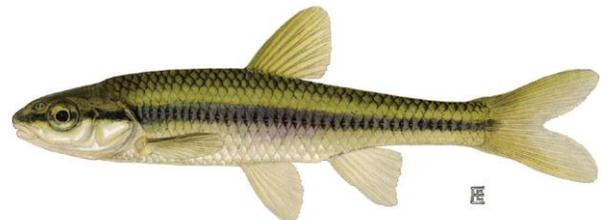




Biogeographic Patterns of Inland Lake Fish Communities at Isle Royale, Voyageurs, and Sleeping Bear Dunes National Park Units

Natural Resource Technical Report NPS/GLKN/NRTR—2014/893



ON THE COVER

Top-to-bottom, left-to-right: Locator Lake (VOYA), northern pike, Lake Harvey (ISRO), yellow perch, Bass Lake–Benzie (SLBE), and blacknose shiner.

Lake photos provided by the NPS Great Lakes Inventory and Monitoring Network. Fish art work from Kraft et al. (2006) and placed in the public domain courtesy of Cornell University and the State of New York.

Biogeographic Patterns of Inland Lake Fish Communities at Isle Royale, Voyageurs, and Sleeping Bear Dunes National Park Units

Natural Resource Technical Report NPS/GLKN/NRTR—2014/893

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Addendum

Gorman, O., L. Kallemeyn, and R. Maki. 2014. Biogeographic patterns of inland lake fish communities at Isle Royale, Voyageurs, and Sleeping Bear Dunes national park units. Natural Resource Technical Report NPS/GLKN/NRTR—2014/893. National Park Service, Fort Collins, Colorado.

Addendum for page 111 concerning status of lake trout in VOYA refuge lakes—Discussion section, end of paragraph four under “Assessment of the Effects of Anticipated Global Warming in the 21st Century”:

Recent genetic studies of the coldwater heritage species lake trout in Cruiser, Little Trout, and Mukooda suggest that these lakes contain distinct populations (Jacob Hennig, Kevin Peterson and Loren Miller, University of Minnesota and Minnesota Department of Natural Resources, unpublished report). Fortunately, a long period of stocking lake trout into these lakes since the 1940s has not eliminated the uniqueness of the endemic populations. To avoid the risk of future losses of genetic diversity in these distinct populations, stocking of lake trout in Cruiser, Little Trout, and Mukooda ceased in 1988, 2006, and 2010, respectively. These findings highlight the heritage value of the lake trout stock in Cruiser—one of the oldest inland VOYA lakes—which may have been derived from colonization ca. 10,000 BP, the time when this lake was estimated to have been isolated.

The National Park Service, Natural Resource Stewardship and Science office in Fort Collins, Colorado, publishes a range of reports that address natural resource topics. These reports are of interest and applicability to a broad audience in the National Park Service and others in natural resource management, including scientists, conservation and environmental constituencies, and the public.

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All manuscripts in the series receive the appropriate level of peer review to ensure that the information is scientifically credible, technically accurate, appropriately written for the intended audience, and designed and published in a professional manner.

This report received formal peer review by subject-matter experts who were not directly involved in the collection, analysis, or reporting of the data, and whose background and expertise put them on par technically and scientifically with the authors of the information.

Views, statements, findings, conclusions, recommendations, and data in this report do not necessarily reflect views and policies of the National Park Service, U.S. Department of the Interior. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

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Abstract

Composition of the inland lake fish communities at Isle Royale National Park (ISRO), Voyageurs National Park (VOYA) and Sleeping Bear Dunes National Lakeshore (SLBE) were examined as examples of modern biological communities shaped by post-glacial history. We considered the roles of historical biogeography, local habitat factors, and human impacts in structuring modern fish communities. Finally, we evaluated the potential impact of pending global climate change on these inland lakes. Differences in community composition within regions were correlated with a gradient of lake habitats determined by lake size and depth and corresponding changes in environmental-physical characteristics (temperature, oxygen, clarity of water). Lake environments ranged from small lakes characterized by shallow depth, low oxygen levels and warm water, to large lakes characterized by greater depth, moderate to high oxygen levels and cold hypolimnions. Small lakes had simple fish communities characterized by thermally tolerant and coolwater species and frequently harbored northern pike, yellow perch, and blacknose shiner, while larger lakes had more diverse communities that included coldwater, coolwater, warmwater, and thermally tolerant species. Relative lake ages and distances among lakes were generally unrelated to species composition of lake communities. Comparison of inland lake fish communities across regions revealed a primary gradient of warmwater, coolwater, and coldwater communities with overlying gradients of temperature, conductivity, alkalinity, pH, and shoreline complexity. Communities of the three regions were arrayed across these gradients such that fish communities of ISRO were distinct from those of SLBE, and VOYA was intermediate between ISRO and SLBE. Fish communities of ISRO were characterized by a mix of coldwater, coolwater, and tolerant species, while VOYA lake communities contained fewer coldwater species and more thermally tolerant species. Fish communities of SLBE were characterized by an absence of coldwater species and a mix of coolwater, warmwater, and thermally tolerant species. Our analysis of community assembly by regions showed that ISRO contains communities most similar to the presumptive faunal source pool dating back to the early Holocene. A cline of sequential losses of coolwater and coldwater species and gains of thermally tolerant and warmwater species from ISRO to VOYA to SLBE suggests a pattern of community assembly associated with different degrees of climate change across the three regions since the early Holocene. A strong underlying gradient of temperature driving differences in community assembly across the regions provides a historical example of the influence of climate change in shaping modern communities. Within each region, we identified “heritage” species and communities as those dating from the early Holocene and valuable for conservation of regional biodiversity. Application of climate change models allowed us to identify refuge lakes for heritage species and communities in the face of an anticipated warming climate in the 21st century. To facilitate the preservation of heritage lake communities against anticipated impacts of climate change, we provided recommendations for research, monitoring, conservation, and management.

Acknowledgments

We wish to thank USGS technicians Jill Falck and Lori Evrard for their support in generating maps and estimating inter-lake distances. NPS aquatic ecologist Joan Elias demonstrated much patience and moral support to ensure completion of this ambitious undertaking. We are also indebted to Wendy Gorman, for her patience and understanding for the considerable personal time the senior author devoted to the completion of this project. Suggestions provided by Joan Elias, William Route, Jay Glase, Walter Loope, William Tonn, and Nickolas Mandrak were very helpful in revising the manuscript. This research was supported by Interagency Agreement # F21050600024 with the National Park Service.

Acronyms Used in This Report

ANOSIM	Analysis of similarities
APIS	Apostle Islands National Lakeshore (Wisconsin)
BOD	Biological Oxygen Demand
BP	Calendar years before present
DEM	Digital Elevation Models
GR	Geometry ratios
ISRO	Isle Royale National Park (Michigan)
KNR	Proto-glacial lakes Kabetogama, Namakan, and Rainy
LiDAR	Light detection and range
LIS	Laurentian Ice Sheet
MCCM	Minnesota Climate Change Model
SIMPER	Similarity percentage
SLBE	Sleeping Bear Dunes National Lakeshore (Michigan)
SLD	shoreline development
TDO3	Temperature at DO = 3 mg/L. An oxythermal parameter variable to define fish habitat in inland waters using dissolved oxygen (DO) and water temperature limits.
VOYA	Voyageurs National Park (Minnesota)
Zmax	Maximum depth

Introduction

Considerable effort has been expended in studying attributes of fish communities of northern North American lakes and the biotic and abiotic factors affecting them (Johnson et al. 1977, Werner et al. 1977, Eadie and Keast 1984, Rahel 1984, Schindler et al. 1985, Hinch et al. 1991). In particular, the number, identity, and relative abundance of fish species in small lakes can be viewed as the product of a series of “filters” acting at continental, regional and local spatial scales (Figure 1; Tonn 1990; Tonn et al. 1990). Moreover, historical processes— particularly geological, glacial, and climatic— may affect filters, particularly at the continental and regional levels (Tonn 1990). Regionally, watershed boundaries and geomorphic barriers serve as filters (Tonn 1990). Locally, the presence or absence of essential habitats and physical-chemical conditions may serve as critical filtering processes (Tonn and Magnuson 1982, Rahel 1984, Jackson and Harvey 1989, Matuszek et al. 1990), but biotic factors, particularly predation, may serve to limit species composition at the local level (Jackson et al. 2001).

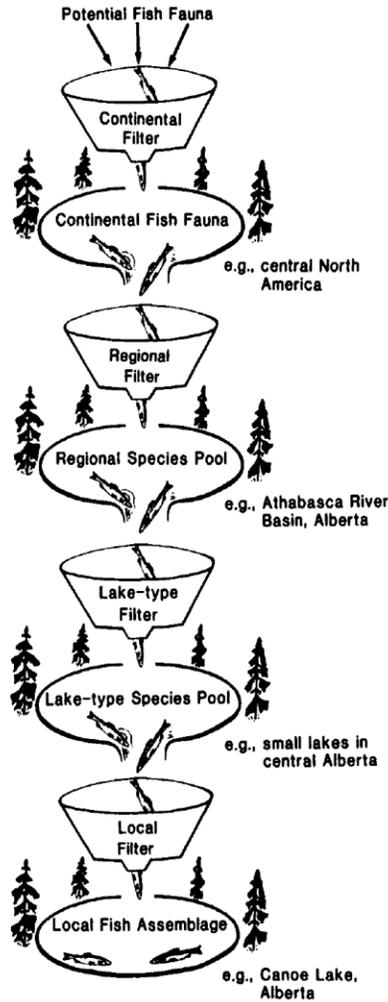


Figure 1. Generalized conceptual framework for fish community assembly (Tonn 1990).

Post-glacial species dispersal and associated historical processes were especially important in shaping the present-day distributions of freshwater fish in the Great Lakes region (Crossman and McAllister 1986, Underhill 1986, Mandrak and Crossman 1992, Mandrak 1995). The inland lakes of National Park Service (NPS) units Isle Royale National Park (ISRO), Voyageurs National Park (VOYA), and Sleeping Bear Dunes National Lakeshore (SLBE) are contained within the Laurentian drainage. As such, their fish communities have been shaped by historical processes. For example, the timing of expansion and contraction of ice sheets during the late Pleistocene Wisconsinan glaciation and the final retreat of the glaciers and emergence of the modern Great Lakes in the Holocene had profound effects on regional faunal source pools. As the Wisconsinan ice sheet began its final retreat north after ca. 13,300 BP (calendar years before present), migration of fishes through a series of outlets and connections among the proto-Great Lakes and the various Pleistocene refugia determined the pre-modern composition of inland lakes in the Laurentian drainage (Crossman and McAllister 1986, Dyke and Prest 1987, Lowell et al. 1999, Larson and Schaetzl 2001, Dyke 2004, Derouin et al. 2007, Hill 2007) (Figures 2 and 3). The inland lake fish communities of the Canadian Shield region that includes VOYA were very much determined by immigration of species from the Mississippian faunal refuge via the Warren River connection to the south (Figure 2) and to lesser degree from more recent connections through lakes Minong–Houghton (proto-Superior), Kelvin (proto-Nipigon) and Ojibway–Barlow to the east (Figure 3). Inland lakes of ISRO did not begin to emerge until the last withdrawal of the Wisconsinan ice sheet from Lake Superior ca. 11,000 BP and were likely colonized by the Lake Keweenaw–Duluth–Minong (proto-Superior) source fauna, which in turn was closely linked to Mississippian faunal refugia through the St. Croix River outlet (Figure 2). The Traverse Bay region containing SLBE was first open for colonization ca. 13,000 BP from the Lake Chicago (proto-Michigan) fauna, which was composed mostly of fish from the Mississippian refugia via the Chicago River outlet (Figure 2). As the ice sheet retreated, connections to Lake Stanley (proto–Huron) allowed colonization of species from the eastern post-glacial lakes and their associated refugia (Figure 3). Since the retreat of the glaciers and subsequent isostatic rebound, most connections of the Great Lakes to the Mississippian faunal source pool were lost, leaving the principal connection eastward to the St. Lawrence River (Figure 4). European settlers in the 19th and 20th centuries constructed additional connections in the east to the Hudson River via the Erie Barge Canal and in the west to the Illinois–Mississippi River system via the Chicago River/Sanitary Canal.

At the present point in the Holocene, ISRO and SLBE remain within the Great Lakes drainage while VOYA is isolated from the Great Lakes, and is connected to the Lake Winnipeg–Red River–Hudson Bay drainage. To guide our investigation into the patterns of species distribution, community assembly, and biogeographical history for inland lake communities of ISRO, VOYA, and SLBE, we constructed a conceptual framework for fish community assembly (*sensu* Tonn 1990) (Figure 5). We recognized the overriding influence of the Mississippian glacial refugia in the west as the principal source pool for the present-day native fish communities of the Great Lakes, and we recognized that sub-regional and local filters and histories determine the composition of the fish communities in the individual lakes of each region.

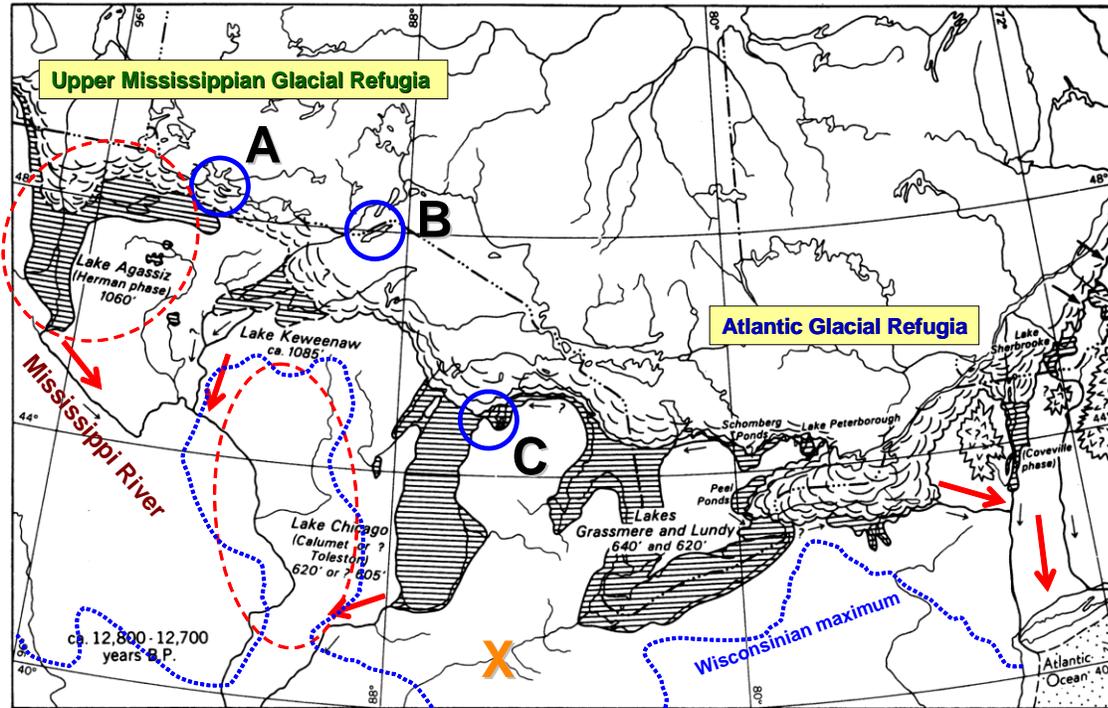


Figure 2. Retreat of the Wisconsinian glaciation from the proto Great Lakes drainage, ca. 13,000 BP (calendar years before present; see Appendices I and II). Blue dotted line shows the maximum extent of the Wisconsinian Glaciation, ca. 20,000 BP. Arrows indicate connections and dispersal routes between glacial lakes and river systems, and X indicates blocked outlet. Lake Agassiz was connected to the Mississippi River through the Warren Outlet, and the proto Lake Superior (Lake Keweenaw) was connected through the St. Croix River outlet (Crossman and McAllister 1986, Dyke and Prest 1987, Lowell et al. 1999, Dyke 2004, Hill 2007). The upper Mississippi River drainage with connected glacial lakes constituted the extensive Mississippian Glacial Refugia. SLBE (C) began to emerge from ice cover ca. 13,000 BP, VOYA (A) ca. 12,600 BP, and ISRO (B) ca. 11,000 BP (see Appendices I and II). The Atlantic Glacial Refugia was more restricted due to extensive ice cover at the glacial maximum. Base map from Prest (1957).

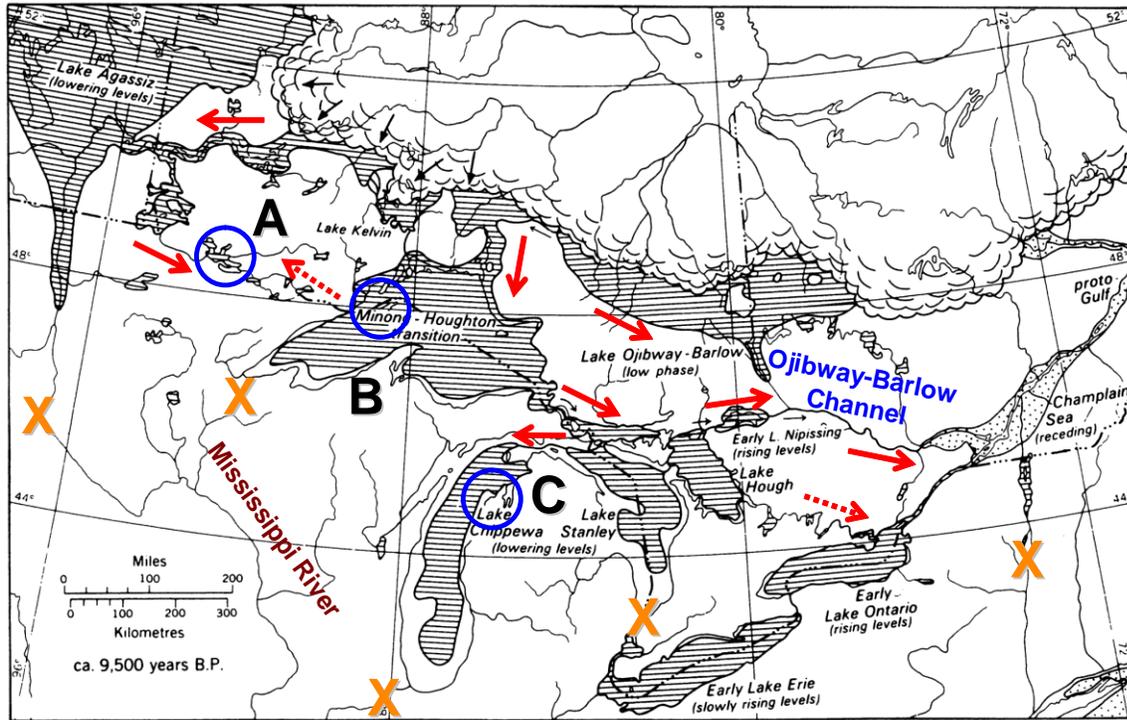


Figure 3. Retreat of the Wisconsin glacial front from the proto Great Lakes drainage, ca. 9,500–10,000 BP (see Appendices I and II). Arrows indicate connections and dispersal routes between glacial lakes and river systems, and Xs indicate blocked outlets. VOYA, ISRO, and SLBE are shown as A, B, and C, respectively. Base map from Prest (1957).

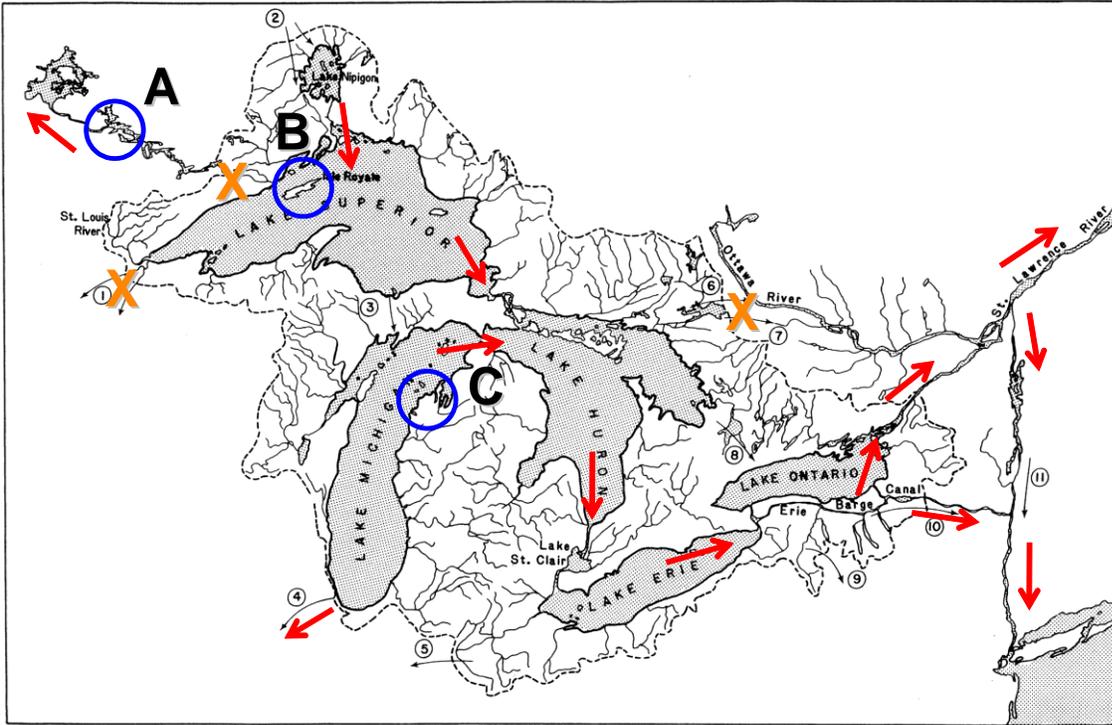


Figure 4. Modern dispersal routes and lost connections among the Great Lakes and adjacent river systems. Arrows indicate connections and dispersal routes between glacial lakes and river systems, and Xs indicate blocked outlets. VOYA, ISRO, and SLBE are shown as A, B, and C, respectively. Base figure from Underhill (1986).

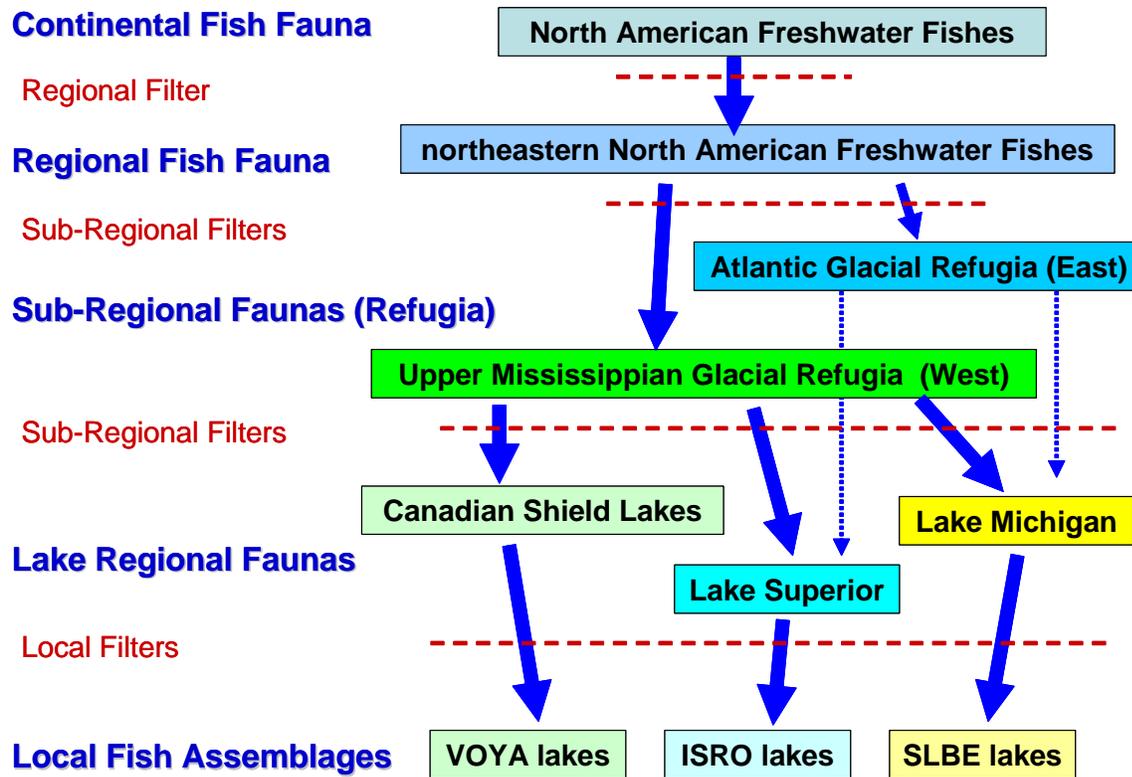


Figure 5. Conceptual framework for assembly of inland lake fish communities at VOYA, ISRO, and SLBE.

The lack of detailed information about the fish communities of VOYA, ISRO, and SLBE and the factors that may influence them were identified by Lafrancois and Glase (2005) in their synthesis of aquatic resources in the NPS units in the Great Lakes states. To better understand the composition of these fish communities, we applied the historical-biogeographical approach of Jackson and Harvey (1989) and Mandrak and Crossman (1992) to the available data from the inland lakes of ISRO, VOYA, and SLBE. Our analysis seeks to increase understanding of the distribution of species across the inland lakes of these park units by identifying the environmental factors that limit or determine the composition of lake fish communities within and across park units. In addition, our analysis attempts to identify “heritage” or pristine communities in need of protection, and the anthropogenic factors affecting composition of lake fish communities. The increased understanding of the effects of post-glacial climate changes on inland lake fish communities that our analysis provides should be useful in predicting future changes arising from anthropomorphically-driven climate change anticipated in the 21st century. Finally, we applied climate change models to identify refuge lakes where heritage species and communities are likely to persist, and we provide research, conservation and management recommendations that should be useful in efforts to preserve heritage species and communities. In pursuit of these goals, this report will address the following objectives:

1. Regional factors influencing lake fish community composition. Determine relationships among lake fish community composition, limnological and lake morphological parameters, and inter-lake distances and differences in elevation at the regional level (ISRO, VOYA, SLBE). Relate the distribution of species and composition of lake communities to the

temperature tolerances of constituent species. Identify species and groups of species (faunal assemblages) that share common patterns of distribution.

2. Factors influencing differences in lake fish community composition across regions.
Determine relationships between lake fish community composition and limnological and lake morphological parameters across regions (global comparisons). Assess the distinctness of the regional lake environments and their faunas and communities; identify species and groups of species (faunal assemblages) that are shared across regions or unique to regions.
3. Influence of history and biogeography in determining lake fish community composition.
Relate faunal composition of inland lakes of ISRO, VOYA, and SLBE to regional and Great Lakes faunal source pools. Identify faunal sources for fish communities of each region and address the effects of historical processes, particularly glacial and climatic. Construct an area cladogram to summarize the biogeographical events that shaped the fish faunas of each region.
4. Potential for future climate change to affect lake fish communities. Identify heritage lake fish communities and species associated with post-glacial lakes. Assess the effects of anthropogenic stressors on habitat, and of physical-chemical conditions and fish introductions on native fish communities. Assess the anticipated effects of global climate change in the 21st century on inland lakes and their fish communities; apply climate change models to identify refuge lakes for heritage communities.
5. Recommendations for research, monitoring, and conservation of inland lake fish communities. Provide specific recommendations for research, monitoring, and conservation measures to stem the loss of heritage species and communities in the face of anticipated climate warming in the 21st century. Findings and recommendations in this report are intended to guide the development of management and conservation plans for each region and for specific lakes, with the aim of preserving biodiversity and heritage species and communities for future generations.

Methods

Description of Regional and Local Faunas

Distributional information of freshwater fishes summarized in Scott and Crossman (1973), Crossman and McAllister (1986), Underhill (1986), and Mandrak and Crossman (1992) was used to describe the sub-regional faunal (glacial refugia) source pool from which the lake regional faunal source pools were derived (Figure 5, Table 2). Composition of lake regional faunas (Canadian Lakes, Lake Superior, Lake Michigan; Figure 5) was provided by information found in Underhill (1957, 1986), Crossman and McAllister (1986), Mandrak and Crossman (1992), Wepruk et al. (1992), Cudmore-Vokey and Crossman (2000), and Hubbs et al. (2004). The largest contributor to the faunas of ISRO, VOYA, and SLBE regions was the upper Mississippian glacial refuge (Crossman and McAllister 1986; Figure 5). Local source pools (lake regional faunas) for each park unit were developed from published and unpublished survey records provided by state, provincial, and federal agencies. For ISRO, we used published results from surveys by Hubbs and Lagler (1949), Kallemeyn (2000), Gorman et al. (2008), and Gorman and Moore (2009). For VOYA, we relied on results of surveys conducted by the NPS, Minnesota Department of Natural Resources (MNDNR), and U.S. Geological Survey (USGS) from 1975 to 2009 and summarized in Kallemeyn et al. (2003). For SLBE, we relied on results of surveys conducted by the NPS and tribal personnel during 2003–2006 (Fessell 2007). Based on our understanding of glacial history and relative age of faunas of each region, we assumed the source pool that was able to rapidly colonize each region following the retreat of the Wisconsin glacialiation was best represented by a combination of species that inhabit the inland lakes and coastal waters of Isle Royale. Thus, the most primitive, closest-to-source fauna would be that of ISRO, which is the youngest (ca. 10,000 BP), followed by VOYA (ca. 11,000 BP) and then SLBE, the oldest and likely the most derived fauna (>12,000 BP).

Treatment of Introduced Species

Introduced species were excluded from our analyses. Status as native and introduced species in each region was determined by comparison of our survey records with regional faunal sources pools listed in Crossman and McAllister (1986) and Underhill (1986). An inspection of distribution data in Lee et al. (1980), Crossman and McAllister (1986), and Underhill (1986) indicated that introduced species have not displaced native species on a regional basis, but their inclusion would obscure historical patterns of distribution and result in differences due to recent anthropogenic impacts. Moreover, inclusion of introduced species would make some inland lakes appear different only because they contained introduced species while others did not. Some species in VOYA appear to be native at the regional level but have not historically been present in inland lakes. Species included in this category include small and largemouth bass, bluegill, green sunfish, black crappie, brown bullhead, and black bullhead. These species were later introduced into VOYA inland lakes through stocking (Kallemeyn et al. 2003). Introduced species in SLBE entered inland lakes via streams and intermittent waterways that connect to Lake Michigan, and included sea lamprey, alewife, coho salmon, Chinook salmon, and common carp. No introduced species were found in ISRO inland lakes.

