, causes and effects of hypoxia, use of eDNA for management of non-invasive species, trophic interactions

**EDUCATION**

**M.S.**, Forestry and Natural Resources, Purdue University, 2014 (expected).

- GPA: 4.0
- Advisor: Dr. Tomas Höök

**B.S.**, Biology (minor in Chemistry), Hillsdale College, 2012.

- Summa cum laude, Top 5

## **GRADUATE RESEARCH EXPERIENCE**

- Thesis Project concerning cisco *Coregonus artedii* in northern Indiana's glacial lakes
  - Working in conjunction with Indiana DNR (Steve Donabauer)
  - Chapter 1: Analysis of stock biology and genetic variation of Indiana's ciscoes
  - Chapter 2: Analysis of lake morphometric and land-use characteristics that promote cisco survival, sustainability, and possible reintroduction in Indiana lakes
- eDNA Project
  - Working in conjunction with Cameron Turner (Notre Dame) and Indiana DNR to use eDNA technology to determine the presence or absence of cisco in northern Indiana lakes and to use the results to help inform management decisions
- Perch Recruitment Synchrony Project
  - Analysis of percid recruitment synchrony across the entire Great Lakes region over the past ~50 years as part of a Great Lakes Fisheries Commission-funded grant; PIs: Drs. Tomas Höök, Cary Troy (Purdue), and David Bunnell (USGS)

## **OTHER EMPLOYMENT EXPERIENCE**

- Student Assistant in Biology (2010-2012), Hillsdale College.
  - Assisted Dr. Anthony Swinehart with sorting fossilized material for his Pipe Creek Sinkhole research, updating and re-labeling the 19th century Hillsdale College herbarium specimens, and caring for one marine and three freshwater aquaria
- Night Assistant in Biology (2011-2012), Hillsdale College.
  - Tutored students in various biological subjects

- Service Worker (Summers, 2009 and 2010), Jackson Township Road Department, Grove City, OH.
  - Repaired drainage tile, repaired and painted fire hydrants, repaired road signs, filled potholes, and mowed township properties
  - Acquired experience in using heavy equipment, a practical knowledge of the use of hand and power tools, and basic problem solving skills
- Research Assistant (Summer 2009), Hillsdale College Biological Station, Luther, MI.
  - Assisted Dr. Jeffrey Van Zant with his research on field mice (*Peromyscus* sp.) by trapping, tracking, and collecting tail samples for DNA analysis

### **RELEVANT COURSES TAKEN**

- Undergraduate (Hillsdale College)
  - Evolution and Biological Diversity, Molecular Genetics and Cell Function, General Chemistry I and II, Organic Chemistry I and II, Analytical Chemistry, Freshwater Biology, General Ecology, Genetics, Animal Behavior, Microbiology, Conservation, Biostatistics, Historical Geology, Marine Biology, Animal Parasitology
- Graduate (Purdue University)
  - Fisheries Science and Management, Ecological Impacts of Climate Change, Individual-based Modeling and Ecology, Modern Applied Statistics, Ecological Statistics, Quantitative Methods for Ecologists, R and Bayesian Analysis in Ecology, Meta-analysis in Ecology

**RELEVANT SKILLS**

- Field Equipment Used
  - Gill nets, seines, plankton tows
  - Eckman dredges, Ponars
  - Boat electrofishing equipment
  - Temperature probes
  - Hydrolab/Sonde
- Laboratory Skills
  - Fish diet analysis
  - Fish ageing
  - DNA digestion and extraction, PCR, sequencing
- Analytical and Statistical Skills/Familiarity
  - All general linear models (e.g., t-test, ANOVA)
  - All generalized linear models (e.g., logistic regression, Poisson regression)
  - Random effects and mixed models
  - Bayesian analysis (any model type)
  - Multivariate analyses (e.g., PCA, NMDS)
  - Individual-based models (in NetLogo language)
  - Statistical programs used: R, JAGS, JMP, STATISTICA

**PRESENTATIONS**

- Honsey, A.E., Bunnell, D.B., Troy, C.D., Fielder, D.G., Thomas, M.V., Lauer, T.E., Knight, C.T., Chong, S.C., Höök, T.O. 2014. Recruitment synchrony of yellow

perch *Perca flavescens* in the Great Lakes region, 1966-2008. Presented at the International Association for Great Lakes Research Conference, Hamilton, ON, CA. Oral presentation.

- Simpson, N., Honsey, A.E.\*, Höök, T.O. 2014. Spatial trends in Lake Michigan salmonid catches: 1992-2012. Presented to the Indiana Chapter of the American Fisheries Society, Muncie, IN. Poster.
- Donabauer, S.B., Porto, M.A., Honsey, A.E., Höök, T.O. 2013. Cisco as the representative species for coldwater glacial lakes habitats in Indiana. Presented to the Indiana Chapter of the American Fisheries Society, Lafayette, IN. Poster.
- Honsey, A.E. 2012. Quantitative ecology and taphonomy of the fishes of Fossil Lake, Green River Formation (Eocene), Kemmerer, Wyoming. Presented to the Hillsdale College Biology Department, Hillsdale, MI. Oral thesis presentation.
- Honsey, A.E. 2012. Quantitative ecology and taphonomy of the fishes of Fossil Lake, Green River Formation (Eocene), Kemmerer, Wyoming. Presented at the Hillsdale College Honors Research Symposium, Hillsdale, MI. Poster.

\*Served as mentor to primary author

### **AWARDS**

- Outstanding Senior Biology Major (Hillsdale College, 2012)
- John A. Catenhusen Scholarship (Hillsdale College, 2011-2)
- LAUREATES Research Program (Hillsdale College, 2011)
- Jensen Science Scholarship (Hillsdale College, 2010-2)
- William McMeekin Scholarship (Hillsdale College, 2008-12)

**MEMBERSHIPS AND ACTIVITIES**

Member, American Fisheries Society (Aug. 2012-present)

IAGLR Volunteer (Purdue University, June 2013)

Sigma Zeta Science Honorary (Hillsdale College, 2011-2012)

Beta Beta Beta Biology Honorary (Hillsdale College, 2010-2012)

Phi Mu Alpha Sinfonia Music Fraternity Hillsdale College, 2010-2012)