Composition of Inland Lake Fish Communities

Because of the lack of standardization of fishing gears used to sample inland lakes across the ISRO, VOYA, and SLBE park units (Lafrancois and Glase 2005), presence/absence rather than relative abundance data were used to determine species composition and to make intra- and inter-park comparisons of fish communities. Similarly, Jackson and Harvey (1989) used presence/absence data to make intra- and inter-regional comparisons of inland lake fish communities. Jackson and Harvey (1997) and Olden and Jackson (2002) demonstrated that presence/absence data are as useful as relative abundance data in understanding spatial patterns of lake fish community compositions. Moreover, presence/absence data may be a more robust data source, as it does not rely on assumptions about comparability of relative abundance measures derived from different gear types.

Contemporary compositions of fish communities for individual inland lakes at ISRO, VOYA, and SLBE were obtained from published and unpublished sources, and we limited our analysis to lakes with two or more species (Table 2). The 32 inland lakes of ISRO (Figure 6) were initially surveyed by Koelz (1929) and the results were presented in a comprehensive review by Hubbs and Lagler (1949). A more recent survey of ISRO inland lakes that repeated Koelz's effort was completed in 1995–1997 by Kallemeyn (2000).

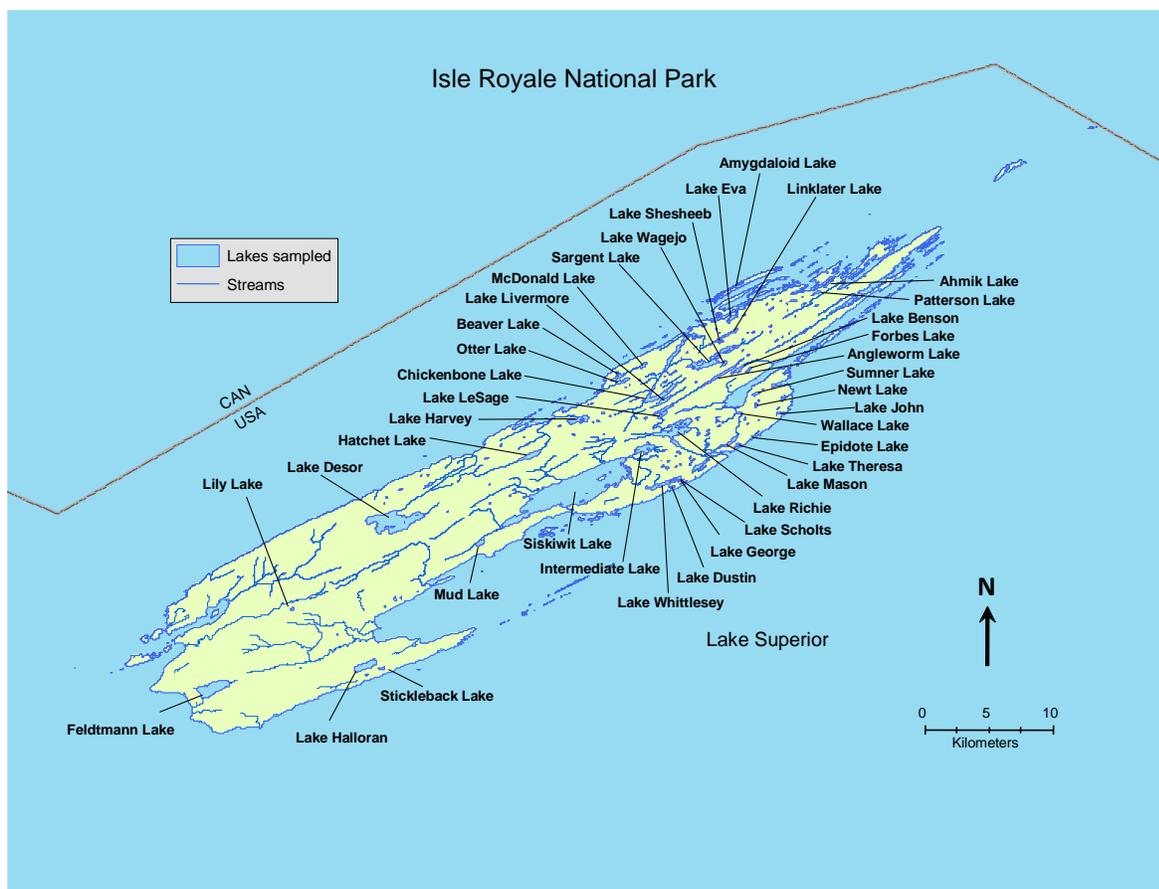


Figure 6. Inland lakes of Isle Royale National Park (ISRO), situated in northern Lake Superior.

Since the establishment of VOYA in 1975, numerous surveys of the 26 smaller interior lakes in the park (Figure 7) have been conducted by the NPS, MNDNR, and USGS. We used records from survey reports and from unpublished NPS data. Initial surveys of the 26 lakes were conducted in the 1970s with subsequent repeated surveys in the 1980s, 1990s, and more recently in 2000–2009. Kallemeyn et al. (2003) summarized the distribution of fishes in VOYA inland lakes up through 2000. Fish communities of Rainy, Kabetogama, Namakan, and Sand Point lakes were not included in our analysis of VOYA fish communities, as these large lake communities have been extensively impacted by stocking, fishing, and water level management throughout the 20th century.

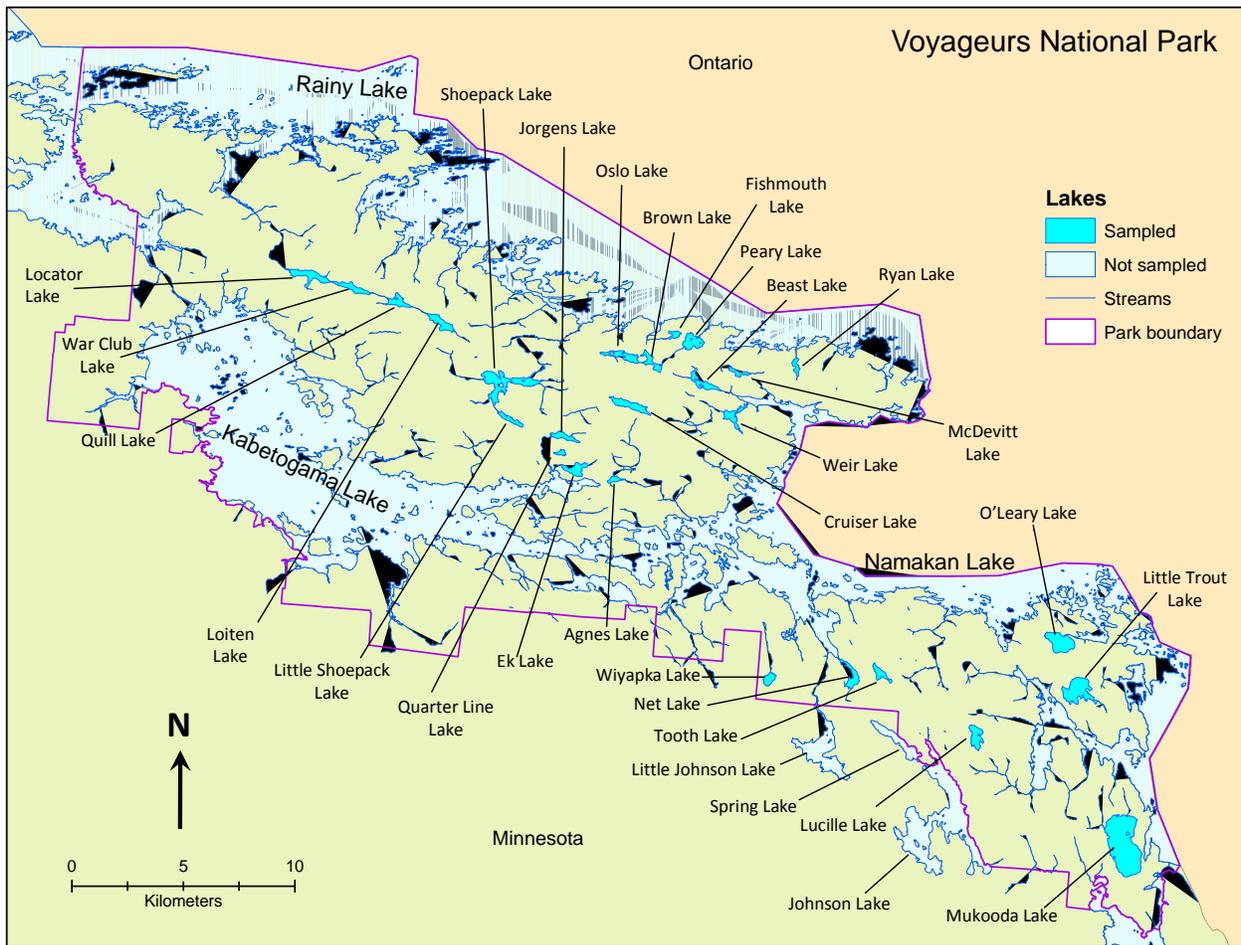


Figure 7. Inland lakes of Voyageurs National Park (VOYA) in northern Minnesota, along the U.S.-Canadian border.

For SLBE we used records from a comprehensive fisheries survey of 20 inland lakes in SLBE (Figure 8) conducted in 2003–2006 by the NPS with the assistance of the Grand Traverse Band of Ottawa and Chippewa Indians (Fessell 2007). SLBE lakes North Bass and South Bass (names used throughout this report) are also known by their county locations as Leelanau Bass and Benzie Bass lakes, respectively.



Figure 8. Inland lakes of Sleeping Bear Dunes National Lake Shore (SLBE), situated along the coast zone of northeastern Lake Michigan. North Bass and South Bass lakes are also known by their county locations as Leelanau Bass and Benzie Bass lakes, respectively.

Lake Morphometry and Limnology

Lake morphometric and limnological data were taken from Kallemeyn (2000), Kallemeyn et al. (2003), and unpublished NPS records for ISRO, VOYA, and SLBE, respectively. We used mid-summer data, as these were the only common data available for all lakes, and mid-summer physical conditions represent those most restrictive physiologically for cool- and coldwater fishes. Lake morphometry measures included lake area, watershed area, maximum depth, and shoreline development (SLD). SLD is a measure of shoreline regularity or convolution and is expressed as:

$$SLD = \frac{S}{2\sqrt{A\pi}}$$

where S is length of shoreline and A is area of the lake. A perfectly round lake has a SLD of 1.0. We also included lake geometry ratio (GR, the fourth root of lake surface area divided by the maximum lake depth), which represents a measure of relative depth and strength of stratification based on lake area and maximum depth (Hondzo and Stefan 1996, Fee et al. 1996). This metric was used in classifying inland lakes as to their likelihood of retaining coldwater habitat in the face of climate warming in the 21st century (Jacobson et al. 2010, Fang et al. 2012, Jiang et al. 2012).

Limnological measures included means of summer epilimnetic temperature, dissolved oxygen, alkalinity, specific conductance, pH, summer hypolimnetic temperature and dissolved oxygen, Secchi depth, and degree days using a base temperature of 65°F (18°C). Data for each lake are presented in Appendix III.

Lake Connectedness

To assess connectedness of inland lakes, interlake distances were estimated from lengths of connecting streams or dry channels from the lowest elevation outlet of one lake to another. For lakes with no apparent connecting streams, we measured distance overland from the lowest outlet channel (essentially a dry stream channel) to the nearest stream or lake. These overland routes were identified and plotted using three-dimensional oblique projections of the topography of each region in Google Earth Maps and a Geographic Information System (GIS) employing Digital Elevation Model (DEM) data layers. Distances across connecting lakes were assigned a value of zero. For example, lakes Desor and Eva in ISRO connect directly to Lake Superior, thus the distance between the connecting channels that empty into Lake Superior were assigned a distance of zero and the estimated interlake distance was the sum of the lengths of the lakes' connecting channels to Lake Superior. Matrices of interlake distances for inland lakes of ISRO, VOYA, and SLBE are provided in Appendix IX.

Thermal Classification of Species and Communities

Species were assigned thermal scores and classified as coldwater, coolwater, cool-warmwater, thermally tolerant, or warmwater fishes (Table 1A) based on distributional and ecological data provided in Scott and Crossman (1973), Smith (1979), Lee et al. (1980), Trautman (1981), Becker (1983), and Hubbs et al. (2004). Based on our criteria of thermal classification we assigned each species a thermal classification and numeric thermal score (Table 2). Coldwater species were defined as those limited to cold oligotrophic lakes with oxygenated hypolimnions or cold water streams not usually distributed south of Laurentian drainage. Coldwater fishes are commonly found in cold lakes

Table 1. Definitions of species (A) and community (B) thermal classifications, and definitions of faunal assemblages (C) in the inland lakes of Isle Royale, Voyageurs, and Sleeping Bear Dunes. Definitions for thermal classification of species is based on distributional and ecological information in Scott and Crossman 1973, Smith 1979, Lee et al. 1980, Trautman 1981, Becker 1983, and Hubbs et al. 2004.

A. Thermal Classification of Species

Thermal Score	Classification	Definition
3	warm	Warmwater. Found in seasonally warm streams and lakes from the Great Lakes to lower Mississippi River and Gulf of Mexico coastal drainages. The Laurentian drainages represent the northern distributional limit for these species.
2	thermally tolerant	Thermally tolerant. Found widely distributed throughout the Mississippi River and Hudson Bay drainages and occupy seasonally cold to warm water habitats. Found in Laurentian drainages south to the lower Mississippi River and coastal drainages of the Gulf of Mexico.
2	cool-warm	Cool-warm water. Similar to cool in distribution, but extend farther south to cooler streams of Tennessee, southern Missouri, and eastern Kansas but are thermally tolerant of seasonally warm habitats within their range.
1	cool	Coolwater. Found in seasonally cold and cool streams and lakes, distributed north to Laurentian drainage and as far south as the upper Mississippi and Ohio River drainages.
0	cold	Coldwater. Limited to cold oligotrophic lakes with oxygenated hypolimnions, cold water streams, not usually distributed south of Laurentian drainage. Found in cold lakes and rivers in the Laurentian, Hudson Bay or arctic drainages.

B. Thermal Classification of Lake Communities

Mean Species Thermal Score	Classification
<1.00	cold (coldwater)
1.00–1.39	cool (coolwater)
1.40–1.79	cool-warm (cool-warmwater, thermally tolerant)
>1.79	warm (warmwater)

C. Definition of Faunal Assemblages

Numeric code	Characteristic species
1	N. Pike and Y. Perch present
2	N. Pike and Y. Perch present; Blacknose Shiner present
3	N. Pike and Y. Perch present; cool or coldwater species present
4	N. Pike and Y. Perch present; Largemouth Bass and Bluntnose Minnow present
5	N. Pike present; Y. Perch absent
6	N. Pike absent; Y. Perch usually present; predators usually absent,
7	N. Pike absent; Y. Perch usually present; other predators present
8	N. Pike and Y. Perch absent
9	Coldwater assemblage: includes Cisco, Lake Whitefish, Lake Trout, Northern Lake Chub, Trout-perch, Burbot, Ninespine Stickleback, Slimy Sculpin

Table 2. Summary of the fish fauna of inland lakes in Isle Royale (ISRO), Voyageurs (VOYA), and Sleeping Bear Dunes (SLBE) park units. Records were compiled from Hubbs and Lagler (1949), Hubbs and Lagler (2004), Lee et al. (1980), Underhill (1986), Crossman and McAllister (1986), Kallemeyn (2000), and Fessell (2007). Early source pool refers to those species that colonized as the glaciers retreated. ISRO coastal waters include embayments, stream mouths, and open lake shorelines. L – at limit of distribution, I – introduced species, E – exotic species. Thermal scores and classification is explained Table 1. Species classified as thermally tolerant or cool-warm receive the same thermal scores.

Common Name	Genus	Species	Species Code	Thermal Score	Thermal Classif.	Early Source Pool	ISRO, Coastal Waters	ISRO	VOYA	SLBE
Longnose gar	<i>Lepisosteus</i>	<i>osseus</i>	LNG	warm	3					L
Bowfin	<i>Amia</i>	<i>calva</i>	BOW	warm	3					X
Brook trout	<i>Salvelinus</i>	<i>fontinalis</i>	BKT	cold	0	X	X	X*		
Lake trout	<i>Salvelinus</i>	<i>namaycush</i>	LKT	cold	0	X	X	X	X	
Cisco	<i>Coregonus</i>	<i>artedi</i>	CIS	cold	0	X	X	X	X	
Round whitefish	<i>Prosopium</i>	<i>cylindraceum</i>	RWF	cold	0	X	X			
Lake whitefish	<i>Coregonus</i>	<i>clupeaformis</i>	LWF	cold	0	X	X	X		
Central mudminnow	<i>Umbra</i>	<i>limi</i>	CMM	cool	1		X [†]		X	X
Northern pike	<i>Esox</i>	<i>lucius</i>	NPK	cool	1	X	X	X	X	X
Muskellunge	<i>Esox</i>	<i>masquinongy</i>	MUS	cool	1				X	
Northern redbelly dace	<i>Phoxinus</i>	<i>eos</i>	NRD	cool	1	X	X [†]	X	X	L
Finescale dace	<i>Phoxinus</i>	<i>neogaeus</i>	FSD	cool	1	X	X [†]	X	X	
Northern lake chub	<i>Couesius</i>	<i>plumbeus</i>	NLC	cold	0	X	X	X		
Longnose dace	<i>Rhinichthys</i>	<i>cataractae</i>	LND	cold	0	X	X			
Blacknose dace	<i>Rhinichthys</i>	<i>atratus</i>	BND	cool	1	X	X [†]			
Hornyhead chub	<i>Nocomis</i>	<i>biguttatus</i>	HHC	cool-warm	2					X
Golden shiner	<i>Notemigonus</i>	<i>crysoleucas</i>	GDS	thrm. tolerant	2	X	X	X	X	X
Pearl dace	<i>Margariscus</i>	<i>margarita</i>	PLD	cool	1	X	X [†]	X	X	
Creek chub	<i>Semotilus</i>	<i>atromaculatus</i>	CKC	thrm. tolerant	2	X	X [†]	X		X
Emerald shiner	<i>Notropis</i>	<i>atherinoides</i>	EMS	thrm. tolerant	2	X	X	X	X	
Blackchin shiner	<i>Notropis</i>	<i>heterodon</i>	BCS	cool	1	X	X [†]	X		
Blacknose shiner	<i>Notropis</i>	<i>heterolepis</i>	BNS	cool	1	X	X	X	X	X
Spottail shiner	<i>Notropis</i>	<i>hudsonius</i>	STS	cool	1	X	X	X	X	X
Sand shiner	<i>Notropis</i>	<i>stramineus</i>	SDS	warm	3					X
Mimic shiner	<i>Notropis</i>	<i>volucellus</i>	MMS	thrm. tolerant	2	X	X [†]	X	X	X
Common shiner	<i>Luxilus</i>	<i>cornutus</i>	CMS	thrm. tolerant	2				L	X
Fathead minnow	<i>Pimephales</i>	<i>promelas</i>	FHM	thrm. tolerant	2	X	X [†]	X	X	X

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Common Name	Genus	Species	Species Code	Thermal Score	Thermal Classif.	Early Source Pool	ISRO, Coastal Waters	ISRO	VOYA	SLBE
Bluntnose minnow	<i>Pimephales</i>	<i>notatus</i>	BNM	warm	3		X [†]		X	X
Longnose sucker	<i>Catostomus</i>	<i>catostomus</i>	LNS	cold	0	X	X			
White sucker	<i>Catostomus</i>	<i>commersoni</i>	WHS	thrm. tolerant	2	X	X	X	X	X
Northern redhorse	<i>Moxostoma</i>	<i>macrolepidotum</i>	NRH	thrm. tolerant	2					X
Black bullhead	<i>Ameiurus</i>	<i>melas</i>	BLB	warm	3				I	X
Brown bullhead	<i>Ameiurus</i>	<i>nebulosus</i>	BRB	warm	3				I	X
Yellow bullhead	<i>Ameiurus</i>	<i>natalis</i>	YLB	warm	3					X
Tadpole madtom	<i>Noturus</i>	<i>gyrinus</i>	TPM	thrm. tolerant	2				L	
Banded killifish	<i>Fundulus</i>	<i>diaphanus</i>	BKF	cool	1					X
Brook silverside	<i>Labidesthes</i>	<i>sicculus</i>	BSS	warm	3					X
Burbot	<i>Lota</i>	<i>lota</i>	BUR	cold	0	X	X	X	X	
Brook stickleback	<i>Culaea</i>	<i>inconstans</i>	BKS	cool	1	X	X	X	X	X
Ninespine stickleback	<i>Pungitius</i>	<i>pungitius</i>	NSS	cold	0	X	X	X		
Trout-perch	<i>Percopsis</i>	<i>omiscomaycus</i>	TRP	cold	0	X	X	X		
Rock bass	<i>Ambloplites</i>	<i>rupestris</i>	RKB	cool-warm	2		X		X	X
Green sunfish	<i>Lepomis</i>	<i>cyanellus</i>	GSF	warm	3				I	X
Pumpkinseed	<i>Lepomis</i>	<i>gibbosus</i>	PKS	cool	1	X	X [‡]	L	L	X
Bluegill	<i>Lepomis</i>	<i>macrochirus</i>	BLG	warm	3				I	X
Northern longear sunfish	<i>Lepomis</i>	<i>peltastes</i>	NLS	cool	1				L	X
Smallmouth bass	<i>Micropterus</i>	<i>dolomieu</i>	SMB	warm	3				I	X
Largemouth bass	<i>Micropterus</i>	<i>salmoides</i>	LMB	warm	3				I	X
Black crappie	<i>Pomoxis</i>	<i>nigromaculatus</i>	BLC	warm	3				I	X
Yellow perch	<i>Perca</i>	<i>flavescens</i>	YLP	cool	1	X	X	X	X	X
Sauger	<i>Sander</i>	<i>canadense</i>	SAU	thrm. tolerant	2				X	
Walleye	<i>Sander</i>	<i>vitreum</i>	WAL	thrm. tolerant	2	X	X	X	X	
Logperch	<i>Percina</i>	<i>caprodes</i>	LGP	thrm. tolerant	2	X	X	X	X	X
Iowa darter	<i>Etheostoma</i>	<i>exile</i>	IOD	cool	1	X	X	X	X	X

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Common Name	Genus	Species	Species Code	Thermal Score	Thermal Classif.	Early Source Pool	ISRO, Coastal Waters	ISRO	VOYA	SLBE
Johnny darter	<i>Etheostoma</i>	<i>nigrum</i>	JOD	thrm. tolerant	2		X		X	X
Slimy sculpin	<i>Cottus</i>	<i>cognatus</i>	SLS	cold	0	X	X	X	X	
Spoonhead sculpin	<i>Cottus</i>	<i>ricei</i>	SPS	cold	0	X	X	X		
Mottled sculpin	<i>Cottus</i>	<i>bairdi</i>	MTS	cool-warm	2		X		X	X
EXOTICS										
Sea lamprey	<i>Petromyzon</i>	<i>marinus</i>	SEL	cool	1		E			E
Alewife	<i>Alosa</i>	<i>pseudoharengus</i>	ALE	cool	1					E
Coho	<i>Oncorhynchus</i>	<i>kisutch</i>	COH	cold	0		E			E
Chinook	<i>Oncorhynchus</i>	<i>tschawytscha</i>	CHI	cold	0					E
Rainbow trout	<i>Oncorhynchus</i>	<i>mykiss</i>	RBT	cold	0		E			
Rainbow smelt	<i>Osmerus</i>	<i>mordax</i>	RBS	cold	0		E			
Common carp	<i>Cyprinus</i>	<i>carpio</i>	CMC	warm	3					E
Species Total, less exotics						33	38	29**	38	36

* brook trout were recorded in three inland lakes by Koelz (1929) and Hubbs and Lagler (1949), but not by Kallemeyn (2000).

** total number of species for ISRO includes brook trout.

‡ pumpkinseed was reported in coastal waters by Hubbs and Lagler (1949) as found in “adjacent stream mouths, marshes, and ponds not more than twenty-five feet higher than Lake Superior”; not reported for Lake Superior by Bailey and Smith (1981) nor in coastal water of ISRO by Gorman and Moore (2009).

† not reported as occurring in Lake Superior waters by Bailey and Smith (1981) but reported as occurring in coastal waters of ISRO by Gorman and Moore (2009).

and rivers in the Laurentian, Hudson Bay, or arctic drainages. Coolwater species were defined as those found in seasonally cold and cool streams and lakes, and distributed north to Laurentian drainage and as far south as the upper Mississippi and Ohio River drainages. Cool–warmwater species are those similar to coolwater species in distribution, but extending farther south to cooler streams of Tennessee, southern Missouri, and eastern Kansas and are tolerant of seasonally warm habitats within their range. Thermally tolerant species were found widely distributed throughout the Mississippi River, Hudson Bay, and Laurentian drainages; they may range north from the Red, English, Winnipeg, and upper Nelson river systems of the Hudson Bay drainage and Laurentian drainages south to the lower Mississippi River and coastal drainages of the Gulf of Mexico. Thermally tolerant species occupy seasonally cold-to-warm-water habitats and can tolerate a wide range of thermal conditions. We found that cool-warmwater and thermally tolerant species had similar distributions so they were treated as a single group to simplify our analyses. Warmwater species are found in seasonally warm streams and lakes from the Great Lakes to lower Mississippi River and Gulf of Mexico coastal drainages. The Laurentian drainages represent the northern distributional limit for warmwater species.

We also identified an early post-glacial source pool of species that was available to colonize emerging lake environments. This early faunal source pool was assumed to be a combination of species that inhabit the inland lakes and coastal waters of Isle Royale, without exotic species and more recent colonizers of coastal waters (i.e., bluntnose minnow, mottled sculpin, central mudminnow, rock bass, and johnny darter). These latter species occur in inland lakes of other regions but not those of ISRO, so we assume that they were not present in coastal waters of ISRO to colonize lakes as they were emerging. This early faunal source pool represents those species able to colonize inland lakes in the early post-glacial period when water temperatures were low and inland lakes had recently emerged from large post-glacial lakes. The mean of the species thermal scores of each lake community was used to classify each community across a thermal gradient as coldwater, coolwater, cool-warmwater (thermally tolerant), or warmwater (see Table 1B).

Within- and Across-Region Analyses

Our approach to describing the patterns of species distribution within and across the three park units or lake regions (see Figure 5) generally followed the historical-biogeographical approach of Jackson and Harvey (1989) and Mandrak and Crossman (1992). We started first with a within-region analysis of fish communities and then proceeded to an across-region analysis. This approach allowed us to understand factors determining species distributions within each region which would facilitate a better understanding of larger-scale influences driving differences in community composition across regions. As with Jackson and Harvey (1989) we eliminated lakes with depauperate fish communities (less than two species) from our analyses since they can add considerable variability (noise) while adding little information regarding the relationship between the fish communities of each lake (McCune and Mefford 1999, McCune et al. 2002).

Within-Region Analysis

The species compositions of the inland lake fish communities for each region were compared with community matrices of species presence-absence (p/a) data (see Appendices VI–VIII). This allowed

us to derive regional profiles from which we identified shared and unique species. The patterns of species distribution across lakes (communities) were evaluated by inspecting the proportion of lakes in which each species occurred and the distribution of species richness across lakes. From this exploratory analysis we identified widespread species (occurring in $\geq 50\%$ of lakes), moderately widespread species (occurring in ≥ 25 -to- 50% of lakes), restricted species (occurring in ≥ 10 -to- 25% of lakes), and rare species (occurring in $< 10\%$ of lakes). We then evaluated the effect of lake size on species richness. Together, these preliminary exercises allowed us to characterize the lake communities within a region in terms of native vs. introduced species, common and rare species, and thermal classification. From this analysis we gained insight to the role of lake size in determining community composition. Rare species were assessed as possible indicator species of unique environmental conditions or biogeographical history. Based on these exercises, we defined faunal assemblages as groups of species that shared common distribution patterns across lakes and regions. As such, these assemblages represented subsets of the lake communities, though in many cases they represented the entire lake fish community. To facilitate cross-region comparisons, we classified these assemblages into nine groups (see Table 1C). Within each region we identified the following faunal assemblages that were present in the inland lake fish communities:

ISRO

- 1) northern pike, yellow perch *present*
- 2) northern pike, yellow perch, blacknose shiner present; subgroup with golden shiner *present*
- 3) northern pike, yellow perch, and coldwater species cisco and slimy sculpin *present*
- 6) northern pike absent; yellow perch, blacknose shiner, pearl dace *present; no predators*
- 8) northern pike and yellow perch *absent; no predators*
- 9) Coldwater assemblage *present*: cisco, lake whitefish, trout-perch, ninespine stickleback, spoonhead or slimy sculpin, and lake trout (lake trout in Siskiwit Lake only)

VOYA

- 1) northern pike and yellow perch *present*
- 2) northern pike, yellow perch, and blacknose shiner *present*; subgroup with golden shiner *present*; subgroup with muskellunge as surrogate for northern pike.
- 3) northern pike, yellow perch, and coldwater species *present*
- 5) northern pike *present*; yellow perch *absent*
- 6) northern pike *absent*; yellow perch *present*
- 8) northern pike and yellow perch *absent; no predators*

SLBE

- 1) northern pike and yellow perch *present*
- 4) northern pike, yellow perch, and largemouth or smallmouth bass *present*
- 5) northern pike and largemouth or smallmouth bass *present*; yellow perch *absent*
- 6) northern pike *absent*; yellow perch *present*
- 7) northern pike and yellow perch *absent*; largemouth or smallmouth bass *present*
- 8) northern pike and yellow perch *absent*; *no predators*

Inspection of the distribution of these faunal assemblages across regions showed that three assemblages (1, 6, 8) were found in all regions, four (2, 3, 5, 6) were found in two regions, and three (4, 7, 9) were restricted to SLBE (Table 3). Fish communities of ISRO and VOYA were generally well differentiated by this faunal assemblage classification, although as expected, similar assemblages showed lower community dissimilarities, such as northern pike–yellow perch (group 1) vs. northern pike–yellow perch–blacknose shiner (group 2) (Table 3). The predominance of wide-spread species in SLBE resulted in less differentiation of communities by our faunal assemblage classification.

Patterns of similarity across lake communities were evaluated with Jaccard's Index of Similarity (Jaccard 1908) applied to community matrices of species p/a data. We used Jaccard's similarity measure because of its simplicity and because it provides relatively conservative estimates of similarity from p/a data (Boyce and Ellison 2001) and because probabilities of significance can be estimated from Jaccard's measure (Real and Vargas 1996). Jaccard's Index of Similarity is expressed as:

$$S^J = \frac{C}{A + B + C'}$$

Where A = number of species unique to sample A,

B = number of species unique to sample B, and

C = number of species shared in samples A and B.

Analysis of Similarities (ANOSIM; Clarke 1993) was used to test for significant differences in species composition among communities grouped by faunal assemblages within regions. ANOSIM is a nonparametric test for significant differences between two or more groups based on Jaccard's measure of similarity (Clarke 1993) and utilizes community matrices of species p/a data divided into designated groups. A value of 1.0 for the ANOSIM test statistic R indicates complete dissimilarity. For within-region comparisons of assemblage groups, we judged groups to be significantly different

Table 3. Thermal and faunal classification of the 32 inland lakes of ISRO with two or more species. Definitions of thermal classifications and faunal assemblages are provided in Table 1.

Lake	Abbrev.	N spp.	Mean Thermal Score	Thermal Classification	Faunal Assemblage ¹
Ahmik	AHM	2	1.00	cool	1
Amygdaloid	AMY	3	1.00	cool	1
Angleworm	ANG	3	1.33	cool	1
Beaver	BEA	4	1.25	cool	2
Benson	BEN	4	1.00	cool	6
Chickenbone	CHI	10	1.20	cool	2
Desor	DES	10	0.50	cold	9
Dustin	DUS	5	1.40	cool-warm	2
Epidote	EPI	2	1.00	cool	1
Eva	EVA	5	1.20	cool	2
Feldtmann	FEL	3	1.33	cool	1
Forbes	FOR	3	1.00	cool	6
George	GEO	2	1.00	cool	1
Halloran	HAL	4	1.25	cool	2
Harvey	HAR	6	1.33	cool	6
Hatchet	HAT	7	1.29	cool	8
Intermediate	INT	6	1.33	cool	2
John	JOH	5	1.20	cool	6
Lesage	LES	2	1.00	cool	1
Linklater	LIN	4	1.25	cool	2
Livermore	LIV	3	1.00	cool	2
Mason	MAS	5	1.20	cool	2
McDonald	MCD	2	1.00	cool	1
Otter	OTT	4	1.00	cool	2
Patterson	PAT	2	1.00	cool	1
Richie	RIC	12	1.00	cool	3
Sargent	SAR	11	1.00	cool	3
Scholts	SCH	3	1.00	cool	2
Shesheeb	SHE	4	1.25	cool	2
Siskiwit	SIS	15	0.67	cold	9
Wagejo	WAG	2	1.00	cool	1
Whittlesey	WHI	8	1.25	cool	2

¹ See Definition of Faunal Assemblages in Table 1C.

with $R > 0.25$ and $P < 0.10$. Similarity Percentage (SIMPER; Clarke 1993) is used in conjunction with ANOSIM to identify species that contribute to the composition of groups and identify species that are shared and not shared among groups. We used SIMPER to identify species that contributed to the composition of communities grouped by faunal assemblages and identify species that were shared or not shared among communities grouped by faunal assemblages. SIMPER is based on the Bray-Curtis similarity measure (Bray and Curtis 1957) and is expressed as:

$$S^{BC} = \frac{2a}{2a + b + c}$$

Where a = number of species shared between two samples, b = number of species unique to sample 1, and c = number of species unique to sample 2.

We note that the Bray-Curtis Similarity is the same as Sørensen's Coefficient of Community (Sørensen 1948), and although Jaccard's index is more sensitive to differences, Bray-Curtis Similarity is more responsive to similarity. The two indices are highly correlated and give similar results in ordination analyses (Boyce and Ellison 2001).

Hierarchical cluster analysis was conducted on community matrices of species p/a data for each region to reveal patterns of grouping of communities based on shared species. We used the unweighted pair-group average (UPGMA) algorithm on measures of Jaccard's similarity to generate dendrograms, or cluster trees, showing patterns of relationship among communities. Community labels at the terminal branches of resulting cluster trees were overlain with color codes and symbols for thermal, faunal assemblage, and lake age classifications to assess agreement of grouping of communities based on community similarity (e.g., clustering by tree branches) vs. our three independent community classifications. Cluster analysis was also conducted to examine grouping of communities by physical closeness based on inter-lake distances. Here again, community labels at the terminal branches of resulting cluster trees were overlain with color codes and symbols for thermal, faunal assemblage, and lake age classifications to assess agreement of grouping of communities based on community similarity vs. our three independent community classifications. Finally, matrices used to generate cluster trees based on community similarities and inter-lake distances were compared for agreement. To make this comparison, inter-lake distances were relativized to match the scale of the Jaccard's similarity measure, i.e., maximum distance was assigned a value of 0 and a distance of 0 was assigned a value of 1. Matrices of Jaccard's similarities and relativized user distances were then compared with the Mantel Test to assess correlation. Mantel test statistics were R (correlation coefficient; agreement of two matrices) and P (probability of no correlation or agreement).

Multivariate ordination analyses were conducted to examine underlying structure in community matrices of species p/a data for each region. Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) projected communities (lakes) in multivariate space based on similarity of community composition. Labels for community scores on DCA plots were overlain with color codes for thermal and faunal assemblage classifications to examine patterns of agreement between multivariate spatial distribution of communities and our independent community classifications. The influence of environmental variables on trends in community composition was then evaluated by Canonical Correspondence Analysis (CCA; Legendre and Legendre 1998). CCA ordinated communities in multivariate space based on community matrices of species p/a data and relevant environmental variables. CCA identified environmental variables that yielded the greatest separation (ordination) of communities in multivariate space. Only environmental variables that were continuous (non-categorical) and measured for each lake were considered. Canonical variables included in development of CCA models were lake area, watershed area, maximum lake depth, summer

epilimnion and hypolimnion temperatures, summer epilimnion and hypolimnion dissolved oxygen, alkalinity, pH, specific conductivity, Secchi depth, and SLD. Lake area, watershed area, maximum lake depth and specific conductivity variables required log-transformation to achieve normality. Canonical variables for CCA with low correlations with ordination axes one and two were eliminated in a stepwise process to derive models restricted to the most informative variables. Labels for community (lake) scores on CCA plots were overlain with color codes for thermal and faunal assemblage classifications to assess agreement between spatial ordination of communities influenced by environmental variables and our independent community classifications. CCA plots of mean species scores in multivariate space revealed the distribution species ordinated by environmental variables. Species scores were overlain with color codes for thermal classification to allow comparison of ordinal distribution of species by environmental variables vs. our thermal classification. Overall, ordination of community and species scores in multivariate space facilitated interpretation of the composite response of communities and individual species to environmental variables and species associations.

Across-Region (Global) Analysis

Community matrices of species p/a data for each region were assembled into a global community matrix grouped by region. ANOSIM was used to determine the distinctiveness of the regions based on species composition, and SIMPER identified species that characterized each region and identified species that were shared and not shared among regions. Communities in the global community matrix were then divided into groups based on thermal classification and a simplified faunal assemblage classification. ANOSIM was used to evaluate the distinctiveness of fish communities grouped by thermal classification and the simplified faunal assemblage classification across regions, and SIMPER was used to identify species that characterized a particular group and identify species that were shared and not shared among groups. For global comparisons of thermal and assemblage groups, we judged groups to be significantly different for the ANOSIM test statistic $R > 0.50$ and $P < 0.10$. Thermal classification of communities (coldwater, coolwater, cool-warmwater, warmwater) was based on the mean of individual species' thermal scores (Table 1B). Simplified faunal groups for global comparisons were defined as: 1–northern pike and largemouth or smallmouth bass absent; 2–northern pike present, largemouth or smallmouth bass absent; 3–northern pike absent, largemouth or smallmouth bass present; 4–northern pike and largemouth or smallmouth present. Use of a simplified faunal classification with fewer groups was necessary to achieve sufficient sample sizes for evaluation of differences among regions based on faunal composition. One-way ANOVA was used to test for significant differences among regions based on species thermal scores and mean thermal scores of lake communities.

As done for individual regions, we conducted hierarchical cluster analysis across regions based on global community matrix of species p/a data grouped by region. Community labels at the terminal branches of the resulting global cluster tree were overlain with color codes and symbols for region and thermal and faunal assemblage classifications. We then assessed agreement of community groupings based on community similarity vs. region and independent community classifications. Overlays of presence/absence for selected species or groups of species (coldwater species, yellow perch, northern pike, blacknose shiner, golden shiner, bluntnose minnow, johnny darter, white

sucker, pumpkinseed, rock bass, smallmouth bass, and largemouth bass) were added to the terminal branches to provide additional insight to the clustering of communities.

As was done for each region, multivariate ordination analyses were conducted to examine underlying structure in the global community matrix. DCA was used to project communities in multivariate space based on similarity of community composition. Overlays of color coding for thermal and faunal assemblage classifications allowed assessment of agreement between multivariate spatial distribution of communities and our independent community classifications. For the global DCA, we included a projection of species mean scores in multivariate space with an overlay of species thermal classification. CCA was used to examine the influence of environmental variables on global trends in community composition. For the global CCA, we included all 10 environmental variables in the model as removal of highly correlated variables did not appreciably improve model outcome and their inclusion showed relationships among variables. Labels for community (lake) scores on CCA plots were overlain with color codes for thermal and faunal assemblage classifications to assess agreement between spatial ordination of communities influenced by environmental variables and our independent community classifications. CCA plots of mean species scores were overlain with color codes for thermal classification to allow comparison of ordinal distribution of species by environmental variables vs. our thermal classification. Overall, ordination of community and species scores derived from the global community matrix in multivariate space facilitated interpretation of the composite response of communities and individual species to environmental variables and species associations across regions.

To summarize historical influences on the development of faunas for each region from a common post-glacial faunal source pool, we constructed an area cladogram that showed the successive gains and losses of species in each region relative to a hypothetical ancestral source pool or outgroup (sensu Mayden 1988, Gorman 1992). Species shared by all regions and the source pool (Early Source Pool, Table 2) constituted the putative post-glacial assemblage that colonized the inland lakes. Parsimony analysis with the Branch and Bound algorithm and Fitch's Character Optimization Criteria (Kitching et al. 1998) were used to find the most parsimonious cladogram topology. Species gained and lost represented changes in regional faunas in response to changing history (e.g., drainage connections, lake formation, and elevation), climatic conditions, and dispersal of species. The cladogram was then overlaid with our thermal classification for the individual species to provide an independent assessment of the influence of climate factors driving differences among regions. One-way ANOVA was used to assess differences in species thermal scores across regions and the source pool, and to assess differences in thermal scores of species gained and lost across regions.

Statistical Software

PAST! Version 1.94 (Hammer et al. 2001, 2009) was used to generate similarity measures and hierarchical cluster trees; compare cluster trees with the Mantel Test; conduct ANOVA, ANOSIM, and SIMPER analyses; and develop multivariate ordination modeling with DCA and CCA. PAST! Cladistics Parsimony Analysis was used to develop area cladograms showing the biogeographical relationships of ISRO, VOYA, and SLBE regions based on shared and derived species in their faunas.

Estimates of Age of Inland Lakes

Ages of ISRO and VOYA lakes were estimated by applying estimated rates of isostatic rebound to lake surface elevations above a reference plane—Lake Superior for ISRO, and Rainy Lake for VOYA (Appendix IV). The resulting age estimates were arrayed in neighbor-joining trees based on expressing age differences as Euclidean distances. Lake names were color-coded by faunal assemblage classification to examine the relationship between lake age and faunal composition.

By about 10,500 BP, the rapidly retreating Laurentian Ice Shield (LIS) in the Lake Superior basin reached the southwest end of ISRO, paused in the vicinity of Lake Desor, then rapidly retreated, deglaciating the remainder of the island by ca. 9,600 BP (Farrand 1969; Huber 1973; Saarnisto 1974, 1975; Boyd et al. 2012). However, Breckenridge (2013) provides a revised chronology based on a new analysis of strand lines utilizing Digital Elevation Models (DEM) and LiDAR data. The southwest end of ISRO was deglaciating ca. 11,000 BP, Lily Lake was isolated ca. 10,700 BP, and the island was fully deglaciating by ca. 10,500 BP. There appears to have been a ca. 50-year pause in the region of Lily Lake at ca. 10,800 BP. Lake Desor was isolated from Lake Minong during this interval, likely after 10,500 BP (ca. 10,100 BP) when lake levels dropped. After 10,500 BP, the LIS retreated rapidly in a northeast direction, fully deglaciating the Lake Superior basin by ca. 10,000 BP (Farrand 1969; Saarnisto 1974, 1975; Barnett 1992; Larson and Schaetzl 2001; Breckenridge 2013).

To reflect the increasing rate of isostatic rebound in the Lake Superior basin from the southwest to northeast (Farrand 1960, Breckenridge 2013), we adjusted the rate of rebound from the southwest to northeast ends of ISRO. The precursor to Lake Superior—Lake Minong—had an elevation 45 m below the current lake level (Farrand 1969, Huber 1973). This value was added to the elevation of the Minong shoreline plane on ISRO, which varied from 23 m to 43 m above lake level from the southwest to northeast ends of the island, respectively (Huber 1973) (Figure 14). Using 9,300 years as the estimated age of the lowest Minong shoreline (Farrand 1969, Huber 1973, Saarnisto 1974, 1975, Boyd et al. 2012, Breckenridge 2013), the estimated total rebound of the Minong plane at the northeast end of ISRO was 88 m, or 0.95 m/100 yr. Total rebound distances in the southwest end were less—67 m, or 0.72 m/100 yr. In the vicinity of Lake Desor, the estimated rate of rebound was 0.76 m/100 yr (see Appendix IV). A second set of estimates were generated by applying higher rebound rates for the first 2,000 years following deglaciation and a lower constant rate afterwards. Our estimates of lake ages based on a constant isostatic rebound rate for each locality of the island is reasonable, as the time frame of our estimates is roughly within the linear phase of rebound (2,000–10,000 yr post-glaciation) reported by Brevik (1994).

Isle Royale

Rebound rates calculated for each ISRO lake position along a southwest-to-northeast transect were used to estimate the relative age of each lake based on its current elevation above Lake Superior. Thus Lake Desor, with an elevation of 77.1 m above lake level, was estimated to be 10,040 yr old, which agrees with estimates of ca. 10,000 yr from Raymond et al. (1975), and Saarnisto's (1974, 1975) estimate of 10,100 BP as the period the LIS stalled near Lake Desor. However, our estimate of the age of Siskiwit Lake (2,200 yr) is much younger than the 8,700 yr estimated in Raymond et al. (1975). Differences in estimates may be due to using radiocarbon dating of sediment cores to

estimate ages of lakes, as in Flakne (2003), versus our aging based on isostatic rebound rates. Embayments may accumulate sediment from the emerging watershed surrounding the lake basin long before isostatic rebound fully isolates and elevates the water body above water level of Lake Superior. This can result in older age estimates based on sediment cores. For fish populations, the time of full isolation of the water body marks the point of population isolation from Lake Superior. Our estimate of the age of Lily Lake, a small, fishless pond with the highest elevation of all ISRO inland lakes (117 m above Lake Superior) was judged to be excessively high (15,700 yr). A possible explanation is that Lily Lake was perched above Glacial Lake Minong when southwestern ISRO was deglaciated ca. 11,000 BP. The estimated time of deglaciation in the vicinity of Lily Lake, based on the estimated elevation of the Minong strandline (68.3 m), was ca. 10,800 BP, which is in line with deglaciation chronologies of Farrand (1969), Saarnisto (1974, 1975), Farrand and Drexler (1985), and Breckenridge (2013). This suggests that Lily Lake was perched above the surrounding terrain at the time of deglaciation. Our estimate based on the elevation of the Minong strandline is also within the range of Flakne's (2003) estimated age of Lily Lake (10,510–11,040 BP) based on C¹⁴ dating of sediment cores. However, our estimated age for Lake Ojibway (8,200 BP) is younger than Flakne's (2003) estimate (9,700–10,100 BP). We suspect Flakne's estimate reflects the accumulation of sediments in the Lake Ojibway basin prior to being cut off from Glacial Lake Minong. More accurate estimated ages of ISRO inland lakes are possible by using the elevations of glacial lake strandlines identified in the DEM of ISRO by Breckenridge (2013) and estimating the age of reference organic material contained in those strandlines based on C¹⁴ aging techniques.

Voyageurs

Like ISRO, the estimated ages of VOYA lakes were based on present elevation and estimated dates of deglaciation and emergence of uplands from inundation by proto-glacial lakes Kabetogama, Namakan, and Rainy (KNR). Thorliefson (1996) estimated that the VOYA region first became deglaciated before ca. 12,600 BP, and the isostatic rebound model in Yang and Teller (2005) estimates that the VOYA uplands emerged ca. 11,000 BP. Using an estimate of 11,000 BP as the age of the highest elevation lake (Cruiser), which is 40.935 m above Rainy Lake, the average rate of rebound was 0.372 m/100 yr. This is remarkably close to Brevik's (1994) estimated rebound rate of 0.358 m/100 yr for bedrock landscapes in the southern Lake Agassiz basin. Brevik (1994) showed that rebound rates were relatively constant 2,000–10,000 yr post-glaciation. Prior to 2,000 yr, rebound rates were high and rapidly falling; after 10,000 yr, rebound rates declined slowly; and by ca. 30,000 years, rebound is complete. Brevik's estimated rebound rate of 0.358 m/100 yr was used to estimate ages of VOYA lakes based on present elevation above Rainy Lake. This is justified because most of the apparent rebound occurred after the uplands began to emerge nearly 2,000 yr after deglaciation. Also, using Rainy Lake as reference plane was judged as reasonable because Yang and Teller's (2005) model showed the configuration of KNR shorelines to be similar to modern ones by ca. 10,000 BP. Using Brevik's rebound rate, the oldest VOYA lake (Cruiser) was estimated to be 11,442 years old, and the youngest lake (Mukooda) was estimated to be 1,198 years old.

Sleeping Bear Dunes

The SLBE region became ice-free more than 12,000 BP (Crossman and McAllister 1986). Inland lake formation has been intimately connected to the post-glacial history of the northern Lake

Michigan coastal environment and is a complex and ongoing process (Calver 1946, Drexler 1974, NPS 2005). The basins of SLBE lakes likely formed during the Nipissing high stand (5,000–4,000 BP) when elevated lake levels carved bluffs and created large perched sand dunes (Arbogast and Loope 1999, Arbogast 2000, Loope and Arbogast 2000, Larson and Schaetzl 2001, Thompson et al. 2011, Johnston et al. 2012). SLBE's inland lakes formed following declining lake levels in the late Nipissing phase, which ended ca. 3,500 BP. Thus, while the lake basins may have formed much earlier, SLBE's inland lakes did not become isolated until relatively recently. Moreover, many of the inland lakes are interconnected intermittently or permanently and all have similar water plane elevations that are affected by the level of Lake Michigan.

Impacts of 21st Century Climate Change on Inland Lake Communities

Global climate change is expected to result in the warming of aquatic environments over the 21st century and, in turn, will result in changes in distributions of aquatic species (Magnuson et al. 1990, 1997; Kling et al. 2003). A warming climate is predicted to result in the expansion of many warmwater fish species into the Great Lakes basin (Mandrak 1989; Shuter and Post 1990; Minns and Moore 1992, 1995) and a contraction of coolwater and coldwater species (Meisner 1990; Schindler et al. 1990, 1996a, 1996b; Minns and Moore 1992; Stefan et al. 1996, 2001). Recent modeling of the impacts of future climate change on Minnesota inland lakes (hereafter referred to as the Minnesota Climate Change Model, or MCCM) has predicted which lakes will likely retain coldwater species or lose them (Jacobson et al. 2010, Fang et al. 2012, Jiang et al. 2012). These investigators showed that lake geometry ratio, maximum depth, and Secchi depth were important predictors of whether a lake will likely serve as refuge for coldwater species by the end of the 21st century. In essence, their model predicts the presence of sufficient cold, oxythermal habitat in hypolimnions as a function of Secchi depth (a surrogate of lake productivity) and lake geometry ratio (a measure of relative depth and strength of stratification). Refuge lakes have Secchi depths >2.3 m, maximum depths >11.6 m, and geometry ratios <2.7 m^{-0.5}. Jacobson et al. (2010) showed that the combination of increased temperature and nutrient loading would deplete the hypolimnetic oxygen in stratified lakes to values <3 mg/L (TDO3) and result in complete loss of minimally oxygenated coldwater habitat. Modeling exercises predict that 74% of Minnesota lakes and 70% of Wisconsin lakes containing cisco will lose this coldwater species by the end of the 21st century if mean July air temperatures increase 4 °C, as predicted by climate change models (Jiang et al. 2012, Sharma et al. 2011).

We applied the MCCM criteria to predict the persistence of sufficient cold, oxygenated habitat in inland lakes of VOYA, ISRO, and SLBE in the face of predicted climate warming in the 21st century. Geometry ratios (GR) were calculated for each lake, and together with measures of maximum depth (Zmax) and Secchi depth, lakes were classified as tier 1 and 2 refuge lakes or tier 3 and 4 non-refuge lakes according to MCCM criteria. Tier 1 refuge lakes had Zmax >13.7 m, GR <1.8, and Secchi depths >3.2 m. Tier 2 refuge lakes had Zmax 11.3–13.7 m, GR 1.8–2.7, and Secchi depths 2.3–3.2 m. Tier 3 non-refuge lakes had Zmax 3.1–11.2 m, GR 2.8–11.9, and Secchi depths 0.7–2.2 m. Tier 4 non-refuge lakes had Zmax <3.1 m, GR >11.9, and Secchi depths <0.7 m.

Because MCCM criteria were developed for lakes affected by continental climates, in particular, Minnesota, and because ISRO lakes are situated on an island in a large, cold Great Lake (Superior),

the MCCM criteria are likely too stringent for ISRO lakes. For example, Lake Desor, a large lake on ISRO, has maintained a coldwater fish community for ca. 10,000 years (Table 14) and has endured the mid-Holocene warming period (Davis et al. 2000), yet would be classified as a non-refuge lake by MCCM criteria. To include Desor as a tier 2 refuge lake, we modified the MCCM criteria for ISRO as follows: tier 1 refuge lakes had $Z_{max} > 11.0$ m, $GR < 2.6$, and Secchi depths unchanged at > 3.2 m. Tier 2 refuge lakes had Z_{max} 8.0–11.0 m, GR 2.6–3.6, and Secchi depths unchanged at 2.3–3.2 m. Tier 3 non-refuge lakes had Z_{max} 3.1–7.9 m, $GR > 3.7$ –11.9, and Secchi depths unchanged at 0.7–2.2 m. Tier 4 non-refuge lakes followed MCCM criteria: Z_{max} of 3.1 m, $GR > 11.9$, and Secchi depths < 0.7 m.

A potential problem we are aware of is that Secchi depths in some ISRO and VOYA lakes may be lower than expected because of high levels of tannins in the water. In those particular lakes, Secchi depth may not be an accurate indicator of relative productivity. However, because tannin levels are likely to be higher in smaller, shallower lakes, the Z_{max} and GR values would already be low, resulting in their classification as non-refuge lakes. Also, the critical Secchi depth for refuge lakes is relatively low (2.3 m). Taken together, the reduction of Secchi depths in some lakes with high tannin levels is not likely to be a deciding factor in its classification as a refuge lake.

An additional predictor of the refuge status of a lake is the presence of suitable summer oxythermal habitat (TDO3) for the coldwater species lake trout, burbot, lake whitefish, and cisco (Jacobson et al. 2010). To evaluate summer oxythermal habitat available in each lake, we inspected summer records of hypolimnetic temperature and oxygen. However, our values were measured near the lake bottom where DO levels are typically < 3 mg/L and temperatures are at their minimum. Estimating TDO3 for evaluation under the MCCM requires measuring a lake temperature-oxygen profile to identify the stratum below the thermocline where DO is ≥ 3.0 mg/L (Jacobson et al. 2010). Thus, our assessment of TDO3 is imprecise and excessively conservative; lakes with DO ≥ 3.0 mg/L and temperatures $< 8^{\circ}\text{C}$ at the lake bottom clearly meet TDO3 requirements as a refuge lake, and lakes with excessively warm temperatures at the lake bottom ($> 15^{\circ}\text{C}$) do not meet requirements as refuge lake, regardless of DO levels. However, lakes with DO < 3.0 mg/L may meet the TDO3 requirements for higher strata, but we lack that information. Lakes that meet Z_{max} , GR , and Secchi depth criteria, and have sufficiently cold lake bottom temperatures, but DO levels are < 3.0 mg/L, are considered candidate refuge lakes pending further information on available oxythermal habitat. The presence of coldwater species in a candidate lake serves as an indicator that the lake likely meets TDO3 criteria as a refuge lake and the absence of coldwater species suggests that oxythermal habitat is lacking and is not a refuge lake.

Species we classified as coldwater fishes were judged to be most susceptible to climate change and coolwater fishes less so (Table 2). Species classified as cool-warmwater, thermally tolerant, and warmwater were expected to maintain or increase their distribution across lakes or prevalence within lake communities. Our thermal classification of species allowed us to identify species as likely to be retained or lost from each lake in the context of the MCCM classification of refuge and non-refuge lakes. Next, we compared our thermal classification of lake communities with the MCCM classification of refuge–nonrefuge lakes. We expected lake communities that were classified as

thermally tolerant or warmwater to be non-refuge lakes and not likely to be affected by climate change, while those that were classified as coolwater communities were expected to be non-refuge lakes and susceptible to shifting toward a warmer classification. Lake communities classified as coldwater were expected to be candidate refuge lakes and least likely to be affected by climate change. From this analysis we predicted the composition and thermal classification of each lake community for the year 2100.

Results

ISRO

Areas of the 32 inland lakes of ISRO with two or more fish species ranged from the 1.3 ha Epidote to the 1,635.2 ha Siskiwit; 56% of the lakes were ≤ 40 ha (Figure 9). Maximum depth ranged from 1.5 to 46 m, and 72% of the lakes were ≤ 10 m deep (Figure 10).

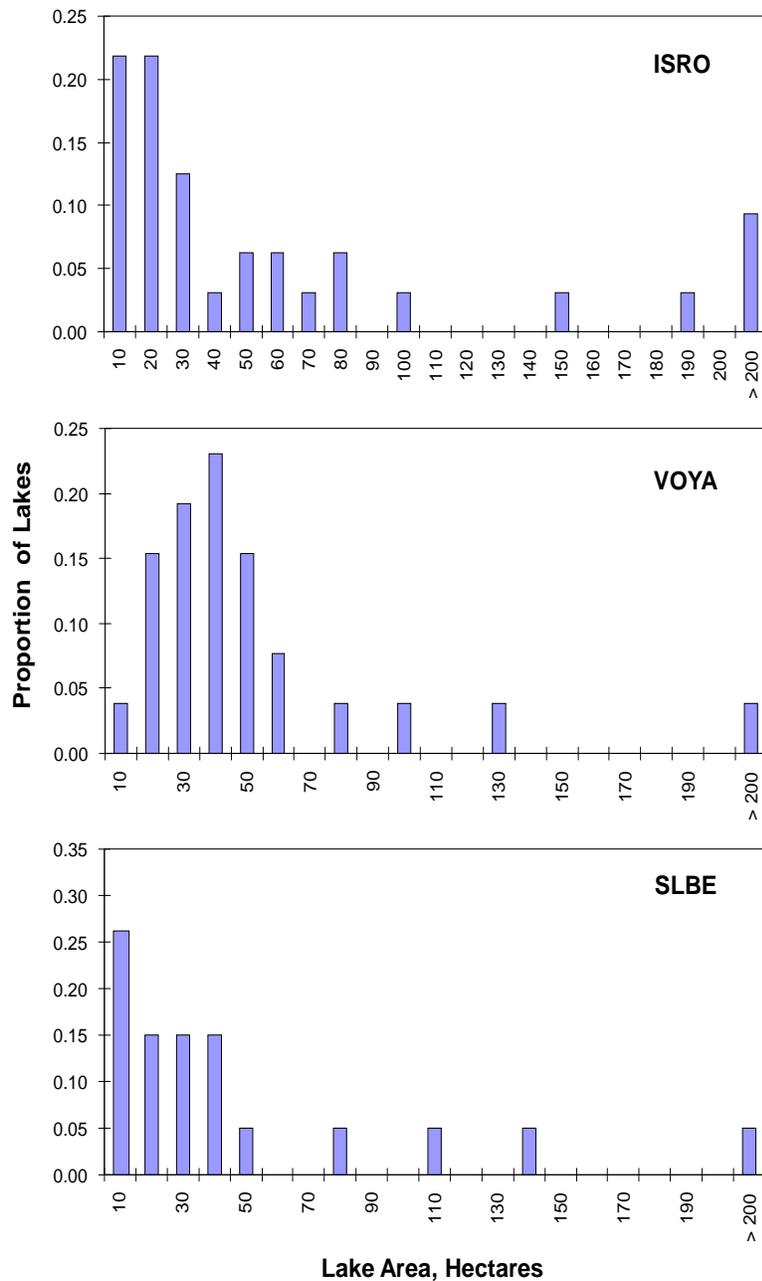


Figure 9. Frequency distribution of surface area (ha) of inland lakes at ISRO, VOYA, and SLBE.

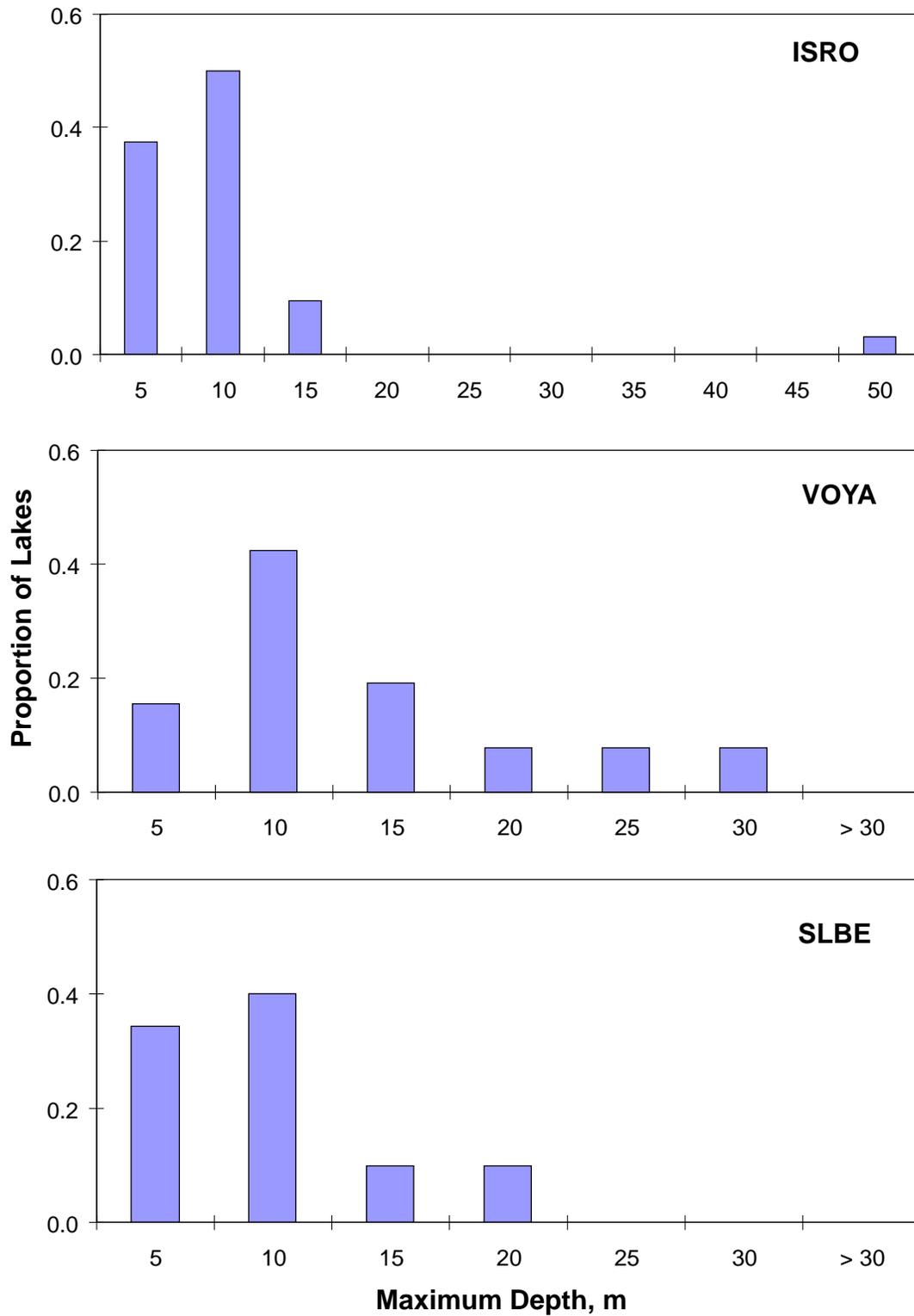


Figure 10. Frequency distribution of maximum depth (m) of inland lakes at ISRO, VOYA, and SLBE.

There were no correlations between lake area and maximum depth or between lake area and summer hypolimnetic temperature (not shown). However, there was a predictable relationship between

maximum depth and summer hypolimnetic temperature; deeper lakes tended to have lower summer hypolimnetic temperatures (Figure 11). Most of the lakes (63%) had summer hypolimnetic temperatures >15°C (Figure 12), a result of the preponderance of small, shallow lakes. The ISRO inland lakes included 28 species (see Table 2), with the larger lakes tending to have more species (Figure 13). The largest lake, Siskiwit, contained 15 species, and the smallest lake, Epidote,

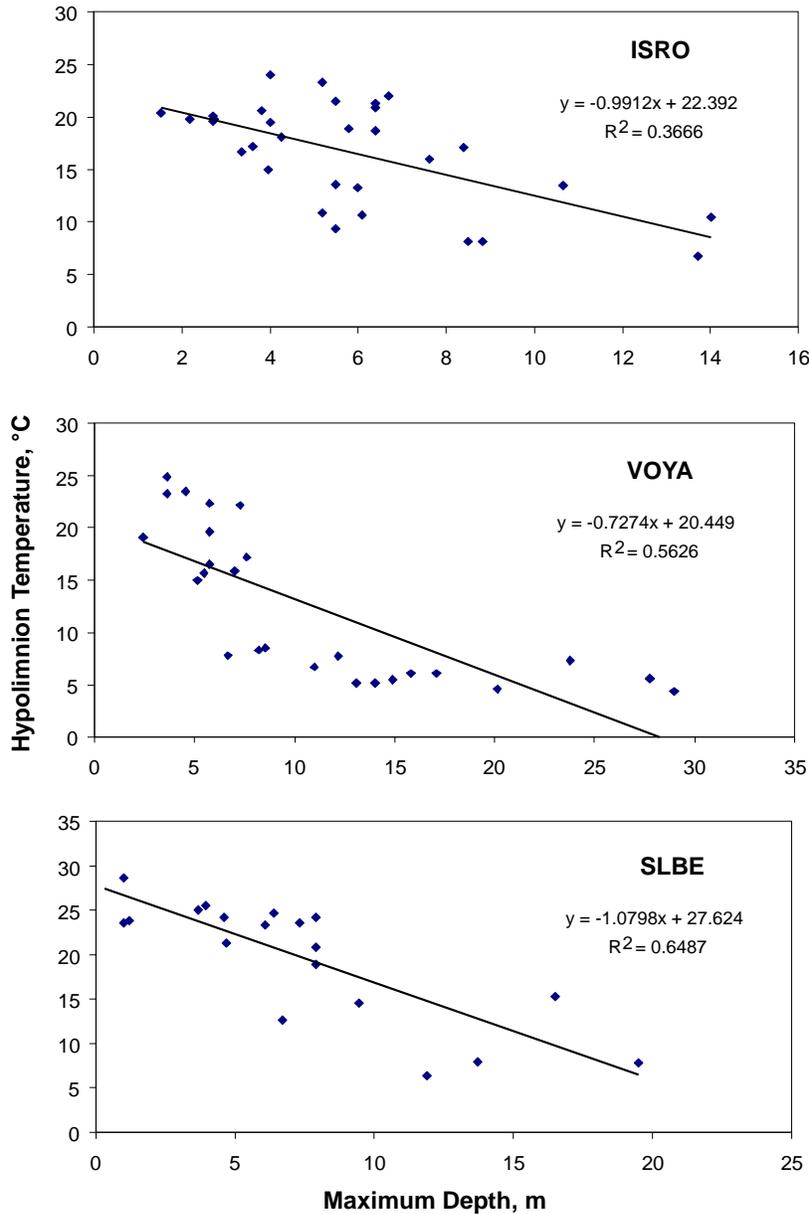


Figure 11. Summer hypolimnetic temperature (°C) vs. depth (m) of inland lakes at ISRO, VOYA, and SLBE.

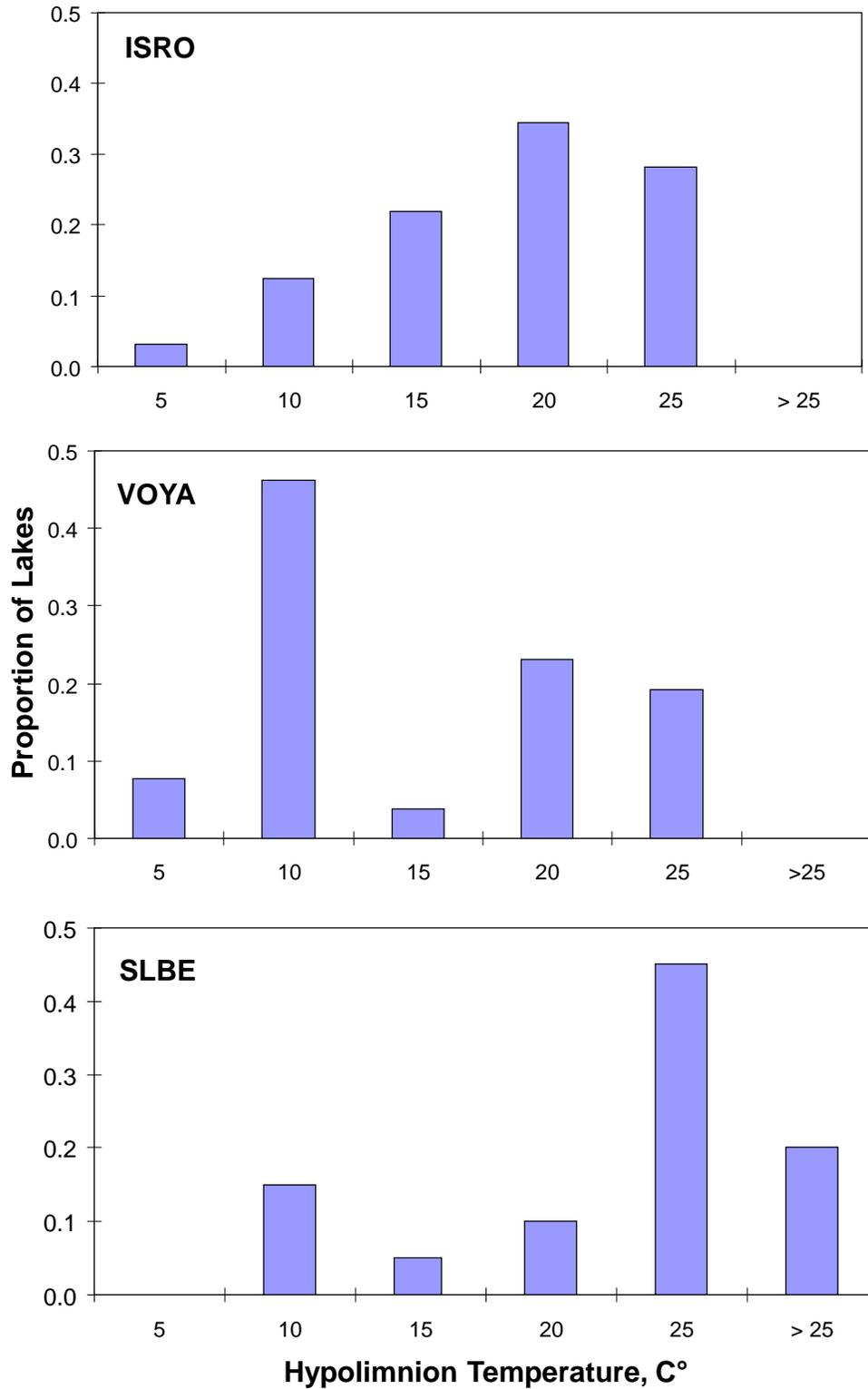


Figure 12. Frequency distribution of summer hypolimnetic temperature (°C) of inland lakes of ISRO, VOYA, and SLBE.

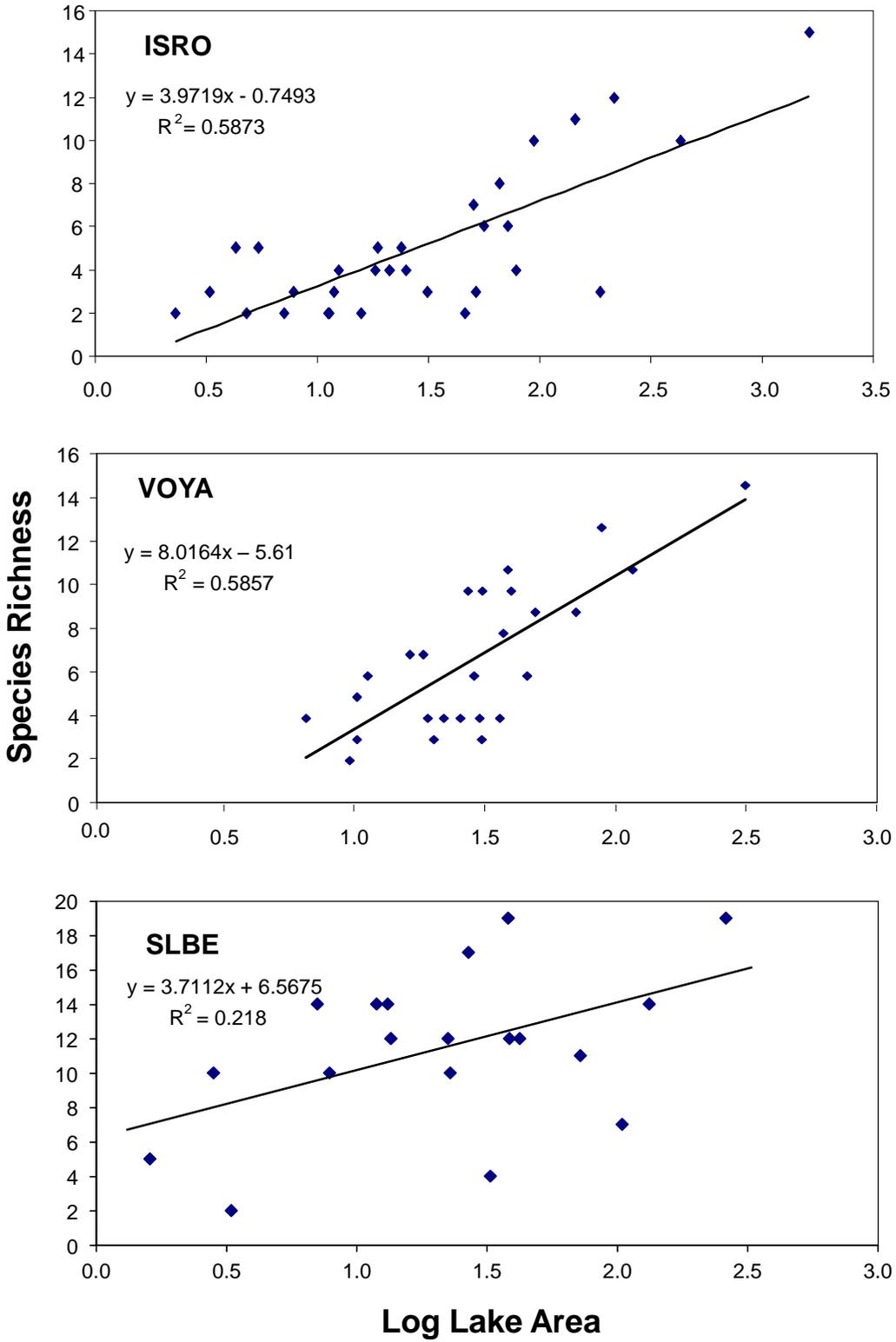


Figure 13. Species area plots of inland lakes of ISRO, VOYA, and SLBE.

contained two species (Table 4). A large majority of lakes (72%) had fewer than six species (Figure 14). Most of the 29 species had restricted distributions; 22 were found in five or fewer lakes, and 17 were found in one-to-three lakes (Figure 15). The most widespread species were yellow perch, northern pike, blacknose shiner, and white sucker; they were found in 94%, 81%, 63%, and 41% of the lakes, respectively. Most of the 28 species were classified as cold or coolwater species (9 and 11 species, respectively), and the remaining eight species were classified as thermally tolerant (see Table 2). Mean thermal scores for all but one lake fish community were <1.4. Dustin was classified as a mixed cool-warmwater community; 29 lakes were classified as coolwater communities, and the two largest lakes—Desor and Sikiwit—were classified as coldwater communities (Table 4).

Table 4. Comparison of species composition among inland lake fish communities of ISRO based on grouping by faunal assemblages 1–9. Probabilities of no difference (P) and dissimilarities (R) were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.25$. An R of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of assemblage groups lists 28 species. Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded. Faunal assemblages are defined in Table 1.

ANOSIM, probabilities of no difference (P) and dissimilarity (R)

Faunal Assemblage	Faunal Assemblage					
	1	2	3	6	8	9
1	-	0.000	0.0178	0.002	0.099	0.019
2	0.519	-	0.018	0.000	0.067	0.006
3	1.000	0.653	-	0.046	0.329	0.331
6	1.000	0.829	1.000	-	0.203	0.065
8	1.000	1.000	1.000	0.833	-	0.662
9	1.000	0.973	0.500	0.664	0.000	-

Overall P / R values: $P(\text{same}) < 0.0001$; $R = 0.7779$

SIMPER, % dissimilarity (Bray-Curtis Similarity)

Faunal Assemblage	Faunal Assemblage					
	1	2	3	6	8	9
1	-					
2	38.63	-				
3	67.72	46.94	-			
6	66.64	54.67	66.01	-		
8	95.56	94.13	78.68	66.74	-	
9	85.44	78.75	57.87	75.54	61.50	-

Overall dissimilarity: 57.32%

Table 4 (continued). Comparison of species composition among inland lake fish communities of ISRO based on grouping by faunal assemblages 1–9. Probabilities of no difference (P) and dissimilarities (R) were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.25$. An R of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of assemblage groups lists 28 species. Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded. Faunal assemblages are defined in Table 1.

SIMPER, Pooled			Mean Species Abundances Within Faunal Assemblages					
Taxon	Contrib. %	Cum. %	1	2	3	6	8	9
Blacknose.Shiner	7.802	13.61	0	0.929	1	1	0	0.5
White.Sucker	5.124	22.55	0.222	0.286	1	0.5	1	1
Golden.Shiner	4.699	30.75	0	0.5	1	0	0	0
N.Pike	4.616	38.80	1	1	1	0	0	0.5
Spottail.Shiner	4.072	45.91	0	0.429	1	0	0	0.5
Pearl.dace	3.754	52.45	0	0	0	0.75	1	0.5
Brook.Stickleback	3.249	58.12	0	0	0.5	0.5	1	0.5
Trout-Perch	2.450	62.40	0	0.071	0.5	0	1	1
Cisco	1.987	65.87	0	0	1	0	0	1
Pumpkinseed	1.843	69.08	0	0.143	1	0	0	0
Finescale.Dace	1.794	72.21	0	0	0	0.5	0	0
N.Redbelly.Dace	1.604	75.01	0	0.071	0	0	1	0.5
Fathead.Minnow	1.473	77.58	0	0	0	0.25	1	0
Slimy.Sculpin	1.451	80.11	0	0	1	0	0	0.5
Yellow.Perch	1.317	82.41	1	1	1	1	0	0.5
Walleye	1.310	84.69	0	0.214	0	0	0	0
Spoonhead.Sculpin	1.020	86.47	0	0	0	0	0	1
NS.Stickleback	1.020	88.25	0	0	0	0	0	1
L.Whitefish	1.020	90.03	0	0	0	0	0	1
Iowa.Darter	0.869	91.55	0	0.071	0.5	0	0	0
Blackchin.Shiner	0.869	93.06	0	0.071	0.5	0	0	0
Logperch	0.816	94.49	0	0.071	0	0	0	0.5
Creek.Chub	0.761	95.82	0	0	0	0	1	0
L.Chub	0.588	96.84	0	0	0	0	0	0.5
Mimic.Shiner	0.513	97.74	0	0	0.5	0	0	0
Lake.Trout	0.432	98.49	0	0	0	0	0	0.5
Burbot	0.432	99.25	0	0	0	0	0	0.5
Emerald.Shiner	0.432	100.00	0	0	0	0	0	0.5

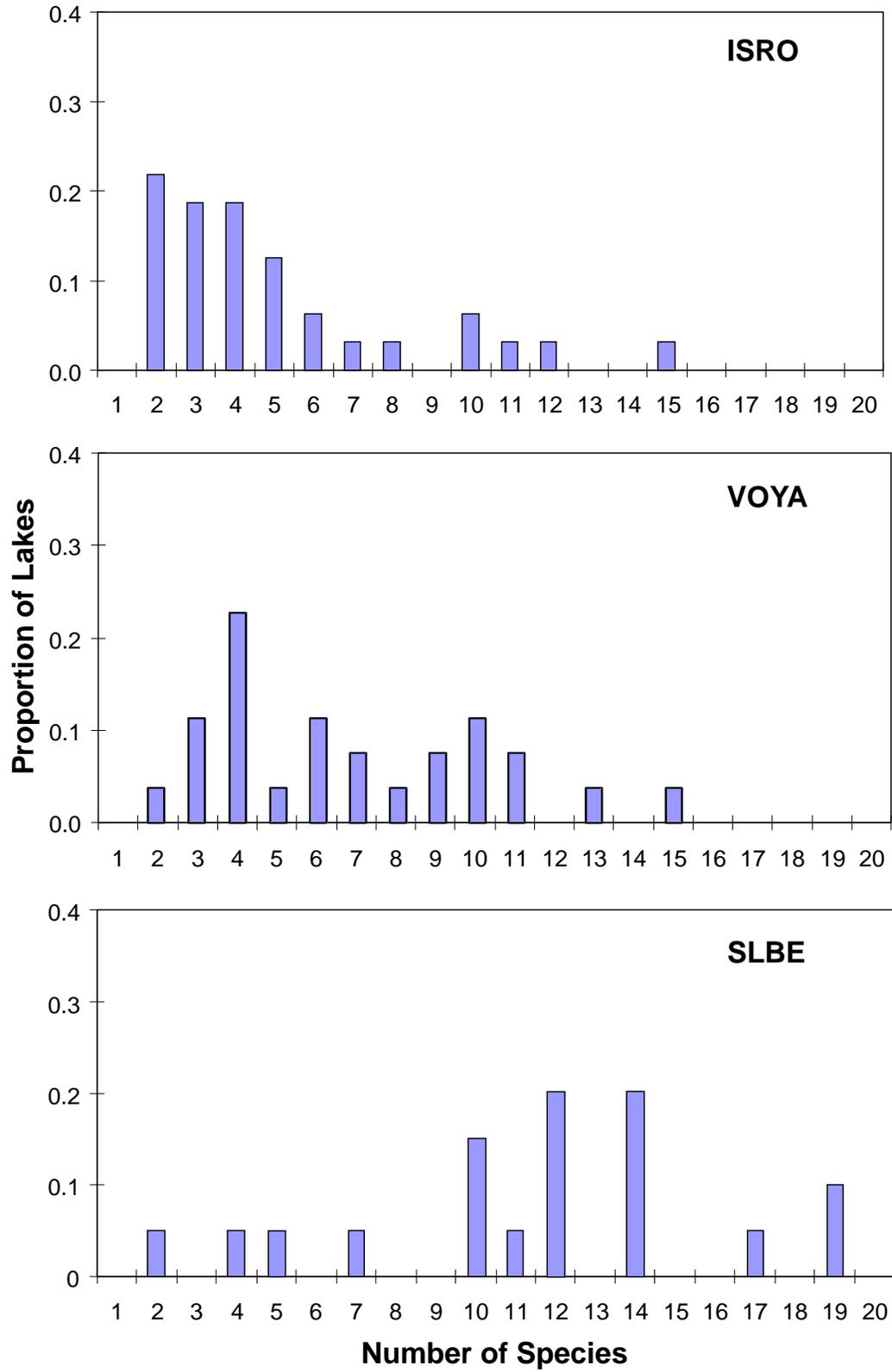


Figure 14. Distribution of species richness of the inland lakes of ISRO, VOYA, and SLBE.

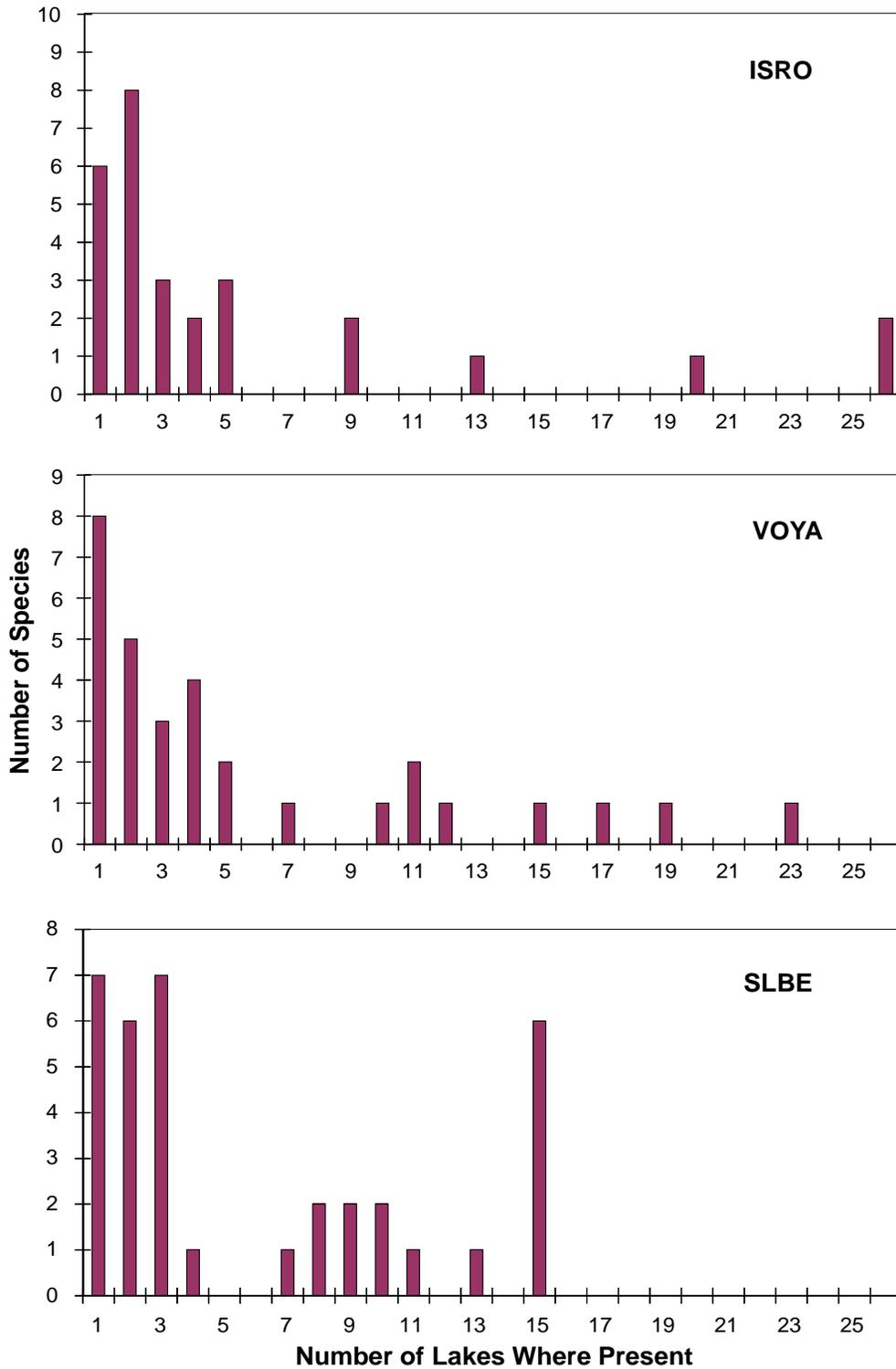


Figure 15. Frequency of species occurrence across the inland lakes of ISRO, VOYA, and SLBE.

The 32 inland lake communities of ISRO comprised six faunal assemblages (see Table 3). The most widespread assemblages were northern pike and yellow perch (assemblage 1), represented in 10 lakes, and northern pike, yellow perch, and blacknose shiner (assemblage 2) represented in 13 lakes. Assemblage 6, containing yellow perch but without northern pike, was found in four lake communities (see Table 4). Coolwater and coldwater assemblages (3 and 9) were represented in two lakes each. Hatchet Lake lacked both northern pike and yellow perch (assemblage 8), but Desor also lacked these species even though it contained a coldwater assemblage. Overall, northern pike with yellow perch were present in 25 of the 32 lakes (78%). Application of ANOSIM demonstrated significant differences in composition of ISRO lake communities based on these faunal groupings (see Table 4). Communities containing assemblages 1 or 2 were distinct from all other assemblages (except for the 1 vs. 8 comparison). Communities with assemblage 6 were distinct only from assemblages 1 and 2. Communities containing the coldwater assemblage 9 (Desor and Siskiwit), the coolwater assemblage 3 (Richie and Sargent), and assemblage 8 that lacked both northern pike and yellow perch (Hatchet), were not distinct from each other (see Table 4). SIMPER showed that lake communities containing assemblages 1 and 2 shared the same species (northern pike, yellow perch, and white sucker) but communities containing assemblage 2 had 10 additional species, of which three were widespread (blacknose shiner, golden shiner, and spottail shiner) (see Table 4). Assemblage 3, represented by communities in Richie and Sargent, added coldwater species cisco, trout perch, and slimy sculpin, and Richie was unique in containing mimic shiner. Communities with assemblage 6 lacked northern pike but contained yellow perch and were unique in containing finescale dace and fathead minnow. Assemblage 8, lacking both northern pike and yellow perch, was represented by the community in Hatchet, which was unique in containing creek chub. Assemblage 9, represented by communities in Desor and Siskiwit, was unique in containing nine coldwater species.

Hierarchical cluster analyses based on similarities of lake community compositions and distances between lakes produced very different linkage trees (Figure 16). A comparison of matrices of Jaccard's similarities and relativized inter-lake distances with the Mantel test showed no correlation ($R = -0.037$, $P = 0.961$). Cluster analysis based on inter-lake distances showed no relationship with grouping by faunal assemblages, i.e., lakes with similar or different assemblages were as likely to be nearby as far away (Figure 16A). Cluster analysis based on similarities of lake communities showed a high degree of concordance with grouping by faunal assemblages (Figure 16B), though lakes Siskiwit (SIS) and Desor (DES) were exceptions. Thermal classification of communities did not show a discernable pattern of association with branches of the distance or similarity linkage trees, an expected outcome as 29 of 32 lakes were classified as having coolwater assemblages. Overall, there was little correspondence between relative lake age and inter-lake distance or community similarity; although some lake pairs of similar age clustered at terminal branches of the distance linkage trees (Figures 16 and 17). This is not surprising given that lakes of similar age have similar elevations and distances from Lake Superior, which the principal connecting lake (Figure 17). Examples included Patterson-Ahmik, Shesheeb-Linklater, Forbes-Benson, and these pairs also clustered in terminal branches of the community similarity linkage tree (Figure 16B). These examples notwithstanding, similarity of community composition could not be reliably predicted based on measures of distance between lakes or relative lake age.

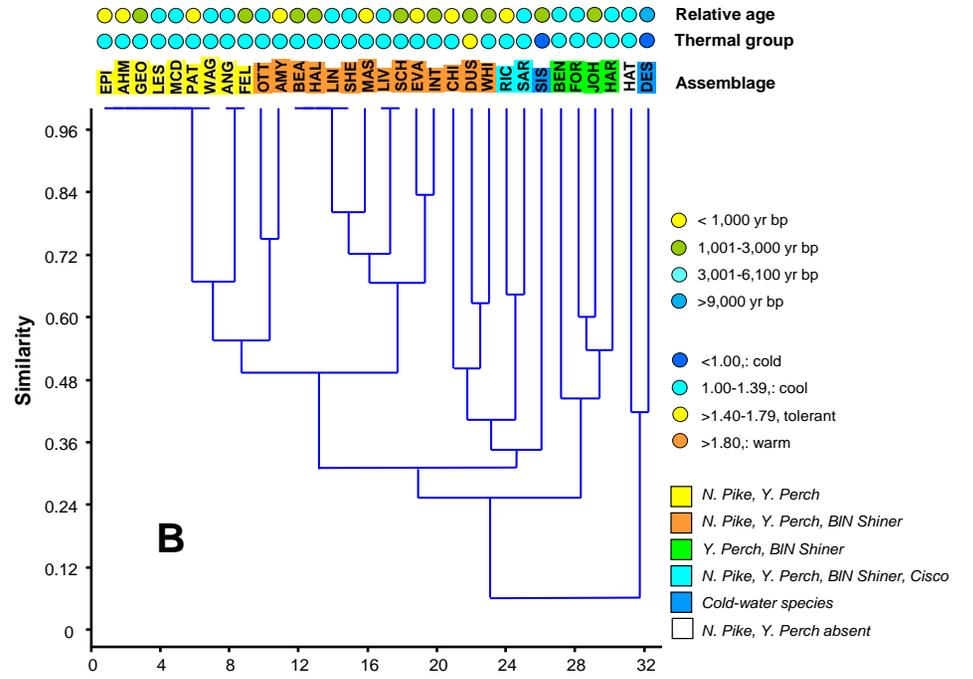
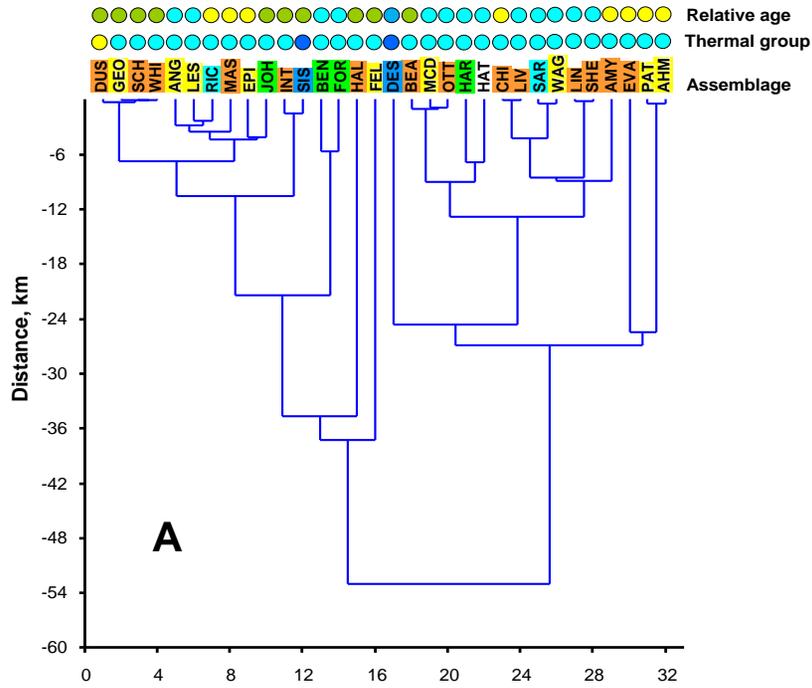


Figure 16. Cluster analysis of 32 ISRO inland lakes based on unpaired distances (A) and lake communities based on paired Jaccard's Similarities (B), with overlays of relative ages of lakes, thermal groups, and faunal assemblages. Correlation Coefficient A: 0.9382, B: 0.9203. See Table 3 for lake name abbreviations.

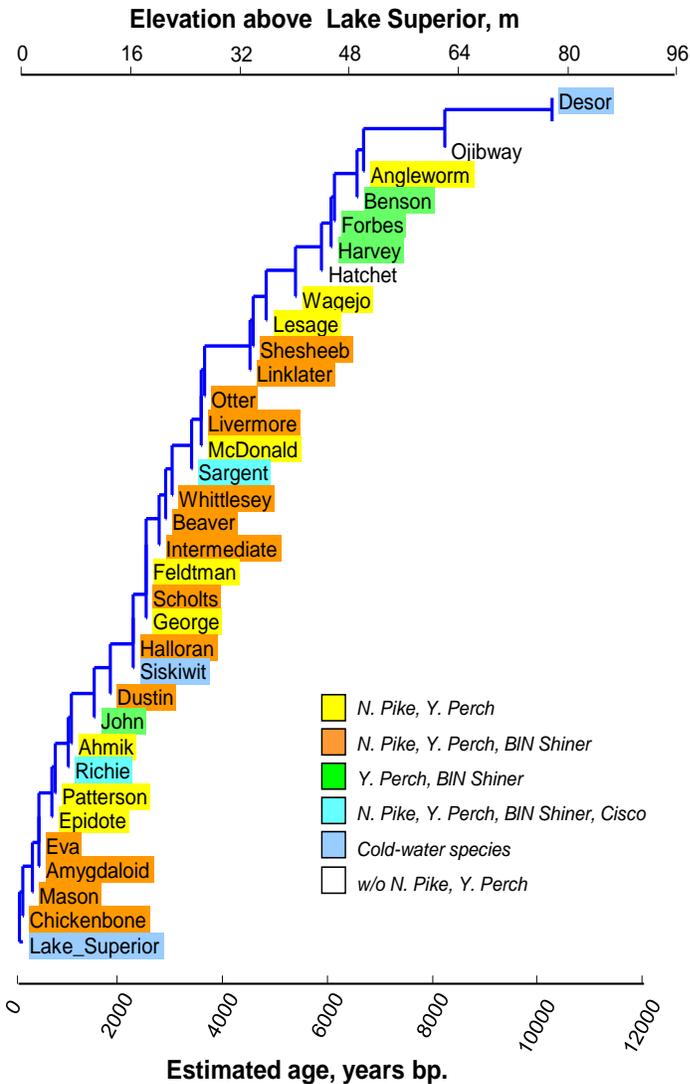


Figure 17. Neighbor-joining tree of ISRO inland lake fish communities based on estimated ages, using Euclidean distances with overlay of assemblage groups. Lake Superior serves as the out-group. Ojibway, a fishless lake, is included for comparison.

DCA separated lake communities based on species composition along two axes that accounted for 75% of the total variance (Figure 18; see Appendix XII). Axis 1 represented a gradient of communities with northern pike and yellow perch to those that lacked northern pike and yellow perch and contained minnows not shared with other lakes (Hatchet) or were dominated by coldwater species (Desor). Axis 2 provided greater separation of lakes that lacked northern pike from those with coldwater species. The two principal axes of the DCA showed that the coldwater communities of Siskiwit (SIS) and Desor (DES) were distinct from the 28 coolwater communities of ISRO (Figure 18A). The lake communities clustered into four assemblage groups: those that contained northern pike and yellow perch (assemblages 1, 2, and 3); those that lacked northern pike but contained

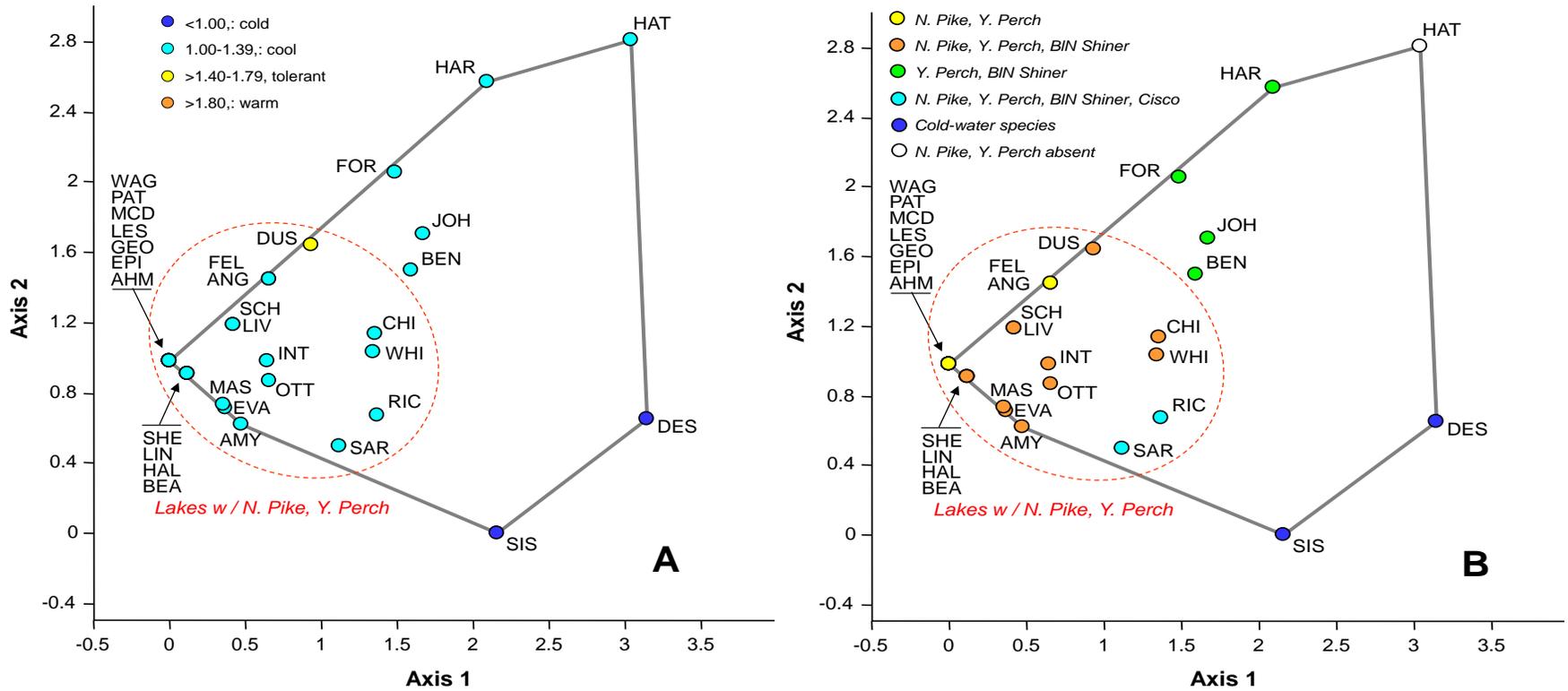


Figure 18. Detrended Correspondence Analysis (DCA) plots for 32 ISRO inland lake communities based on similarity of composition with overlays of mean community thermal scores (A) and assemblage groups (B). The polygon circumscribes the community scores. Axis 1 explained 49% of the total variance and Axis 2 explained an additional 26%. The DCA model is based on 18 segments. See Table 3 for lake name abbreviations.

yellow perch and blacknose shiner (assemblage 6); Hatchet lacking both northern pike and yellow perch; and Desor and Siskiwit containing nine coldwater species (assemblage 9) (Figure 18B). Many of the simplest communities had the same composition, particularly those that contained northern pike and yellow perch, or northern pike, yellow perch, and blacknose shiner (assemblages 1 and 2).

CCA provided a projection of lake communities and species in multivariate space in response to environmental variables (Figures 19 and 20). Axis 1 explained 43% of the total variance. Environmental variables with the highest correlations with Axis 1 were log maximum depth (Zmax_log), log lake area (L.Area_log), Secchi depth, watershed area (Wshd.Area_log), and hypolimnetic temperature (Hypo_temp) (see Appendix XIII). Axis 1 may be interpreted as a gradient of communities in small, shallow lakes with reduced transparency and warm hypolimnions (negative scores) to communities in deep, large lakes with clear water and cold hypolimnions (positive scores). Axis 2 explained an additional 23% of the total variance and was largely complementary to the Axis 1 gradient. The variable with the highest correlation to Axis 2 was shoreline development (Shore_D) (see Appendix XIII). Axis 2 may be interpreted as a gradient of communities in more convoluted lakes (negative scores) to more round lakes (positive scores). The triplots for environmental variables indicated the general environmental gradient along which the lake communities were distributed (Figures 19 and 20). With the exception of Hypo_temp, scores for all environmental variables increased with increasing values along Axis 1 and declined with increasing values along Axis 2 (see Appendix XIII). Thus, communities in larger, deeper, colder lakes scored higher along the environmental gradient coincident with Axis 1, and communities in smaller, shallower, warmer lakes scored lower.

Coding of lake communities by thermal classification in CCA plots showed similar results as in DCA plots; coldwater communities of SIS and DES were distinct from the 28 coolwater communities of ISRO (Figures 18A and 19A). Coding of lake communities by faunal assemblages resulted in clustering similar to that observed as in DCA (Figures 18B and 19B). Plotting species scores coded by thermal classification on CCA plots provided further insight into the dispersion of lake communities along environmental gradients just described (Figure 20). Coldwater species loaded positively on Axis 1 while most coolwater and thermally tolerant species loaded negatively. Both groups were widely distributed along Axis 2.

Integration of information from CCA plots provided insights as to the relationship of species distributions, community composition, and environmental conditions (Figures 19 and 20). The smallest, warmest lakes (BEN, FOR, HAR, HAT, and JOH; see Table 3 for lake names) contained three-to-seven species that included yellow perch and blacknose shiner but lacked northern pike (assemblages 6 and 8). A group of slightly larger lakes (AHM, AMY, ANG, EPI, FEL, GEO, LES, MCD, PAT, and WAG) contained two-to-three species that included northern pike and yellow perch (assemblage 1). A diverse range of smaller and medium size lakes (BEA, CHI, DUS, EVA, HAL, INT, LIN, LIV, MAS, OTT, and SHE) contained three-to-ten species that included northern pike, yellow perch, and blacknose shiner (assemblage 6). Two intermediate size lakes, RIC and SAR, contained 12 and 11 species, respectively, and included northern pike, yellow perch, blacknose shiner, and the coldwater species cisco (assemblage 3). Finally, the largest lakes, DES and SIS,

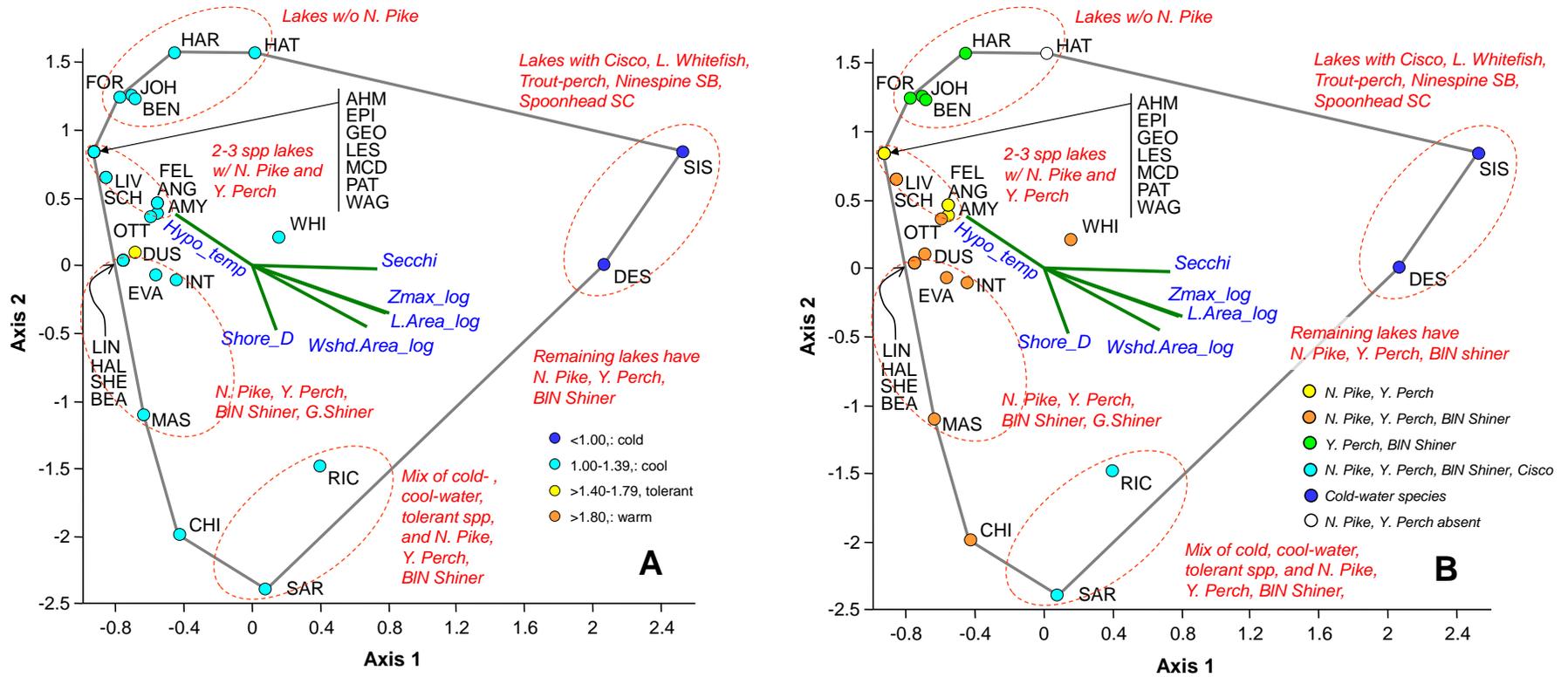


Figure 19. Canonical Correspondence Analysis (CCA) plots for 32 ISRO lake communities set by environmental variables, with overlays of mean community thermal scores (A) and assemblage groups (B). The polygon circumscribes the community scores. Axis 1 explains 43% of the variance and Axis 2 explains an additional 23%. See Table 3 for lake name definitions.

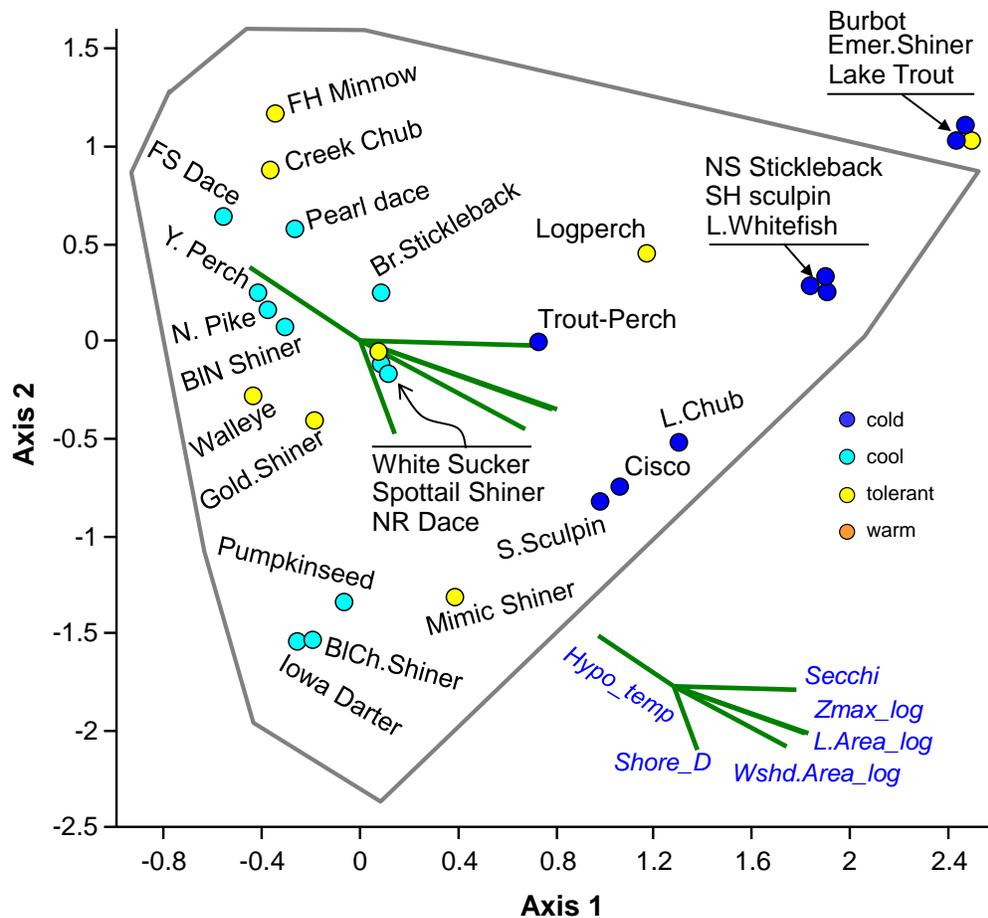


Figure 20. CCA plot for ISRO lake communities showing positions of species mean scores in canonical space set by environmental variables and coded by species thermal classification. The polygon represents the area circumscribing the community scores (not shown; see Figure 19).

contained 10 and 15 species, respectively, which included an array of 9 coldwater species (assemblage 9).

VOYA

Areas of the 26 inland lakes of VOYA with two or more fish species ranged from the 8.3 ha Quarter Line to the 305 ha Mukooda; 62% of the lakes were ≤ 40 ha (see Figure 9). Maximum depth ranged from 2.4 to 29 m, and 58% of the lakes were ≤ 10 m deep (see Figure 10). There were no correlations between lake area and maximum depth or lake area and summer hypolimnetic temperature (not shown). However, there was a predictable relationship between maximum depth and summer hypolimnetic temperature, with deeper lakes tending to have lower summer hypolimnetic temperatures (see Figure 11). Approximately 46% of the lakes had summer hypolimnetic temperatures $> 15^{\circ}\text{C}$ (see Figure 12). The VOYA inland lakes included 31 endemic species and seven introduced species (see Table 2). Larger lakes tended to have more endemic species (see Figure 13); the largest, Mukooda, contained the greatest number of species (15), while the smallest, Quarter Line, contained just four species (Table 5). Less than half of the lakes (42%) had fewer than six species (see Figure 14). Most of the 31 endemic species had restricted distributions; 22 were found in

five or fewer lakes, and 16 were found in one-to-three lakes (see Figure 15). The most widespread species were yellow perch, northern pike, blacknose shiner, and white sucker, which were found in 88%, 73%, 65%, and 58% of the lakes, respectively. Most of the 31 endemic species were classified as coldwater or coolwater species (4 and 13, respectively); 13 were classified as thermally tolerant species, and one as a warmwater species (see Table 2). No lake fish communities were classified as coldwater (Table 5). Of the 26 lake communities, 19 were classified as coolwater and seven as cool-warmwater communities.

Table 5. Thermal and faunal classification of the 26 inland lakes of VOYA with two or more species. Definitions of thermal classifications and faunal assemblages are provided in Table 1.

Lake	N Spp.	Thermal Score	Thermal Classification	Faunal Assemblage
Agnes	3	1.33	cool	1
Beast	10	1.30	cool	5*
Brown	4	1.25	cool	2
Cruiser	10	1.30	cool	6
Ek	4	1.25	cool	1
Fishmouth	5	1.40	cool-warm	2
Jorgens	3	1.00	cool	1*
Little Shoepack	7	1.29	cool	2 [‡]
Little Trout	13	1.46	cool-warm	3*
Locator	9	1.22	cool	3*
Loiten	3	1.33	cool	6*
Lucille	6	1.17	cool	5*
McDevitt	2	1.00	cool	1
Mukooda	15	1.20	cool	3*
Net	8	1.63	cool-warm	2
O'Leary	9	1.44	cool-warm	2*
Oslo	4	1.25	cool	2
Peary	11	1.73	cool-warm	2
Quarter Line	4	1.25	cool	2*
Quill	6	1.50	cool-warm	6*
Ryan	6	1.17	cool	2
Shoepack	11	1.36	cool	2 [‡]
Tooth	4	1.00	cool	2
War Club	10	1.20	cool	3*
Weir	4	1.50	cool-warm	6
Wiyapka	7	1.29	cool	8

* introduced largemouth bass present; [‡] Muskellunge for northern pike.

The 26 inland lake communities of VOYA comprised six faunal assemblages (see Table 5). The most widespread assemblage was northern pike, yellow perch, and blacknose shiner (assemblage 2), represented by 11 lakes; in two of these lakes (Shoepack and Little Shoepack) muskellunge is the functional substitute for northern pike. Northern pike and yellow perch without blacknose shiner (assemblage 1) were found in four lakes. Coldwater species with northern pike and yellow perch

(assemblage 3) were found in four lakes. Northern pike was absent in only five lakes, and yellow perch was absent in three lakes. Overall, northern pike (or muskellunge) together with yellow perch (assemblages 1, 2, and 3) were present in 19 of the 26 lakes (73%). Application of ANOSIM showed significant differences in 9 of 15 community comparisons grouped by faunal assemblages (Table 6). The most distinctive communities contained northern pike and yellow perch (assemblage 1), and northern pike/muskellunge, yellow perch, and blacknose shiner (assemblage 2). The least distinctive communities were those that contained assemblage 6 (northern pike absent) and 8 (northern pike and yellow perch absent). SIMPER showed considerable overlap in species across communities grouped by assemblages, especially for communities containing assemblages 1–3; principal shared species were northern pike, yellow perch, white sucker, pumpkinseed, Iowa darter, and golden shiner (Table 6). Communities with assemblage 3 were unique in containing coldwater species cisco, lake trout, burbot, and slimy sculpin; and coolwater species spottail shiner, northern longear sunfish, and mottled sculpin (Table 6). Communities containing assemblages lacking northern pike (assemblages 6 and 8) shared three species (Iowa darter, northern redbelly dace, and finescale dace). However, Wiyapka, the only lake containing assemblage 8, differed in harboring fathead minnow, brook stickleback, and mudminnow, and was unique in harboring logperch (Table 6).

Hierarchical cluster analysis based on similarities of lake communities and distances between lakes produced very different linkage trees (Figure 21). A comparison of matrices of Jaccard's similarities and relativized inter-lake distances with the Mantel test showed no correlation ($R = 0.07$, $P = 0.423$). Cluster analysis based on similarities of community composition showed some concordance with faunal assemblage groups (Figure 21B). A group of 12 lake communities containing northern pike formed a major branch; four terminal branches (communities) contained northern pike and yellow perch (assemblage 1); seven contained northern pike, yellow perch, and blacknose shiner (assemblage 2); and one (Lucille) contained northern pike without yellow perch (assemblage 5). Communities containing northern pike, yellow perch, and coldwater species (Locator, War Club, Little Trout, Mukooda; assemblage 3) were clustered into two separate branches. Wiyapka, lacking both northern pike and yellow perch (assemblage 8), served as an outgroup to other VOYA lake communities. No clear pattern of clustering was evident based on thermal classification, likely a result that 19 of 26 lakes were classified as having coolwater communities. Though the matrices based on community similarities and inter-lake distances were uncorrelated, the linkage tree based on distances between lakes (Figure 21A) showed some evidence that lakes with similar assemblages tended to be nearby, particularly in terminal pairs; for example, Locator–War Club, Quill–Loiten, Brown–Oslo, and Little Trout–Mukooda shared the same assemblage group and were likewise clustered as terminal pairs in the linkage tree based on similarity of community composition (Figure 21B). However, the distance linkage tree was less successful in aggregating other lake communities by assemblage groups. For example, a group of five lake communities (Brown, Oslo, Peary,

Table 6. Comparison of species composition among inland lake fish communities of VOYA based on grouping by faunal assemblages 1–8. Probabilities of no difference (P) and dissimilarities (R) were generated from Analysis of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.25$. An R of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of assemblage groups lists 30 species. Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded. For this analysis, Muskellunge was coded as N. Pike. Assemblage groups are defined in Table 1.

ANOSIM, probabilities of no difference (P) and dissimilarity (R)

Faunal Assemblage	Faunal Assemblage					
	1	2	3	5	6	8
1	-	0.005	0.029	0.064	0.030	0.193
2	0.433	-	0.000	0.037	0.001	0.080
3	0.922	0.702	-	0.065	0.177	0.200
5	0.929	0.528	0.982	-	0.206	0.330
6	0.458	0.674	0.203	0.250	-	0.205
8	1.000	1.000	1.000	1.000	0.750	-

Overall P / R values: P(same) < 0.0001; R = 0.6522

SIMPER, % dissimilarity (Bray-Curtis Similarity). Overall dissimilarity: 59.16%

Faunal Assemblage	Faunal Assemblage					
	1	2	3	5	6	8
1						
2	45.53					
3	64.71	53.95				
5	69.62	48.5	64.47			
6	65.68	56.89	60.53	70.11		
8	95.00	90.91	89.79	55.2	91.18	

SIMPER, Pooled

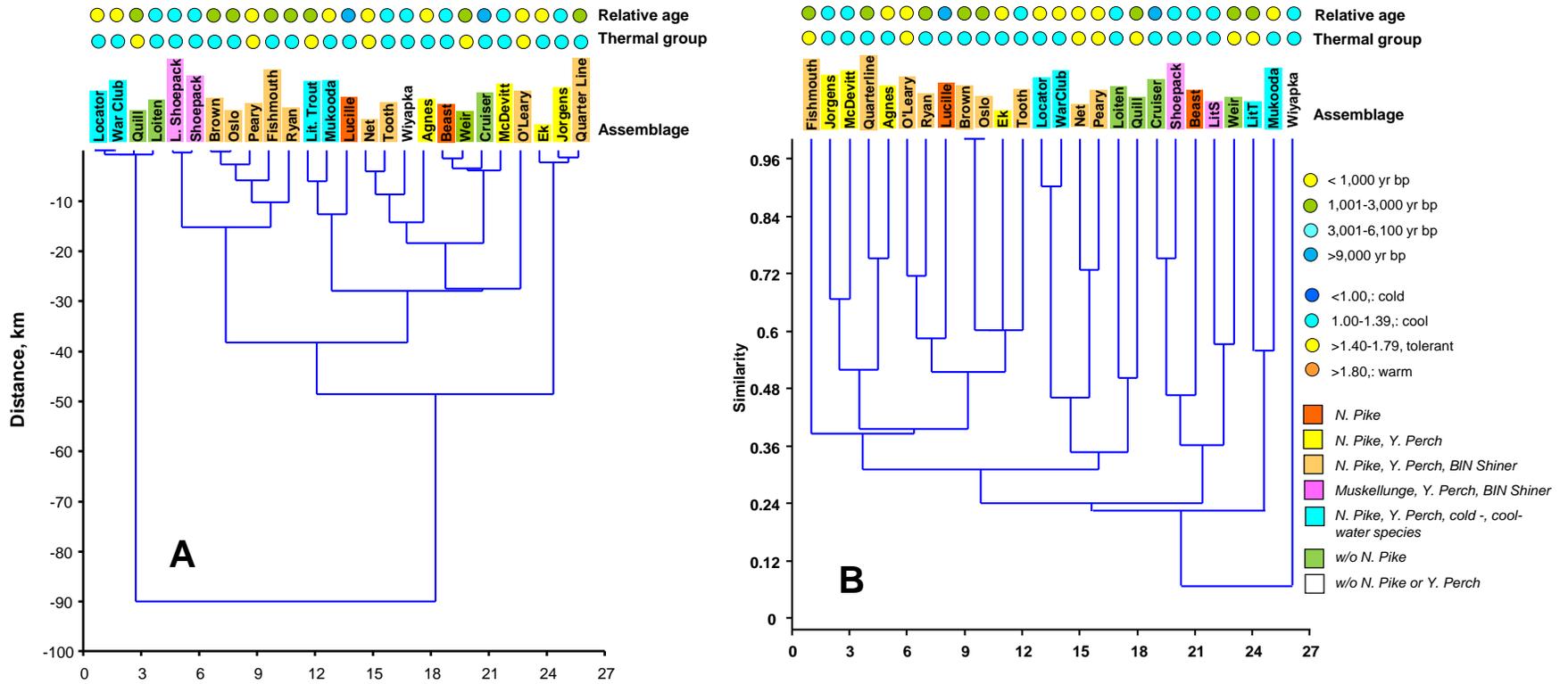
Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Faunal Assemblages					
			1	2	3	5	6	8
Blacknose.Shiner	5.084	8.59	0	1	0.5	1	0.5	0
White.Sucker	4.303	15.87	0.25	0.727	0.5	1	0.5	0
Pumpkinseed	4.140	22.86	0.25	0.455	0.75	0.5	0.5	0
Iowa.Darter	3.915	29.48	0.25	0.364	0.5	1	0.25	1
Golden.Shiner	3.908	36.09	0.25	0.545	0.5	0	0.5	0
Johnny.Darter	3.690	42.32	0	0.273	1	0.5	0.5	0
N.Pike	3.616	48.43	1	1	1	1	0	0
Rock.Bass	3.466	54.29	0	0.091	1	0	0.5	0
N. Redbelly.Dace	2.632	58.74	0	0.091	0	1	0.25	1
Finescale.Dace	2.316	62.66	0	0.091	0.25	0.5	0.25	1
Cisco	2.067	66.15	0	0	1	0	0	0
Yellow.Perch	2.053	69.62	1	1	1	0	1	0
Pearl.dace	2.008	73.01	0	0.182	0	0.5	0.25	0

Table 6 (continued). Comparison of species composition among inland lake fish communities of VOYA based on grouping by faunal assemblages 1–8.

SIMPER, Pooled (continued)			Mean Species Abundances Within Faunal Assemblages					
Taxon	Contribution %	Cumulative %	1	2	3	5	6	8
Fathead.Minnow	1.903	76.23	0	0.182	0	0.5	0	1
Bluntnose.Minnow	1.532	78.82	0	0.182	0.5	0	0	0
Lake.Trout	1.365	81.13	0	0	0.5	0	0.25	0
Br.Stickleback	1.311	83.34	0	0	0	0.5	0	1
Mudminnow	1.282	85.51	0	0	0.25	0	0	1
Walleye	1.222	87.57	0	0.091	0.5	0	0	0
Spottail.Shiner	1.170	89.55	0	0	0.5	0	0	0
Emer.Shiner	1.153	91.50	0	0.182	0	0	0.25	0
Mimic.Shiner	0.978	93.15	0	0.091	0.25	0	0	0
Logperch	0.764	94.44	0	0	0	0	0	1
Common.Shiner	0.720	95.66	0	0	0	0	0.25	0
Sauger	0.472	96.46	0	0	0.25	0	0	0
Burbot	0.425	97.18	0	0	0.25	0	0	0
N.Longear.Sunfish	0.425	97.90	0	0	0.25	0	0	0
Mottled.Sculpin	0.425	98.61	0	0	0.25	0	0	0
Slimy.Sculpin	0.425	99.33	0	0	0.25	0	0	0
Tadpole.Madtom	0.395	100.00	0	0.091	0	0	0	0

Fishmouth, and Ryan) clustered in a terminal branch based on distances (Figure 21A) contained northern pike, yellow perch, and blacknose shiner (assemblage group 3), but did not cluster together in the tree based on similarity of community composition (Figure 21B). Other lake communities showed little concordance in clustering between the distance tree and the community similarity tree.

Comparing lake community groupings based on relative lake age with grouping based on relative distance and similarity of community composition (Figures 21 and 22) did not reveal any congruent patterns of clustering. Only communities <ca. 3,000 years old contained assemblage 3, which is characterized by the presence of northern pike, yellow perch, and coolwater and coldwater species (Mukooda, Little Trout, War Club, Locator). However, the fish community in Cruiser, estimated to be ca. 11,000 yr old, lacked northern pike (assemblage 6), but contained lake trout, a coldwater species. Northern pike (or surrogate muskellunge) and yellow perch were present in most inland VOYA lakes (assemblages 1, 2, and 3), which ranged from ca. 1,200 to ca. 11,000 years old. Lakes with muskellunge as a surrogate for northern pike—Shoepack and Little Shoepack—clustered close together, shared similar community composition, and were estimated to have formed 7,000–9,000 BP (Figures 21 and 22; see Appendix IV).



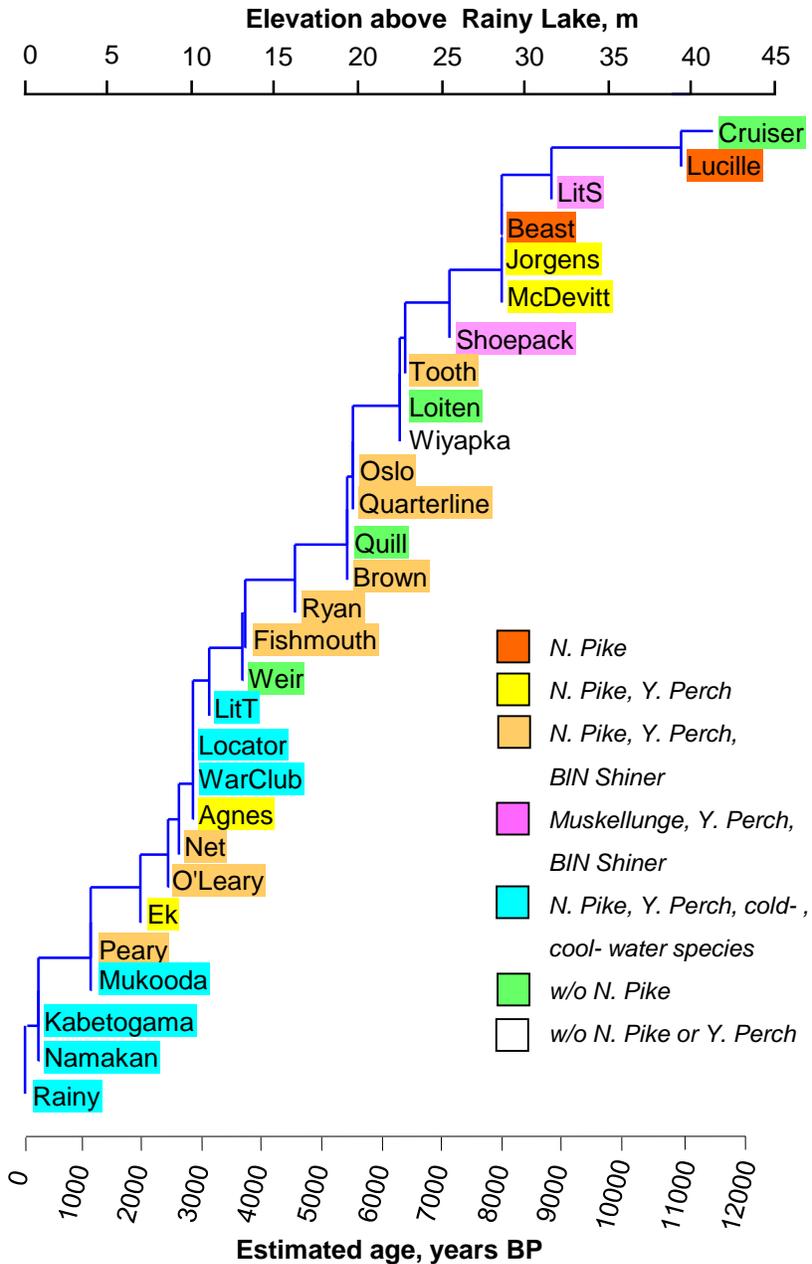


Figure 22. Neighbor-joining tree of VOYA inland lake fish communities based on estimated ages, using Euclidean distances with overlay of assemblage groups. Rainy Lake serves as the baseline (outgroup).

DCA separated lake communities based on species composition along two axes that accounted for 80% of the total variance (Figure 23; see Appendix XIV). Axis 1 represented a gradient of communities with coldwater species (lake trout, cisco, burbot, and slimy sculpin) to communities with coolwater and thermally tolerant species (pearl dace, emerald shiner, northern redbelly dace, finescale dace, fathead minnow, white sucker, brook stickleback, Iowa darter, and logperch) and

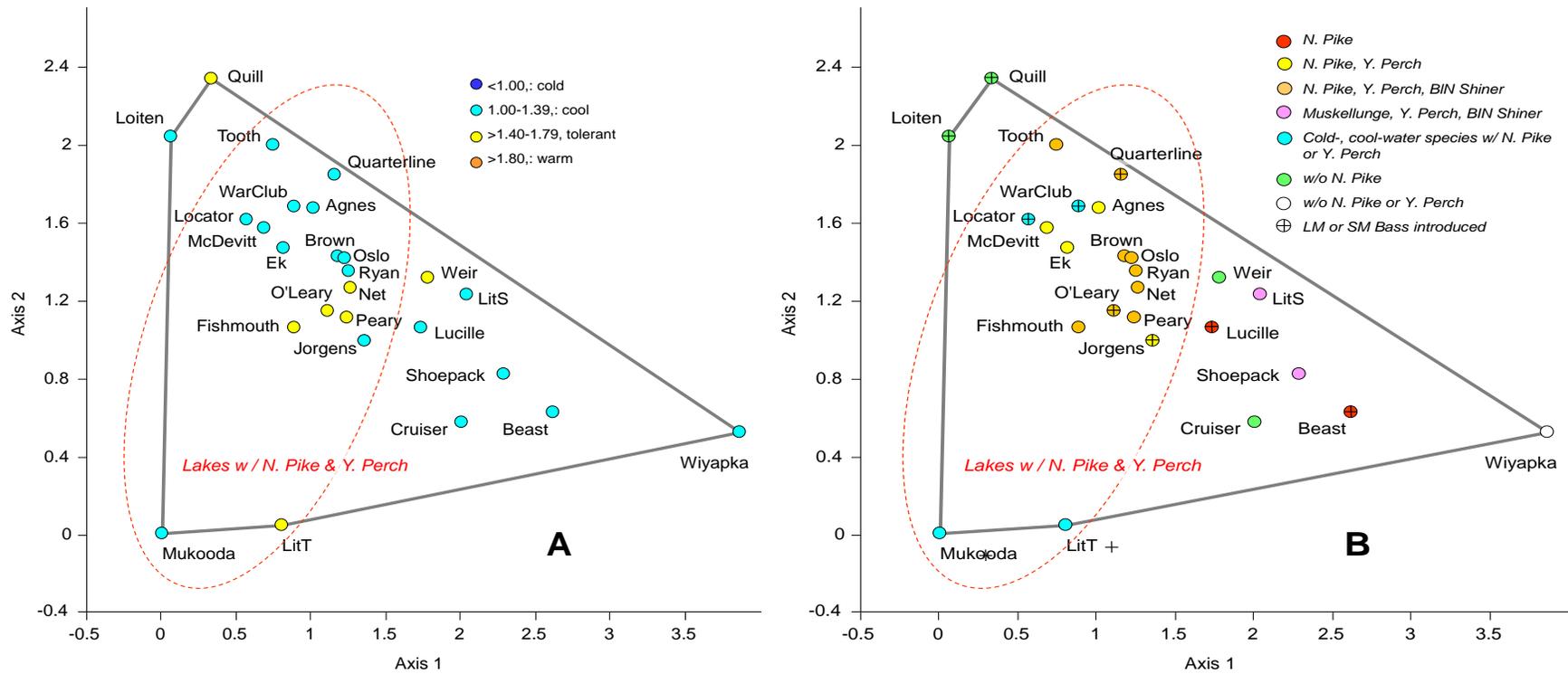


Figure 23. DCA plots for 26 VOYA inland lake communities based on similarity of composition with overlays of mean community thermal scores (A) and assemblage groups and presence of largemouth or smallmouth bass (B). The polygon circumscribes the community scores. Axis 1 explained 47% of the total variance and Axis 2 explained an additional 33%. The DCA model is based on 10 segments. Largemouth and smallmouth basses and other introduced species were not included in the analysis.

explained 47% of the total variance. Communities that loaded high on Axis 1 lacked blacknose shiner and northern pike or yellow perch. Axis 2 provided greater separation among communities containing coldwater, coolwater, and thermally tolerant species and explained an additional 33% of the total variance. Communities that loaded low on Axis 2 tended to have more diverse communities that included coldwater species (Mukooda and Little Trout contained 21 and 14 species, respectively). Communities that loaded high on Axis 2 tended to have fewer species and lacked coldwater species, with the most extreme communities (Loiten and Quill) lacking northern pike. An overlay of community thermal classifications showed no discernible pattern (Figure 23A). Similarly, an overlay of faunal assemblages (Figure 23B) did not yield a clear pattern of segregation; communities in the middle of the distribution contained northern pike and yellow perch, and those outside were lacking one or both of these species. Thus, segregation of VOYA lake communities in the DCA projection appears to be based on differences in the presence of less common species and on the absence of widespread species in less diverse communities. Lake communities and species at VOYA were projected in CCA multivariate space to evaluate the influence of environmental variables on structuring communities (Figures 24 and 25). Axis 1 explained 32% of the total variance, and all environmental variables were correlated with Axis 1; L. Area_log, Secchi depth, Zmax_log, log specific conductivity (SpCond_log), and Alk (alkalinity) were positively correlated, and Hypo_temp was negatively correlated (see Appendix XV). Axis 1 may be interpreted as a gradient of communities distributed from small, shallow lakes with reduced transparency, soft water, and warm hypolimnions (negative scores) to deep, large lakes with clearer water, higher conductivity, and colder hypolimnions (positive scores). Axis 2 explained an additional 20% of the total variance and accommodated exceptions to the Axis 1 gradient. The most informative variables for Axis 2 were L.Area_log, Secchi depth (both positive), and SpCond_log (negative) (see Appendix XV). Axis 2 may be interpreted as a gradient of communities in smaller lakes with higher conductivities and less transparent water to communities in larger lakes with softer, clearer water.

The triplots for environmental variables indicated the general gradient along which the lake communities were distributed (Figure 24). Scores for all environmental variables except Hypo_temp increased with increasing values along Axis 1 and had a mixed pattern of loadings along Axis 2. In general, communities in larger, deeper, colder lakes scored higher along the environmental gradient coincident with Axis 1 and communities in smaller, shallower, warmer lakes scored lower. Coding of lake communities by thermal classification did not reveal any clustering of lakes (Figure 24A). Coding of lake communities by faunal assemblages (Figure 24B) showed that the 13 communities in the central region of the canonical projection contained northern pike and yellow perch (assemblages 1 and 2), eight of which also contained blacknose shiner (assemblage 2). Lake communities outside the central region had various exceptions or additions to these elements: Two communities contained northern pike and yellow perch but also cisco (Locator and War Club; assemblage 3); four lacked northern pike (Weir, Wiyapka, Loiten, and Quill; assemblages 6 and 8); two lacked yellow perch (Beast and Lucille; assemblage 5); two substituted muskellunge for northern pike (Shoepack and Little Shoepack; assemblage 2); two had both lake trout and cisco (Little Trout and Mukooda; assemblage 3), and one contained lake trout (Cruiser; assemblage 6). Plotting species scores coded by thermal classification in the CCA plot did not reveal a pattern of clear segregation of species into

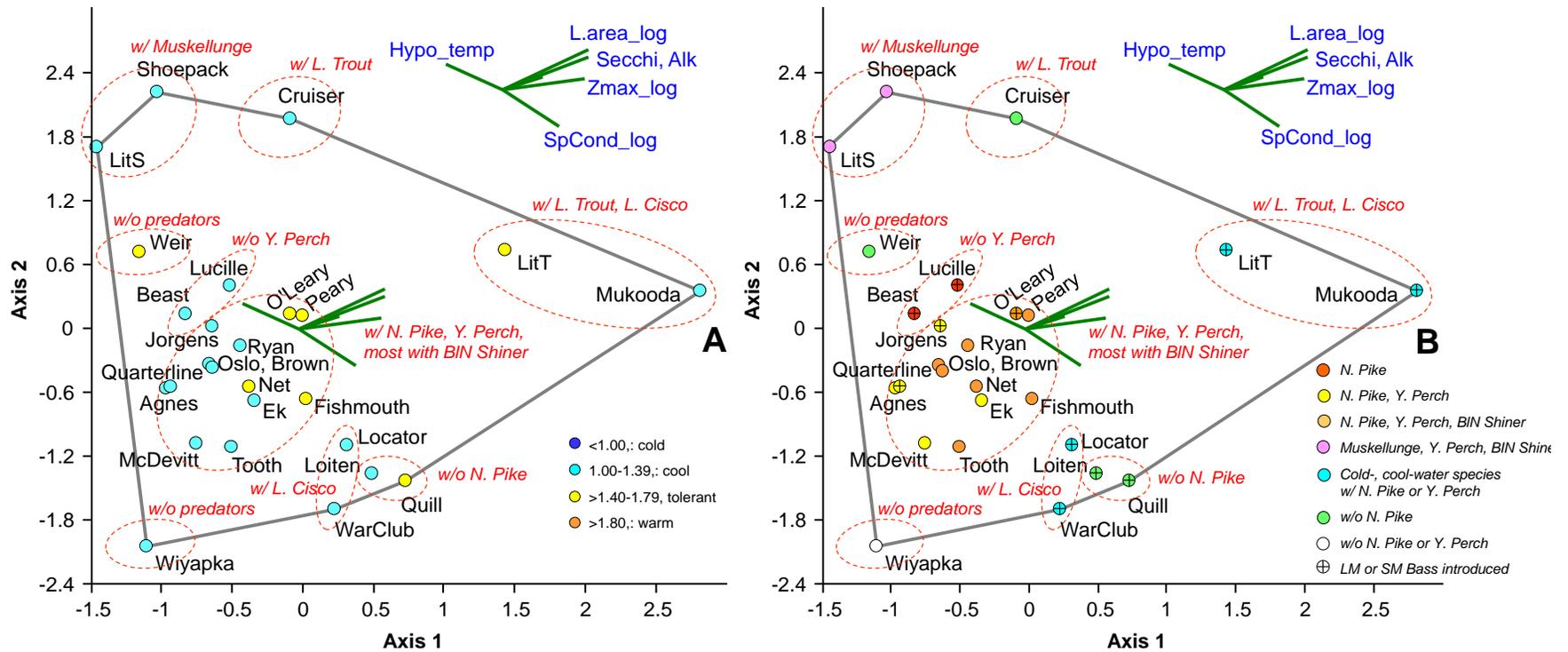


Figure 24. CCA plots for 26 VOYA lake communities plotted in canonical space set by environmental variables with overlays of mean community thermal scores (A) and assemblage groups and presence of largemouth or smallmouth bass (B). The polygon circumscribes the community scores. Axis 1 explained 32% of the total variance and Axis 2 explained an additional 20%. Largemouth and smallmouth basses and other introduced species were not included in the analysis.

clusters (Figure 25). One cluster of cold, cool, and thermally tolerant species (burbot, slimy sculpin, northern longear sunfish, and mottled sculpin) occurred in the same area, a result of these species being present in the larger lakes (Mukooda and Little Trout), which had the most diverse communities (see Appendices I and IV).

In both DCA and CCA projections we provided overlays showing the presence of introduced largemouth or smallmouth bass into VOYA lakes (see Figures 23 and 24). These species were not included in the analyses that generated the DCA and CCA projections but were included to detect potential patterns of community clustering as a result the impacts of these introductions on community composition. No patterns were apparent.

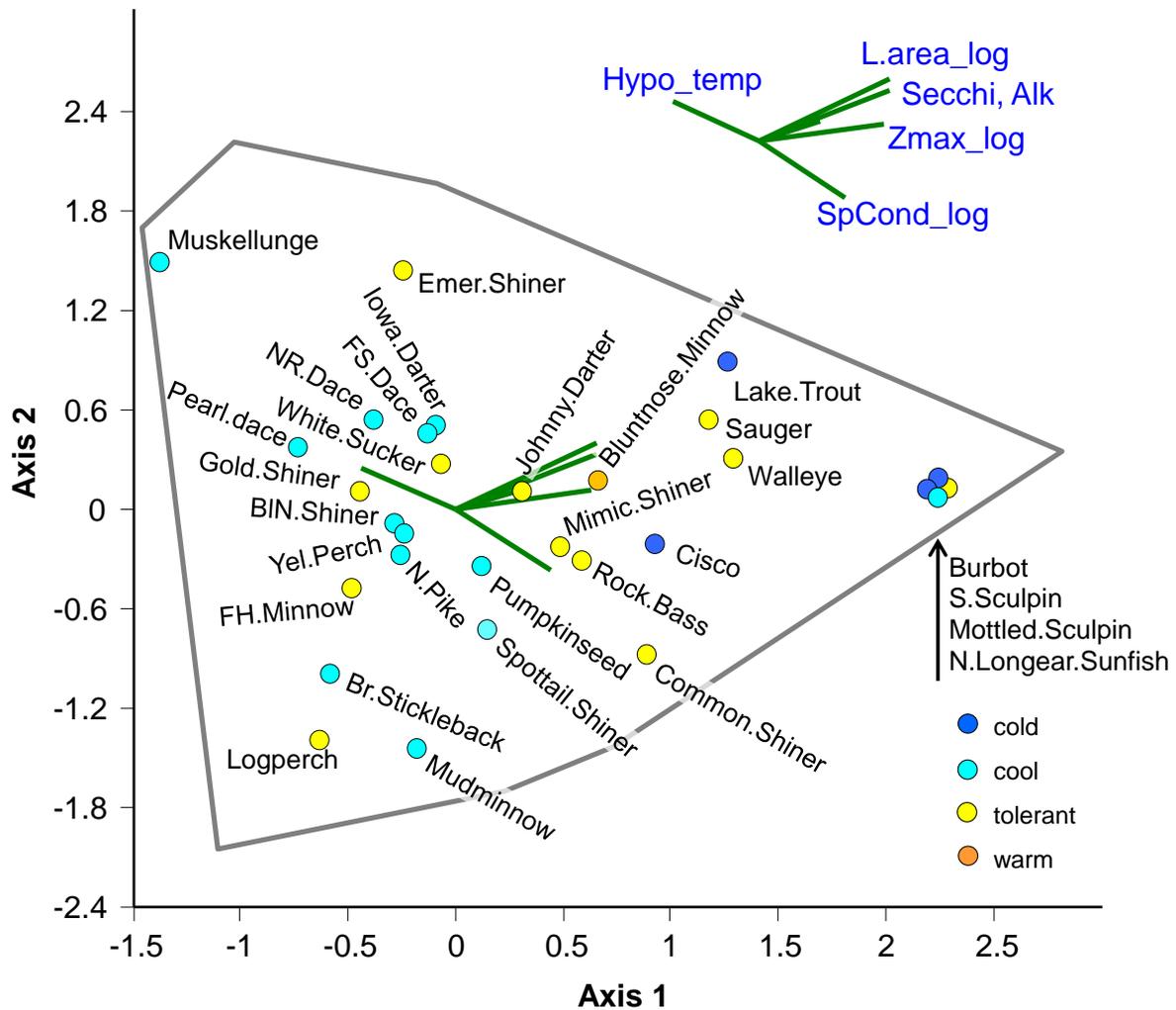


Figure 25. CCA plot for VOYA lake communities showing positions of species mean scores in canonical space set by environmental variables and coded by species thermal classification. The polygon represents the area circumscribing the community scores (not shown; see Figure 24).

SLBE

Areas of the 19 inland lakes at SLBE with two or more fish species ranged from 0.6 ha (Hidden) to 261 ha (Little Traverse), and 74% of the lakes were ≤ 40 ha (see Figure 9). Maximum depth ranged from 0.3 to 19.5 m, and 75% were ≤ 10 m deep (see Figure 10). There were no correlations between lake area and maximum depth, or between lake area and summer hypolimnetic temperature (not shown). However, there was a predictable relationship between maximum depth and summer hypolimnetic temperature; deeper lakes tended to have lower summer hypolimnetic temperatures (see Figure 11). Most (74%) of the lakes had summer hypolimnetic temperatures $>15^{\circ}\text{C}$ (see Figure 12). The SLBE inland lakes included 36 native species and five exotics (see Table 2). Unlike ISRO and VOYA, there was no significant relationship between species richness and lake area (see Figure 13), and only 16% of the lakes had fewer than six species (see Figure 14). This result suggests homogenization of lake communities is characteristic for SLBE inland lakes.

Little Traverse—the largest lake—and intermediate-sized Loon Lake each contained 19 species (excluding introduced species) (see Appendix VIII). The smallest lakes (Day Mill, Deer, and Hidden) contained two, ten, and five species, respectively. Most of the 36 native species had restricted distributions; 20 were found in three or fewer lakes, and 13 were found in one-to-two lakes (see Figure 15). The most widespread species—northern pike, yellow perch, pumpkinseed, bluntnose minnow, and largemouth bass—were found together in 11 of the 19 lakes. Northern pike, pumpkinseed, yellow perch, bluntnose minnow, bluegill, and largemouth bass were each present in 15 lakes. Other widespread species included rock bass, smallmouth bass, johnny darter, Iowa darter, white sucker, banded killifish, sand shiner, and brown bullhead, and were found in 68%, 58%, 53%, 53%, 47%, 47%, 42%, and 42% of the lakes, respectively. The widespread distribution of these species among SLBE lakes is indicative of community homogenization (see Figure 15). Most (25) of the 36 native species were classified as thermally tolerant or warmwater species (12 and 13 species, respectively), and the remaining 11 were classified as coolwater species (see Table 2). No lake fish communities were classified as coldwater. Of the 19 lake communities, one was classified as coolwater, two as cool-warmwater, and 16 as warmwater communities (Table 7).

The 19 inland lakes of SLBE comprised five faunal assemblages (Table 7). The most widespread was assemblage 4, which was found in 11 lakes and included northern pike, yellow perch, largemouth bass, and bluntnose minnow. Assemblage 5—containing northern pike without yellow perch—occurred in three lakes, and assemblage 7—lacking northern pike, but containing yellow perch and largemouth or smallmouth bass—occurred in three lakes. Assemblage 1—containing northern pike and yellow perch without largemouth bass and bluntnose minnow—was found only in Florence. Assemblage 8, which lacked northern pike, yellow perch, and basses, was found only in Hidden. Overall, northern pike together with yellow perch were present in 12 of the 19 lakes (63%). Application of ANOSIM demonstrated significant differences in just 4 of 10 community comparisons grouped by faunal assemblages (Table 8). The large number of shared species across communities resulted in low levels of differentiation among communities grouped by faunal assemblages (Table 8). Most species found in assemblages 4, 5, and 7 were shared. Assemblage 1, represented by Florence, contained four species that were shared with assemblage 4, the most

widespread. Assemblage 8, represented by Hidden, was the most unique and contained five species, two of which were unique (brook stickleback and northern redbelly dace).

Table 7. Thermal and faunal classification of the 20 inland lakes at SLBE with two or more species. Definitions of thermal classifications and faunal assemblages are provided in Table 1. Bass, South and Bass, North lakes are also known as Bass, Benzie and Bass, Leelanau lakes, respectively.

Lake	No. Spp.	Thermal Score	Thermal Classification	Faunal Assemblage
Bass, South	14	1.93	warm	4
Bass, North	12	2.08	warm	4
Day Mill	2	1.00	cool	5
Deer	10	2.10	warm	5 ^{‡^}
Fisher	10	1.90	warm	4
Florence	4	1.50	cool-warm	1 [‡]
Hidden	5	1.60	cool-warm	8
Long	14	2.00	warm	4
Loon	19	2.16	warm	4
Manitou	7	2.14	warm	7 ^{‡^}
Mud	12	2.00	warm	5 ^{‡^}
Narada	12	1.92	warm	4
North Bar	14	2.00	warm	4
Otter	17	2.06	warm	4
Round	14	2.07	warm	7 ^{‡^}
School	11	2.09	warm	4
Shell	12	2.08	warm	7 ^{‡^}
Little Traverse	19	2.21	warm	4
Tucker	10	1.90	warm	4 [°]

* Largemouth Bass present, ‡ Smallmouth Bass present, ^ Bluntnose Minnow present, ° Bluntnose Minnow absent

Table 8. Comparison of species composition among inland lake fish communities of SLBE based on grouping by faunal assemblages 1–8. Probabilities of no difference (*P*) and dissimilarities (*R*) were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Assemblage groups are defined in Table 1. Values in bold indicate a significant difference at *P*<0.10 and *R*≥0.25. An *R* of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of assemblage groups lists 36 species. Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥0.20 are shaded.

ANOSIM, probabilities of no difference (*P*) and dissimilarity (*R*)

Faunal Assemblage	Faunal Assemblage				
	1	4	5	7	8
1	-	0.076	0.756	0.243	1.000
4	0.952	-	0.114	0.063	0.083
5	-0.222	0.262	-	0.093	0.490
7	0.556	0.336	0.296	-	0.256
8	1.000	1.000	0.556	1.000	-

Overall *P* / *R* values: *P*(same)= 0.005; *R*= 0.5086

SIMPER, % dissimilarity (Bray-Curtis Similarity). Overall dissimilarity: 58.74%

Faunal Assemblage	Faunal Assemblage				
	1	4	5	7	8
1					
4	65.63				
5	66.87	51.82			
7	61.91	47.53	67.25		
8	100.00	79.53	83.27	81.63	

SIMPER, Pooled

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Faunal Assemblages				
			1	4	5	7	8
Rock.Bass	3.128	5.324	0	0.909	0.667	0.333	0
Yellow.Perch	3.049	10.51	1	1	0	1	0
Largemouth.Bass	2.938	15.52	0	1	0.667	0.667	0
Smallmouth.Bass	2.811	20.30	1	0.545	0.333	1	0
N.Pike	2.804	25.08	1	1	1	0	0
White.Sucker	2.753	29.76	0	0.545	0	1	0
Iowa.Darter	2.734	34.42	1	0.455	0.667	0.667	0
Bluntnose.Minnow	2.624	38.88	0	0.909	0.667	1	0
Johnny.Darter	2.612	43.33	0	0.636	0.333	0.667	0
Brown.Bullhead	2.560	47.69	0	0.636	0.333	0	0
Banded.Killifish	2.517	51.97	0	0.545	0.333	0.667	0
Pumpkinseed	2.516	56.26	0	0.909	0.667	0.667	1
Bluegill	2.516	60.54	0	0.909	0.667	0.667	1
Mudminnow	2.423	64.67	0	0.364	0.667	0	0
Sand.Shiner	2.299	68.58	0	0.455	0.333	0.667	0
Fathead.Minnow	1.564	71.24	0	0	0	0.333	1
Black.Crappie	1.387	73.60	0	0.273	0.333	0	0
Blacknose.Shiner	1.371	75.94	0	0.091	0.333	0.333	0

Table 8 (continued). Comparison of species composition among inland lake fish communities of SLBE based on grouping by faunal assemblages 1–8. Probabilities of no difference (*P*) and dissimilarities (*R*) were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Assemblage groups are defined in Table 1. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.25$. An *R* of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of assemblage groups lists 36 species. Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded.

SIMPER, Pooled			Mean Species Abundances Within Faunal Assemblages				
Taxon	Contribution %	Cumulative %	1	4	5	7	8
Brook.Stickleback	1.336	78.21	0	0.091	0	0	1
Mimic.Shiner	1.264	80.36	0	0.182	0	0.333	0
Yellow.Bullhead	1.192	82.39	0	0.273	0	0	0
Golden.Shiner	1.171	84.39	0	0.182	0	0.333	0
N.Redbelly.Dace	1.068	86.20	0	0	0	0	1
Mottled.Sculpin	1.055	88.00	0	0.091	0	0.333	0
Spottail.Shiner	1.033	89.76	0	0.273	0	0	0
Hornyhead.Chub	0.967	91.40	0	0.273	0	0	0
Green.Sunfish	0.852	92.85	0	0	0	0.333	0
Common.Shiner	0.842	94.29	0	0.273	0	0	0
N.Longear.Sunfish	0.677	95.44	0	0.182	0	0	0
Logperch	0.612	96.48	0	0.182	0	0	0
Bowfin	0.546	97.41	0	0.182	0	0	0
Brook.Silverside	0.339	97.99	0	0.091	0	0	0
Black.Bullhead	0.339	98.57	0	0.091	0	0	0
Creek.Chub	0.296	99.07	0	0.091	0	0	0
Longnose.Gar	0.273	99.53	0	0.091	0	0	0
N.Redhorse	0.273	100.00	0	0.091	0	0	0

Hierarchical cluster analysis based on distances between lakes and similarities of lake communities produced very different linkage trees (Figure 26). A comparison of matrices of relativized inter-lake distances and Jaccard's community similarities with the Mantel test showed no correlation ($R = 0.052$, $P = 0.434$). There were no evident patterns of clustering of communities by thermal classification or faunal assemblages overlain on the tree based on inter-lake distances (Figure 26A). This is probably because 16 of 19 lakes were classified as having warmwater communities and 11 of 19 communities contained the widespread assemblage 11. Similarly, there was no clear pattern of clustering of communities by thermal classification or faunal assemblages overlain on the tree based on community similarities (Figure 26B). Simple communities lacking largemouth bass and bluntnose minnow (Hidden and Day Mill) were on separate branches of the tree. Florence and Manitou, located on islands in Lake Michigan, lacked largemouth bass and clustered on the same branch of the tree based on community similarities (Figure 26B). The only instance of two nearby communities sharing faunal assemblages and having similar composition and clustering on a terminal branch was Bass N and School (Figure 26).

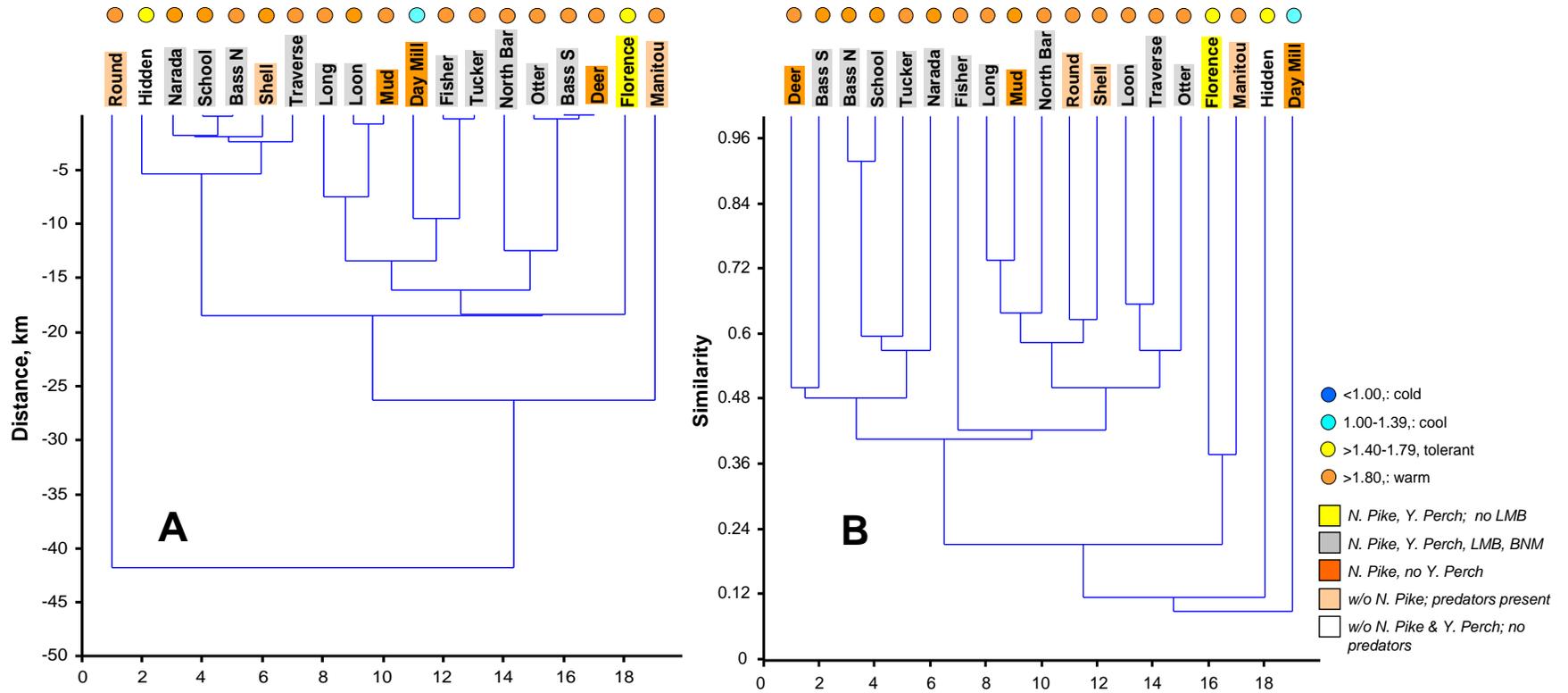


Figure 26. Cluster Analysis of 19 SLBE inland lakes based on unpaired distances (A) and lake communities based on paired Jaccard's Similarities (B) with overlays of thermal groups and faunal assemblages. Corr. Coeff. A: 0.7491, B: 0.9437.

DCA separated lake communities based on species composition along two axes that explained 65% of the total variance (Figure 27; see Appendix XVI). Axis 1 represented a gradient from communities with uncommon thermally tolerant and warmwater species to communities containing widespread warmwater and thermally tolerant species to communities containing uncommon coolwater and thermally tolerant species. Examples of uncommon thermally tolerant and warmwater species in communities that scored low on Axis 1 included longnose gar, bowfin, hornyhead chub, northern redhorse, and green sunfish. Examples of uncommon coolwater and thermally tolerant species present in communities that scored high on Axis 1 included northern redbelly dace, blacknose shiner, fathead minnow, golden shiner, and brook stickleback. Examples of widespread warmwater and thermally tolerant species that were present in communities that scored in the middle of Axis 1 included white sucker, bluntnose minnow, sand shiner, brown bullhead, banded killifish, largemouth bass, rock bass, and johnny darter. Axis 2 provided greater resolution of communities with thermally tolerant and warmwater species vs. coolwater and warmwater species. Examples of thermally tolerant and warmwater species present in communities that scored low on Axis 2 included fathead minnow, creek chub, logperch, sand shiner, mottled sculpin and green sunfish. Examples of coolwater and warmwater species present in communities that scored high on Axis 2 included central mudminnow, yellow bullhead, yellow perch, northern pike, brook stickleback, and northern longear sunfish.

An overlay of community thermal classifications onto the DCA plot showed no discernible pattern (Figure 27A). This was due to a disproportionate number of warmwater communities (16 of 19) in SLBE. Only the coolwater Day Mill community was segregated from the large central cluster of warmwater communities. Similarly, an overlay of faunal assemblages (Figure 27B) did not yield a clear pattern of segregation; the central cluster of 16 communities was characterized by having a combination of northern pike, largemouth bass, bluntnose minnow, pumpkinseed, bluegill, and rock bass. Assemblage 4, which was characterized by the presence of northern pike, largemouth bass, and bluntnose minnow, was the most common assemblage in communities projected in the central portion of the DCA plot. Grouping of some pairs of communities by faunal assemblages in the DCA plot (Figure 27B) showed some concordance with the cluster analysis based on community similarity (Figure 26B). Overall, segregation of SLBE lake communities in the DCA projection appears to be based largely on differences in the presence of less common species and on the absence of widespread species in less diverse communities.

Lake communities and species of SLBE were projected in CCA multivariate space to evaluate the influence of environmental variables on structuring communities (Figures 28 and 29). Axis 1 explained 21% of the total variance. Environmental variables with the highest correlations with Axis 1 were L.Area_log, Zmax_log, Wshd.Area_log, and Hypo_temp (see Appendix XVII). Axis 1 may be interpreted as a gradient of communities in larger, deeper lakes with cooler hypolimnions (positive scores) to communities in small, shallow lakes with warmer hypolimnions (negative scores). Axis 2 explained an additional 17% of the total variance and accommodated exceptions to the Axis 1 gradient. Variables largely responsible for Axis 2 were Secchi, Wshd.Area_log, and Hypo_temp (see Appendix XVII). Axis 2 may be interpreted as a gradient of communities in larger watersheds with

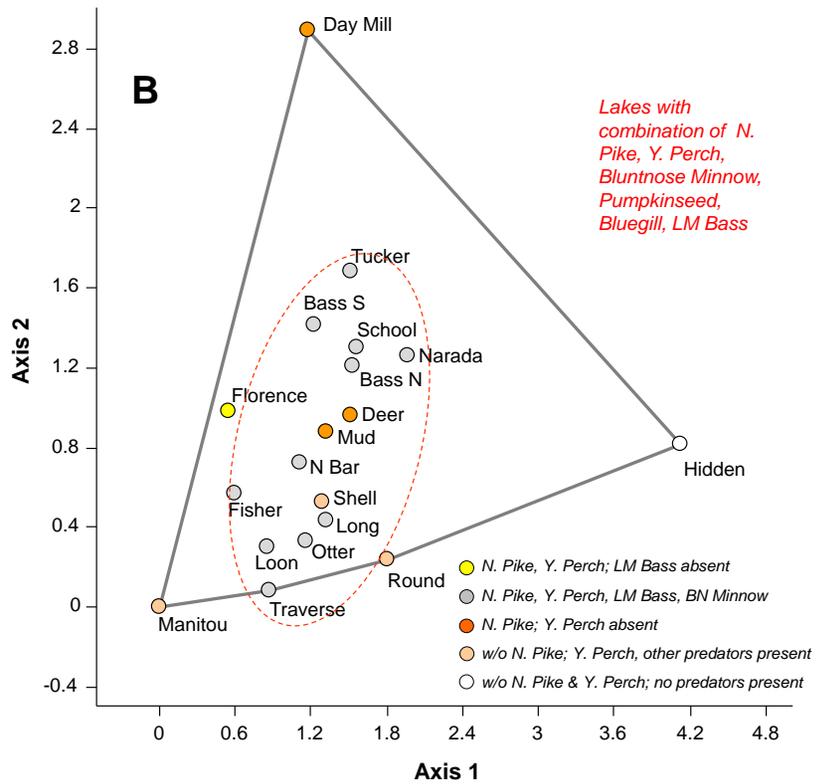
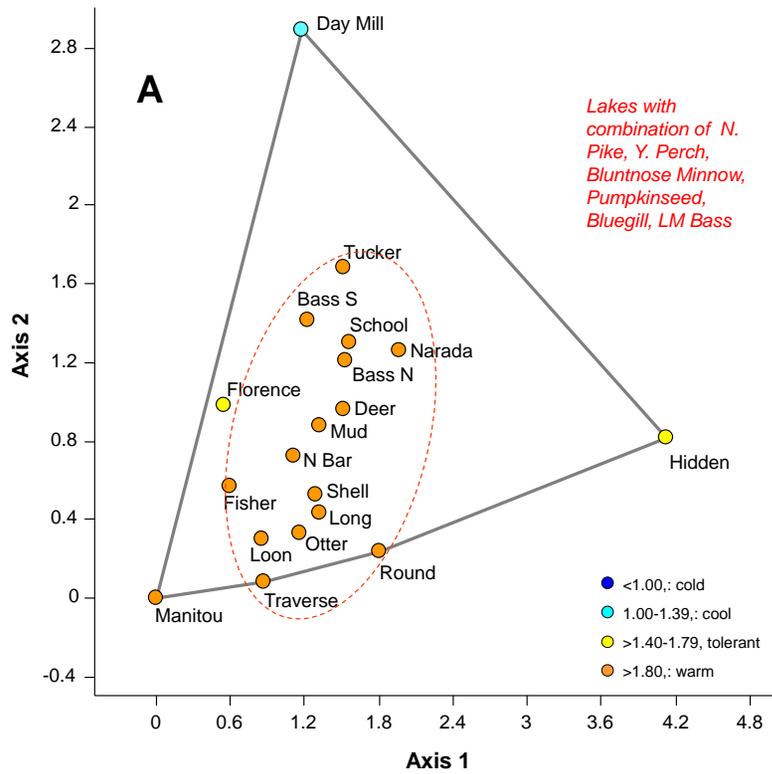


Figure 27. DCA plots for 19 SLBE inland lake communities based on similarity of composition with overlays of mean community thermal scores (A) and assemblage groups (B). The polygon circumscribes the community scores. Axis 1 explained 44% of the total variance and Axis 2 explained an additional 21%. The DCA model is based on 10 segments.

lower water clarity and cooler hypolimnions (positive scores) to lakes in smaller watersheds with higher water clarity and warmer hypolimnions (negative scores).

The triplots for environmental variables indicated the general gradient along which the lake communities were distributed (Figure 28). An overlay of thermal classifications onto the projected communities did not yield a discernable pattern of segregation (Figure 28A). Similarly, an overlay of faunal assemblages did not yield a discernable pattern of segregation (Figure 28B). As with DCA, the high degree of shared species among communities and their faunal assemblages resulted in little segregation of communities based on overlays, though there were some instances of pairs of communities that were physically close, shared the same thermal classification and faunal assemblage, and clustered together in canonical space. Examples include Bass S–Otter and Bass N–School. Fifteen lake communities with a combination of northern pike, yellow perch, bluntnose minnow, pumpkinseed, bluegill, and largemouth bass were clustered at the center of the CCA plot (Figure 28B). Outlying communities in Hidden, Day Mill, Loon, and Manitou differed from communities in the central cluster by the presence of less common species (Loon, Manitou) and the absence of common species (Day Mill, Hidden). Plotting species scores coded by thermal classification in canonical space showed no discernable separation of coolwater vs. warmwater and thermally tolerant species (Figure 29).

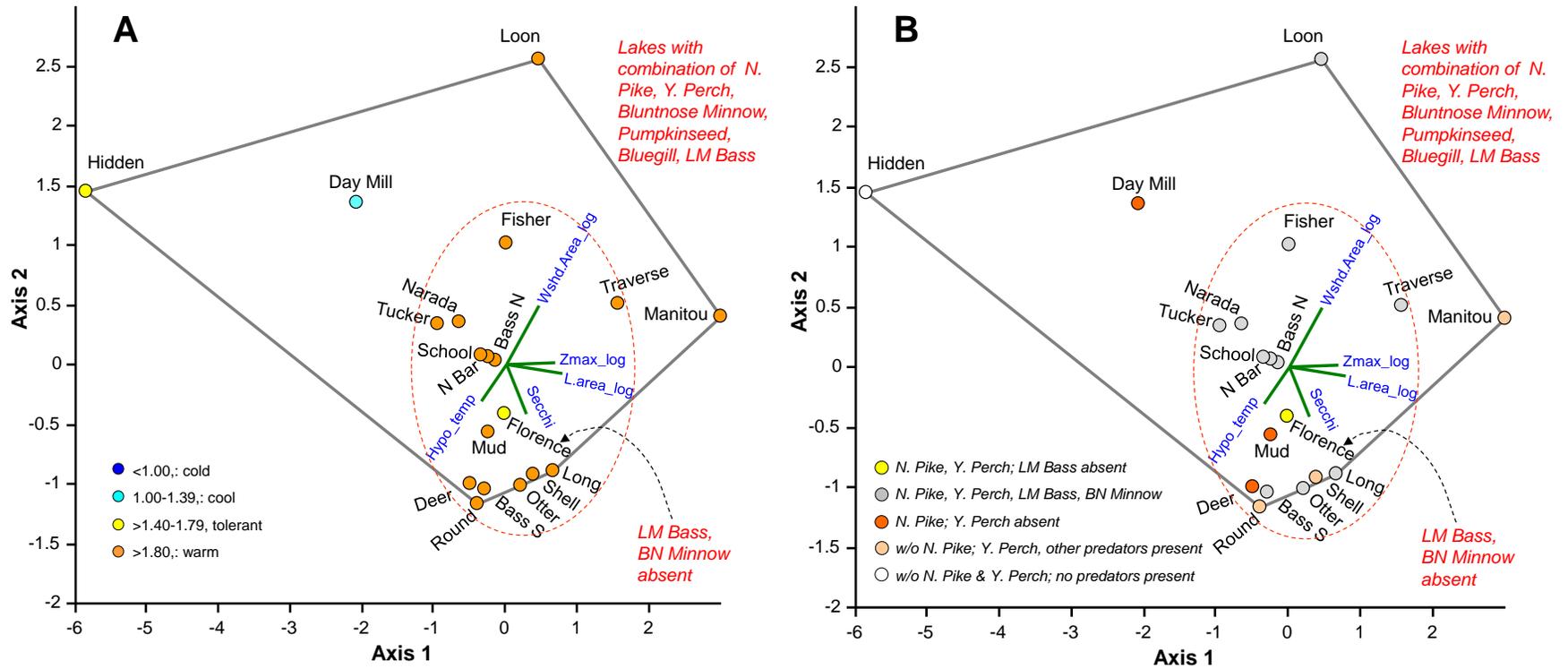


Figure 28. CCA plots for 19 SLBE lake communities plotted in canonical space set by environmental variables with overlays of mean community thermal scores (A) and assemblage groups (B). The polygon circumscribes the community scores. Axis 1 explained 21% of the total variance and Axis 2 explained an additional 17%.

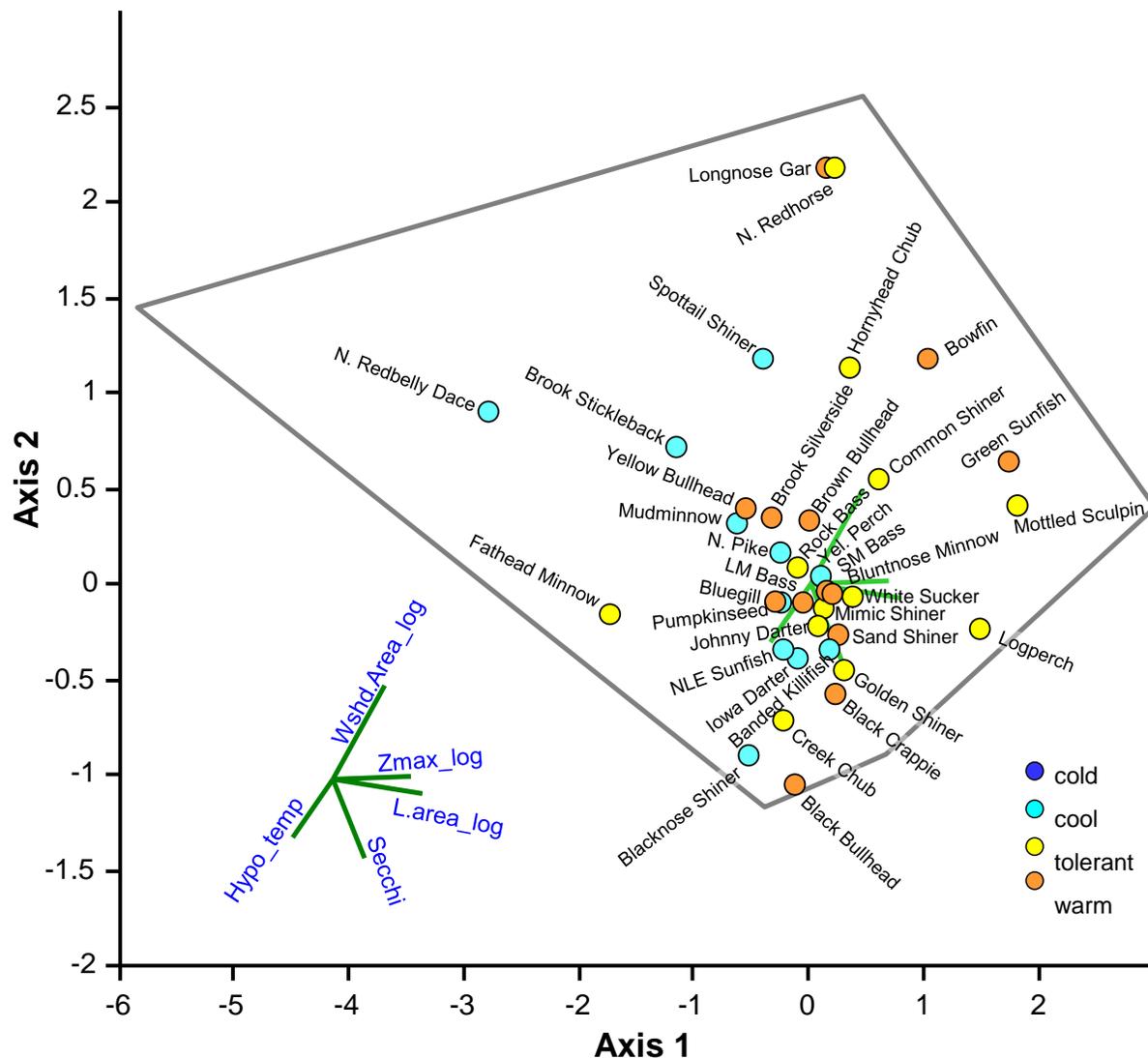


Figure 29. CCA plot for SLBE lake communities showing positions of species mean scores in canonical space set by environmental variables and coded by species thermal classification. The polygon represents the area circumscribing the community scores (not shown; see Figure 28).

Global Comparisons

Global comparisons of species composition in inland lake fish communities grouped by region showed significant differences for all comparisons with ANOSIM (Table 9). The lowest dissimilarity was found between ISRO and VOYA ($R = 0.13$), and the highest dissimilarity was found between ISRO and SLBE ($R = 0.67$). The SLBE and VOYA comparison yielded intermediate dissimilarity ($R = 0.46$). SIMPER analysis identified species that contributed most to inter-regional differences. Species contributing $>1.8\%$ relative difference (63% cumulative) to inter-regional comparisons were blacknose shiner, pumpkinseed, white sucker, Iowa darter, golden shiner, rock bass, bluntnose minnow, johnny darter, northern pike, bluegill, largemouth bass, smallmouth bass, spottail shiner, and yellow perch (Table 9). SIMPER analysis also identified species unique to regions and species shared among regions (Tables 9 and 10).

Table 9. Global comparison of species composition of inland lake fish communities by region (ISRO, VOYA, and SLBE). Probabilities of no regional differences (P) and dissimilarities (R) were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.5$. An R of 1.0 indicates complete dissimilarity. Pooled Similarity Percentage (SIMPER) analysis of regional groups lists 33 species contributing to differences $> 0.5\%$ across regions (20 species contributing $< 0.5\%$ not shown). Mean abundance is the proportion of lakes where a species occurred in region (group). Species with mean abundances ≥ 0.15 are shaded. Exotic species were excluded from the analysis.

ANOSIM , probabilities of no difference (P) and dissimilarity (R)			
	ISRO	VOYA	SLBE
ISRO	-	<i>0.0007</i>	0.0000
VOYA	0.130	-	<i>0.0000</i>
SLBE	0.666	0.458	-

Overall P / R values: P (same): < 0.0001 ; R = 0.3902

SIMPER , % dissimilarity (Bray-Curtis Similarity). Overall dissimilarity: 65.70%			
	ISRO	VOYA	SLBE
ISRO	-		
VOYA	76.0	-	
SLBE	56.1	69.1	-

SIMPER, Pooled

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Parks		
			ISRO	VOYA	SLBE
Blacknose Shiner	4.202	6.40	0.625	0.654	0.158
Pumpkinseed	4.074	12.60	0.125	0.462	0.789
White Sucker	3.887	18.51	0.406	0.577	0.474
Iowa Darter	3.462	23.78	0.063	0.423	0.526
Golden Shiner	3.216	28.68	0.281	0.423	0.158
Rock Bass	3.012	33.26	0	0.269	0.684
Bluntnose Minnow	2.866	37.63	0	0.154	0.789
Johnny Darter	2.805	41.90	0	0.385	0.526
N. Pike	2.759	46.10	0.813	0.731	0.789
Bluegill	2.577	50.02	0	0	0.789
Largemouth Bass	2.472	53.78	0	0	0.789
Smallmouth Bass	1.978	56.79	0	0	0.579
Spottail Shiner	1.967	59.79	0.281	0.077	0.158
Yellow Perch	1.817	62.55	0.938	0.885	0.789
Mudminnow	1.573	64.95	0	0.077	0.316
Pearl Dace	1.520	67.26	0.156	0.154	0
N. Redbelly Dace	1.478	69.51	0.094	0.192	0.053
Brook Stickleback	1.470	71.75	0.156	0.077	0.105
Banded Killifish	1.429	73.92	0	0	0.474
Fathead Minnow	1.366	76.00	0.063	0.154	0.105
Brown Bullhead	1.307	77.99	0	0	0.421
Sand Shiner	1.193	79.80	0	0	0.421

SIMPER, Pooled continued

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Parks		
			ISRO	VOYA	SLBE
Sand Shiner	1.193	79.80	0	0	0.421
Finescale Dace	1.142	81.54	0.063	0.192	0
Cisco	0.998	83.06	0.125	0.154	0
Mimic Shiner	0.976	84.55	0.031	0.077	0.158
Walleye	0.854	85.85	0.094	0.115	0
Logperch	0.696	86.91	0.063	0.039	0.105
Trout-Perch	0.659	87.91	0.156	0	0
Black Crappie	0.610	88.84	0	0	0.211
Common Shiner	0.589	89.73	0	0.039	0.158
Emerald Shiner	0.557	90.58	0.031	0.115	0
Yellow Bullhead	0.556	91.43	0	0	0.158
Lake Trout	0.512	92.21	0.031	0.115	0

Table 10. Species unique to inland lakes of ISRO, VOYA, and SLBE, or a combination of regions.

ISRO	ISRO, VOYA
Trout-perch	Pearl Dace
Blackchin Shiner	Cisco
Spoonhead Sculpin	Finescale Dace
Ninespine Stickleback	Walleye
Lake Whitefish	Emerald Shiner
Lake Chub	Lake Trout
Brook Trout	Slimy Sculpin
	Burbot
VOYA	ISRO, SLBE
Muskellunge	Creek Chub
Sauger	
Tadpole Madtom	
	VOYA, SLBE
SLBE	Rock Bass
Bluegill	Bluntnose Minnow
Largemouth Bass	Johnny Darter
Smallmouth Bass	Mudminnow
Banded Killifish	Common Shiner
Brown Bullhead	Mottled Sculpin
Sand Shiner	Northern Longear Sunfish
Black Crappie	
Yellow Bullhead	ISRO + VOYA + SLBE
Hornyhead Chub	Yellow Perch
Bowfin	Northern Pike
Green Sunfish	White Sucker
Brook Silverside	Blacknose Shiner
Black Bullhead	Pumpkinseed
Longnose Gar	Iowa Darter
Northern Redhorse	Golden Shiner
<i>Sea Lamprey (introduced)</i>	Spottail Shiner
<i>Alewife (introduced)</i>	Northern Redbelly Dace
<i>Chinook (introduced)</i>	Brook Stickleback
<i>Coho (introduced)</i>	Fathead Minnow
<i>Common Carp (introduced)</i>	Mimic Shiner
	Logperch

Global comparison of species composition in inland lake fish communities grouped by thermal classification showed significant differences for all comparisons among thermal groups (coldwater, coolwater, cool-warmwater, warmwater) (Table 11). Each community's assignment to a thermal group was based on the mean of the species' thermal scores (see Tables 1, 2, 3, 5, and 7). Coolwater and cool-warmwater thermal groups were the least distinct groups; ANOSIM dissimilarity was 0.163 but significant, and SIMPER dissimilarity was 59.2%. Species contributing >1.5% relative difference

Table 11. Global comparison of species composition of inland lake fish communities grouped by thermal classification. Included were all lake communities of ISRO, VOYA, and SLBE. Probabilities of no differences (P) and dissimilarities (R) among thermal groups were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Thermal scores and classification of communities are defined in Table 1. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.5$. Pooled Similarity Percentage (SIMPER) analysis of thermal groups lists 38 species contributing to differences $> 0.5\%$ across groups (15 species contributing $< 0.5\%$ not shown). Mean abundance is the proportion of lakes where a species occurred in a thermal group. Species with mean abundances ≥ 0.20 are shaded. Introduced species were excluded.

ANOSIM, Probabilities of no difference (P) and dissimilarity (R)

Thermal Classification	Thermal Classification			
	Cold	Cool	Cool-warm	Warm
Cold	--	0.009	0.032	0.007
Cool	0.644	--	0.063	0.000
Cool-warm	0.576	0.163	--	0.000
Warm	0.994	0.626	0.648	--

Overall P/R values: P (same) < 0.0001 ; R = 0.478

SIMPER, % dissimilarity (Bray-Curtis Similarity). Overall dissimilarity 69.1%

Thermal Classification	Thermal Classification			
	Cold	Cool	Cool-warm	Warm
Cold	--			
Cool	78.6	--		
Cool-warm	80.5	59.2	--	
Warm	87.6	73.7	66.0	--

SIMPER, Pooled

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Thermal Classifications			
			Cold	Cool	Cool-warm	Warm
Pumpkinseed	3.791	5.487	0	0.245	0.5	0.875
Bluntnose Minnow	3.766	10.94	0	0.020	0.3	0.938
Blacknose Shiner	3.536	16.05	0.5	0.612	0.6	0.188
White Sucker	3.491	21.11	1.0	0.408	0.6	0.563
Rock Bass	3.394	26.02	0	0.082	0.3	0.813
Bluegill	3.233	30.7	0	0	0.1	0.875
Largemouth Bass	3.191	35.32	0	0	0	0.938
Iowa Darter	3.054	39.74	0	0.224	0.3	0.563
Johnny Darter	3.033	44.12	0	0.122	0.4	0.625
Golden Shiner	2.695	48.03	0	0.327	0.4	0.188
N. Pike	2.585	51.77	0.5	0.796	0.7	0.813
Smallmouth Bass	2.481	55.36	0	0	0.1	0.625
Banded Killifish	1.844	58.02	0	0	0	0.563
Brown Bullhead	1.687	60.47	0	0	0	0.500
Spottail Shiner	1.628	62.82	0.5	0.204	0	0.188
Sand Shiner	1.539	65.05	0	0	0	0.500
Yellow Perch	1.527	67.26	0.5	0.898	0.9	0.875
Fathead Minnow	1.411	69.3	0	0.082	0.3	0.063
Brook Stickleback	1.368	71.28	0.5	0.122	0.1	0.063

SIMPER, Pooled continued

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Thermal Classifications			
			Cold	Cool	Cool-warm	Warm
Pearl dace	1.347	73.23	0.5	0.143	0.1	0
Mimic Shiner	1.313	75.13	0	0.020	0.2	0.188
Mudminnow	1.312	77.03	0	0.061	0	0.313
N. Redbelly Dace	1.24	78.82	0.5	0.143	0.1	0
Walleye	1.091	80.4	0	0.061	0.3	0
Cisco	1.063	81.94	1.0	0.102	0.1	0
Common Shiner	0.8306	83.14	0	0	0.1	0.188
Finescale Dace	0.801	84.3	0	0.122	0.1	0
Black Crappie	0.7865	85.44	0	0	0	0.250
Trout-perch	0.7653	86.55	1.0	0.061	0	0
Logperch	0.745	87.63	0.5	0.041	0	0.125
Yellow Bullhead	0.7178	88.67	0	0	0	0.188
Emerald Shiner	0.6143	89.55	0.5	0.041	0.1	0
Lake Trout	0.5766	90.39	0.5	0.041	0.1	0
Hornyhead Chub	0.5717	91.22	0	0	0	0.188
Mottled Sculpin	0.5409	92	0	0.020	0	0.125
Spoonhead sculpin	0.5163	92.75	1.0	0	0	0
Ninespine Stickleback	0.5163	93.49	1.0	0	0	0
Lake Whitefish	0.5163	94.24	1.0	0	0	0

(67% cumulative) to comparisons among thermal groups were pumpkinseed, bluntnose minnow, blacknose shiner, white sucker, rock bass, bluegill, largemouth bass, Iowa darter, johnny darter, golden shiner, northern pike, smallmouth bass, banded killifish, brown bullhead, spottail shiner, and yellow perch (Table 11). Species contributing most to communities in the coldwater group were white sucker, cisco, trout-perch, spoonhead sculpin, ninespine stickleback, and lake whitefish (mean abundance = 1.0) (Table 11). Species contributing most to communities in the coolwater group were pumpkinseed, blacknose shiner, white sucker, Iowa darter, golden shiner, northern pike, spottail shiner, and yellow perch (mean abundance ≥ 0.20) (Table 11). Species contributing most to communities in the cool-warmwater group were pumpkinseed, bluntnose minnow, blacknose shiner, white sucker, rock bass, Iowa darter, johnny darter, golden shiner, northern pike, yellow perch, fathead minnow, mimic shiner, and walleye (mean abundance ≥ 0.20) (Table 11). Species contributing most to communities in the warmwater group were pumpkinseed, bluntnose minnow, white sucker, rock bass, bluegill, largemouth bass, Iowa darter, johnny darter, northern pike, smallmouth bass, banded killifish, brown bullhead, sand shiner, yellow perch, mudminnow, and black crappie (mean abundance ≥ 0.20) (Table 11). Comparison of species thermal scores by region with ANOVA yielded highly significant differences among regions ($P < 0.0001$), with the greatest differences occurring between ISRO–SLBE and VOYA–SLBE comparisons (Tukey’s pairwise comparison) (Table 12A). Similarly, comparison of community mean thermal scores by region with ANOVA yielded highly significant differences among regions ($P < 0.0001$), with the largest

differences again occurring between the ISRO–SLBE and VOYA–SLBE comparisons (Tukey’s pairwise comparison) (Table 12B).

ANOSIM and SIMPER were used to compare the distribution of fish communities across inland lakes at ISRO, VOYA, and SLBE, grouped by a simplified faunal assemblage classification (Table 13). To make this comparison more manageable for inter-regional comparisons, we reduced nine faunal assemblages (see Table 1) to four groups (Table 13). The first group lacked northern pike or

Table 12. Comparison of fish communities of ISRO, VOYA and SLBE based on thermal scores of species and mean thermal scores of lake communities. Part A shows results of ANOVA testing for differences in species thermal scores across regions. Part B shows results of ANOVA testing for differences in mean thermal scores of lake communities across regions. Assignments of thermal scores for species are listed in Table 2 and mean thermal scores for lake communities are listed in Tables 4, 5, and 6. Definitions of thermal scores and classification of communities are provided in Table 1.

A. Differences in Species Thermal Scores Across Regions

SUMMARY

Groups	No. Species	Species Thermal Score		
		Sum	Average	Variance
ISRO	29	27	0.93103	0.63793
VOYA	31	42	1.35484	0.56989
SLBE	36	74	2.05556	0.68254

ANOVA, one-way

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	21.14185	2	10.57093	16.70576	6.32962E-07	3.09434
Within Groups	58.84773	93	0.63277			
Total	79.98958	95				
Omega ² :	0.2465		Welch F test in case of unequal variances:	F = 15.83,	df = 61.10	P = 2.883E-06
Levene's test for homogeneity of variances based on means:	0.9175		Levene's test for homogeneity of variances based on medians:		0.8960	
Shapiro-Wilk W =	0.9244		P(normality):	3.460E-05		

Tukey's pairwise comparisons Q \ Probability of being the same

Q \ P	ISRO	VOYA	SLBE
ISRO	--	0.0909	0.0001
VOYA	3.002	--	0.0021
SLBE	7.964	4.963	--

Table 12. Comparison of fish communities of ISRO, VOYA and SLBE based on thermal scores of species and mean thermal scores of lake communities. (continued)

B. Differences in Mean Thermal Scores of Lake Communities Across Regions

SUMMARY

Groups	No. Lakes	Lake Community Thermal Score		
		Sum	Average	Variance
ISRO	32	35.23571	1.10112	0.03847
VOYA	26	33.84000	1.30154	0.03087
SLBE	19	36.74434	1.93391	0.08275

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	8.48041	2	4.24020	90.85416	1.18854E-20	3.12035
Within Groups	3.45361	74	0.04667			
Total	11.93560	76				
Omega^2:	0.7004		Welch F test for unequal variances:	F = 61.66	df = 40.63	P = 4.922E-13
Levene's test for homogeneity of variances base on means:	0.3932		Shapiro-Wilk W =	0.8954		
Levene's test for homogeneity of variances base on medians:	0.6954		P(normality):	1.105E-05		

Tukey's pairwise comparisons Q \ Probability

Q \ P	ISRO	VOYA	SLBE
ISRO	--	0.0051	0.0001
VOYA	4.585	--	0.0001
SLBE	19.110	14.520	--

largemouth bass or smallmouth bass (no predators). The second included northern pike and yellow perch but lacked the basses. The third group lacked northern pike but had one or both of the basses. The last group included northern pike and one or both of the basses. ANOSIM showed that comparisons among groups showed significantly different community compositions (Table 13). However, groups 3 and 4 were the least distinct ($R = 0.26$), the comparison was barely significant ($P = 0.10$), and SIMPER dissimilarity for groups 3 and 4 was 49%—the lowest among the group comparisons. Species contributing $>1.8\%$ relative difference (67% cumulative) to comparisons among assemblage groups were northern pike, blacknose shiner, pumpkinseed, white sucker, rock bass, bluntnose minnow, Iowa darter, bluegill, largemouth bass, golden shiner, johnny darter, smallmouth bass, pearl dace, brook stickleback, banded killifish, and yellow perch (Table 13). Species contributing most to communities containing assemblage group 1 were blacknose shiner,

pumpkinseed, white sucker, pearl dace, brook stickleback, yellow perch, northern redbelly dace, fathead minnow, and finescale dace (mean abundance ≥ 0.20) (Table 13). Species contributing most to communities containing assemblage group 2 were northern pike, blacknose shiner, pumpkinseed, white sucker, Iowa darter, golden shiner, yellow perch, and spottail shiner (mean abundance ≥ 0.20) (Table 13). Species contributing most to communities containing assemblage group 3 were blacknose shiner, pumpkinseed, white sucker, rock bass, bluntnose minnow, Iowa darter, bluegill, largemouth bass, golden shiner, johnny darter, smallmouth bass, yellow perch, banded killifish, fathead minnow, sand shiner, mimic shiner, and mottled sculpin (mean abundance ≥ 0.20) (Table 13). Species contributing most to communities containing assemblage group 4 were northern pike, pumpkinseed, white sucker, rock bass, bluntnose minnow, Iowa darter, bluegill, largemouth bass, johnny darter, smallmouth bass, yellow perch, banded killifish, brown bullhead, spottail shiner, sand shiner, mudminnow, common shiner, black crappie, yellow bullhead, and hornyhead chub (mean abundance ≥ 0.20) (Table 13).

Table 13. Global comparison of species composition of inland lake fish communities by simplified faunal groups. Included were all lake communities of ISRO, VOYA, and SLBE. Probabilities of no differences (P) and dissimilarities (R) among faunal groups were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at $P < 0.10$ and $R \geq 0.5$. Pooled Similarity Percentage (SIMPER) analysis of faunal groups lists 33 species contributing to differences $> 0.5\%$ across groups (19 species contributing $< 0.5\%$ not shown). Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded. Muskellunge was treated as N. Pike and exotic and introduced species were excluded.

Simplified Faunal Groups for Global Comparison	
1	N. Pike absent; LM or SM Bass absent
2	N. Pike present; LM or SM Bass absent
3	N. Pike absent; LM or SM Bass present
4	N. Pike present; LM or SM Bass present

Table 13 (continued). Global comparison of species composition of inland lake fish communities by simplified faunal groups. Included were all lake communities of ISRO, VOYA, and SLBE. Probabilities of no differences (P) and dissimilarities (R) among faunal groups were generated from Analysis Of Similarity (ANOSIM) using Jaccards' Similarity measure. Values in bold indicate a significant difference at P < 0.10 and R ≥ 0.5. Pooled Similarity Percentage (SIMPER) analysis of faunal groups lists 33 species contributing to differences >0.5% across groups (19 species contributing <0.5% not shown). Mean abundance is the proportion of lakes where a species occurred in an assemblage group. Species with mean abundances ≥ 0.20 are shaded. Muskellunge was treated as N. Pike and exotic and introduced species were excluded.

ANOSIM, Probabilities of no difference (P) and dissimilarity (R)

Faunal Groups	Faunal Groups			
	1	2	3	4
1	--	0.000	0.034	0.000
2	0.639	--	0.000	0.000
3	0.276	0.772	--	0.098
4	0.730	0.704	0.262	--

Overall P/R values: P (same) < 0.0001; R = 0.679

SIMPER, % dissimilarity (Bray-Curtis Similarity). Overall dissimilarity 71.52%

Faunal Groups	Faunal Groups			
	1	2	3	4
1	--			
2	72.52	--		
3	76.60	73.38	--	
4	82.44	68.67	49.04	--

SIMPER, Pooled

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Faunal Groups			
			1	2	3	4
N. Pike	4.758	6.65	0	1.000	0	1.000
Blacknose Shiner	3.852	12.04	0.500	0.646	0.333	0.143
Pumpkinseed	3.675	17.18	0.250	0.292	0.667	0.857
White Sucker	3.572	22.17	0.500	0.458	1.000	0.429
Rock Bass	3.368	26.88	0.167	0.104	0.333	0.857
Bluntnose Minnow	3.166	31.31	0	0.083	1.000	0.857
Iowa Darter	3.159	35.72	0.167	0.229	0.667	0.571
Bluegill	3.108	40.07	0.083	0	0.667	0.857
Largemouth Bass	3.079	44.38	0	0	0.667	0.929
Golden Shiner	2.719	48.18	0.167	0.375	0.333	0.143
Johnny Darter	2.660	51.90	0.167	0.167	0.667	0.571
Smallmouth Bass	2.477	55.36	0	0	1.000	0.571
Pearl Dace	2.255	58.51	0.500	0.063	0	0
Brook Stickleback	2.213	61.61	0.500	0.042	0	0.071
Yellow Perch	1.862	64.21	0.667	0.938	1.000	0.857
Banded Killifish	1.809	66.74	0	0	0.667	0.500
N. Redbelly Dace	1.710	69.13	0.417	0.083	0	0

SIMPER, Pooled (continued)

Taxon	Contribution %	Cumulative %	Mean Species Abundances Within Faunal Groups			
			1	2	3	4
Fathead Minnow	1.681	71.48	0.333	0.063	0.333	0
Brown Bullhead	1.664	73.81	0	0	0	0.571
Spottail Shiner	1.629	76.08	0	0.229	0	0.214
Sand Shiner	1.521	78.21	0	0	0.667	0.429
Mudminnow	1.506	80.32	0.083	0.042	0	0.357
Finescale Dace	1.497	82.41	0.333	0.063	0	0
Mimic Shiner	0.942	83.73	0	0.063	0.333	0.143
Cisco	0.804	84.85	0.083	0.146	0	0
Common Shiner	0.799	85.97	0.083	0	0	0.214
Logperch	0.796	87.08	0.083	0.042	0	0.143
Black Crappie	0.776	88.17	0	0	0	0.286
Trout-perch	0.775	89.25	0.167	0.063	0	0
Yellow Bullhead	0.707	90.24	0	0	0	0.214
Walleye	0.592	91.07	0	0.125	0	0
Mottled Sculpin	0.568	91.86	0	0.021	0.333	0.071
Hornyhead Chub	0.564	92.65	0	0	0	0.214

Cluster analysis based on similarities of species composition for all 77 lake communities at ISRO, VOYA, and SLBE revealed a pattern of clustering/branching largely concordant with overlays of thermal classification, faunal assemblages, and distribution of key species (Figure 30). The tree shows a major division between warmwater communities of SLBE and the coldwater, coolwater, and cool-warmwater communities of VOYA and ISRO. One major branch includes 15 of 19 SLBE communities, which are characterized as warmwater communities containing largemouth bass with adjuvants northern pike, yellow perch, rock bass, pumpkinseed, and bluntnose minnow (with few exceptions). All communities with assemblage 4 (northern pike, yellow perch, largemouth bass, and bluntnose minnow present) are included in this branch. The second major branch contains most ISRO and VOYA communities and is divided into several sub-branches. The largest sub-branch includes 31 simple communities (21 from ISRO, eight from VOYA, and one from SLBE) containing northern pike, yellow perch, and few other species. A second sub-branch representing three ISRO and seven VOYA lakes includes more diverse communities characterized by the presence of northern pike, yellow perch, blacknose shiner, pumpkinseed, white sucker, and coldwater species. A third sub-

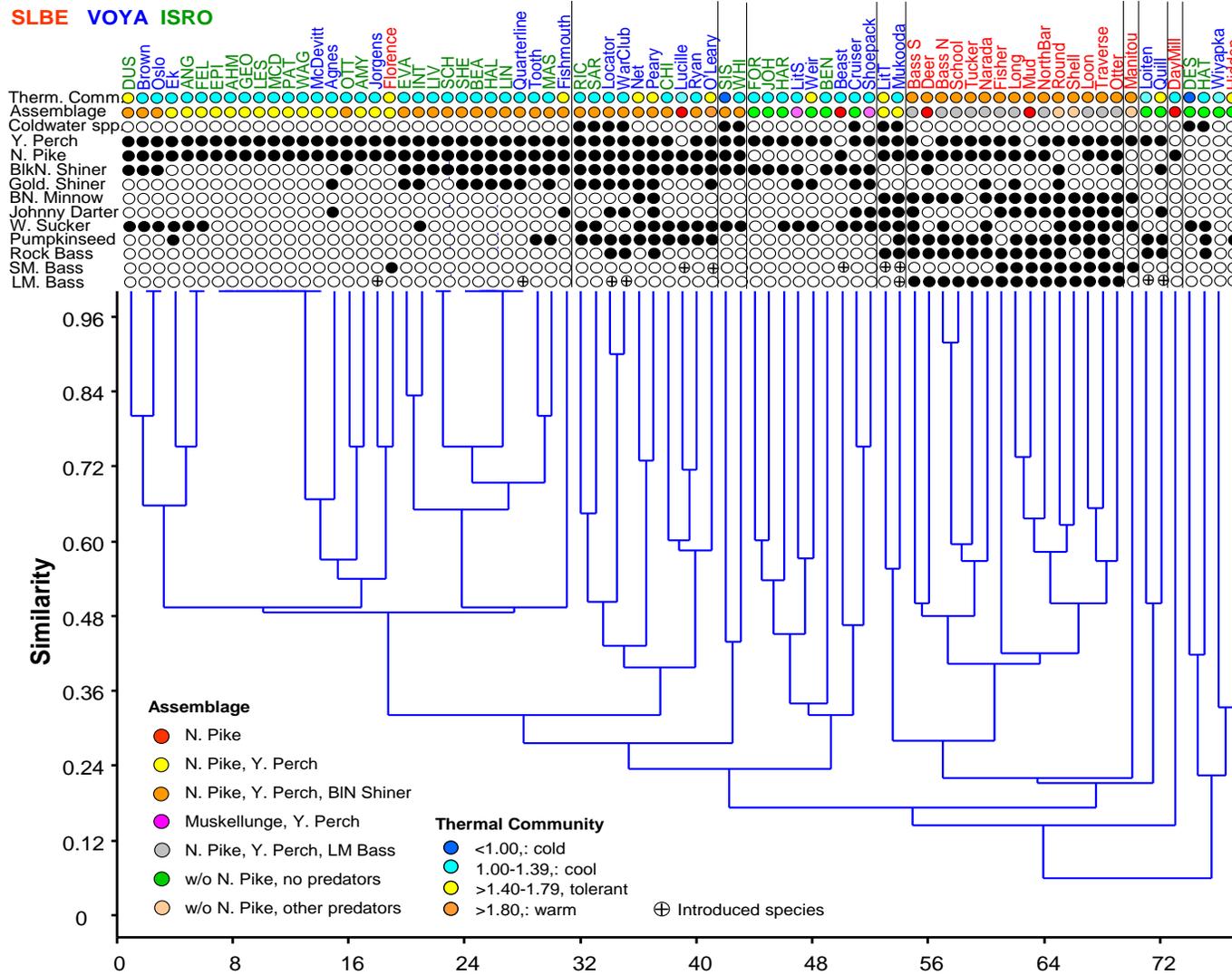


Figure 30. Global Cluster Analysis of 77 inland lake fish communities of ISRO, VOYA, and SLBE based on paired Jaccard's Similarities with overlays of thermal groups, faunal assemblages, selected species, and introduced species. Introduced species (in VOYA) were not included in the cluster analysis. Vertical lines between lake names demark division of major branches or clusters. Corr. Coeff. 0.8874.

branch contains four ISRO and five VOYA communities characterized by the absence of northern pike and the presence of a mixed assortment of species, for example, VOYA communities Shoepack and Little Shoepack are unique in containing muskellunge. The smallest sub-branch includes two ISRO communities (SIS and WHI) and is characterized by the presence of coldwater species and lacking golden shiner and pumpkinseed. The remaining branches of the tree contain one-to-four species. An outlier branch representing all three regions contains four communities that lacked northern pike, yellow perch, or basses (DES, HAT, Wiyapka, and Hidden). VOYA communities Little Trout and Mukooda form a branch characterized by the presence of coldwater and warmwater species. VOYA communities Loiten and Quill form a branch characterized by the absence of northern pike but containing yellow perch, pumpkinseed, and rock bass. SLBE communities Manitou and Day Mill form separate branches; Manitou lacks northern pike, and Day Mill is a simple community containing northern pike and mudminnow.

A global DCA separated lake communities based on species composition along two axes that explained 76% of the total variance (Figure 31; see Appendix XVIII). Overlays of thermal classification and faunal assemblages onto community scores facilitates interpretation of the DCA projection. Axis 1 represented a gradient of warmwater to coldwater communities, and Axis 2 provided greater separation of communities based on the presence of northern pike and yellow perch and warmwater and coldwater species. Polygons encompassing the communities of each region showed relatively little overlap and showed a progression of warmwater communities (SLBE) to a mix of cool-warmwater and coolwater communities (VOYA) to coolwater and coldwater communities (ISRO). Most of the communities in the central cluster contained both northern pike and yellow perch even though they span warmwater, cool-warmwater, and coolwater communities of ISRO, VOYA, and SLBE. Most communities distributed low along Axis 1 contained largemouth bass along with northern pike and yellow perch (all from SLBE). Smaller clusters of communities differing in the presence of northern pike and yellow perch are located below the main cluster. A plot of species scores with an overlay of species thermal classifications (Figure 32) facilitates interpretation of the dispersion of species and community scores. Axis 1 shows a gradient of warmwater to cool-warmwater to coolwater to coldwater species, while Axis 2 provided greater separation of coldwater from other species.

A global CCA projected lake communities in multivariate space in response to environmental variables (Figure 33; see Appendices XX and XXI). Axis 1 explained 37% of the total variance. Environmental variables with the highest correlations with Axis 1 were SpCond_log, alkalinity, pH, surface temperature (Temp), and Shore_D. Axis 1 may be interpreted as a gradient ranging from round, warm lakes with high conductivity, alkalinity, and pH (negative axis scores) to cool lakes with convoluted shorelines and soft water (lower conductivity, alkalinity, and pH) (positive axis scores). Axis 2 explained an additional 26% of the total variance. Variables largely responsible for Axis 2 were L.Area_log, Zmax_log, Wshd.Area_log, and Secchi depth (Secchi). Hypo_temp loaded negatively on both axes, indicating that lakes with warmer summer hypolimnions scored low on both axes. Axis 2 may be interpreted as a gradient from small, shallow, less transparent lakes (negative scores) to large, deep, clear lakes (positive scores). The triplots for environmental variables indicated

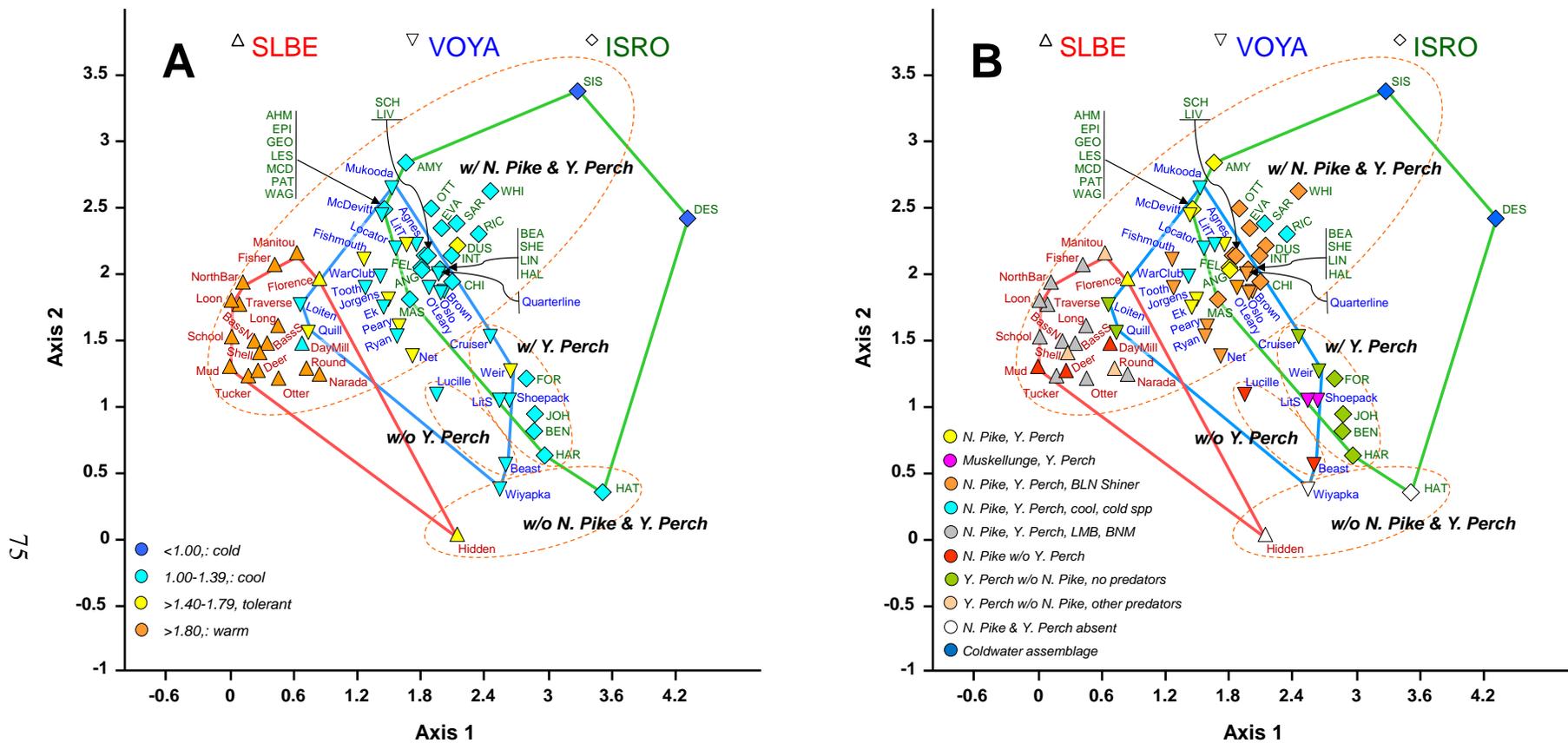


Figure 31. Global DCA plots for 77 ISRO, VOYA, and SLBE inland lake communities based on similarity of composition with overlays of mean community thermal scores (A) and assemblage groups (B). Polygons circumscribe the communities for each region. Axis 1 explained 43% of the total variance and Axis 2 explained an additional 33%. The DCA model is based on 10 segments.

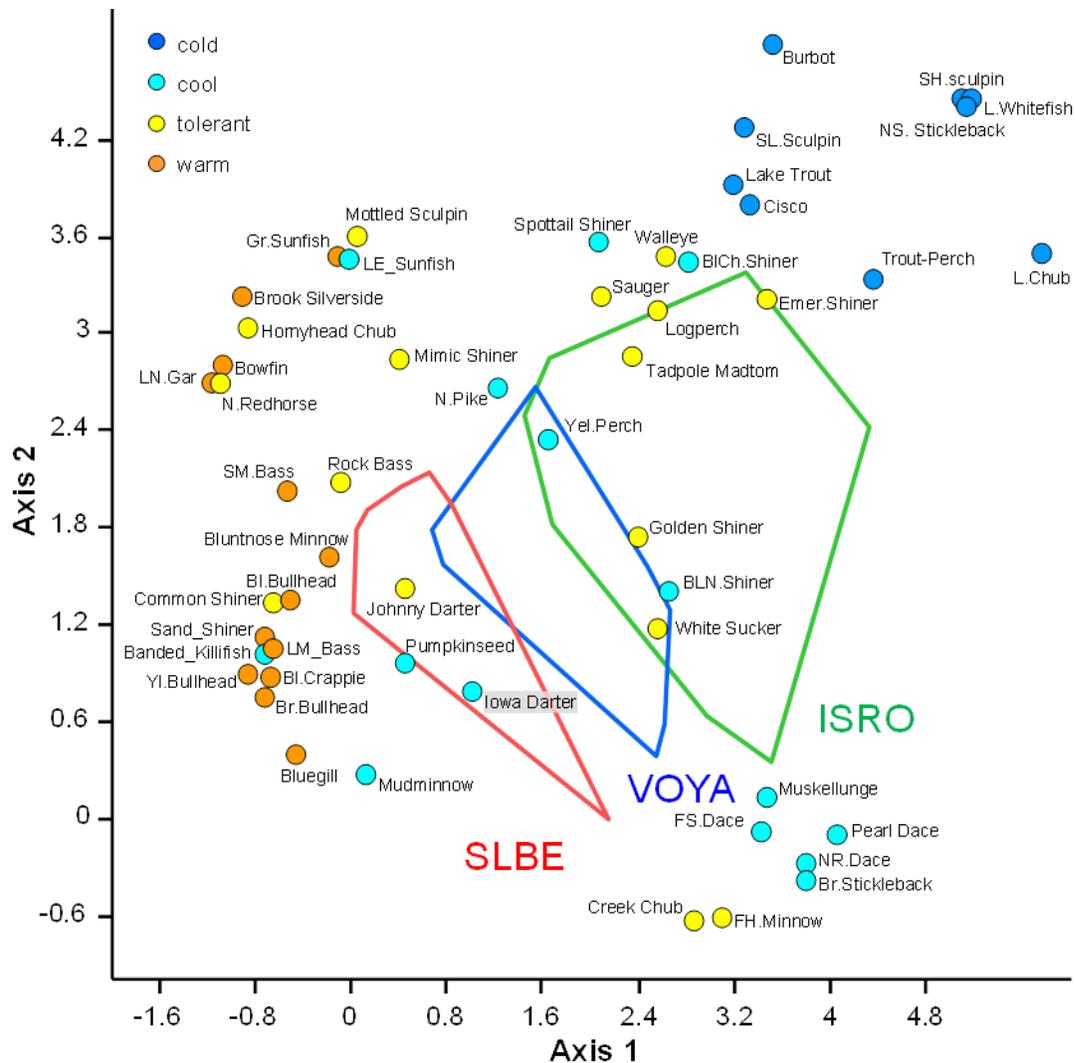


Figure 32. Global DCA plot for ISRO, VOYA, and SLBE inland lake communities based on similarity of composition showing mean species scores coded by thermal classification. The DCA model is based on 10 segments. Polygons represent the area circumscribing the community scores for each region (not shown; see Figure 31).

the direction and strength of the two general gradients (Axis 1 and Axis 2) along which the lake communities were distributed (Figure 33).

The overlay of thermal classification onto community scores in the global CCA showed that lake communities were arrayed into warmwater, cool-warmwater, coolwater, and coldwater communities along Axis 1 (Figure 33A). Axis 2 provided further separation of lakes by size and depth, with Desor and Siskiwit lakes (ISRO) being outstanding examples of deep, cold lakes populated by coldwater fishes. The overlay of the faunal assemblage classification onto community scores in the global CCA provided further interpretation of community dispersion along the two axes. Along Axis 1, communities containing assemblages with largemouth bass (scores <-0.8) were separated from those without largemouth bass (scores >-0.8) (Figure 33B). Communities containing other assemblages showed no discernable pattern of grouping along Axis 1 other than ISRO communities Desor and

Siskiwit, which contained the coldwater assemblage. Along Axis 2 communities from smaller lakes with fewer species had lower scores (<0.6), while larger lakes with more diverse communities had higher scores (>0.6). The largest, deepest, coldest lakes (Desor and Siskiwit) with predominately coldwater species had scores >3.9 (Figure 33). Plotting species scores in CCA space with an overlay of thermal classification provided greater insight into the underlying causes of the dispersion of communities and species (Figures 33A and 34). Along Axis 1, warmwater species scored low (<0) and coldwater species scored high (>0.6), but coolwater and thermally tolerant species were not well segregated and overlapped with other thermal groups (Figure 34). Axis 2 provided greater segregation of coolwater and thermally tolerant species and provided greater separation of coldwater species from other thermal groups. Coolwater species tended to score lower (negatively) on Axis 2 while warmwater and thermally tolerant species scored in the center of the axis, and coldwater species scored higher (≥ 1.0).

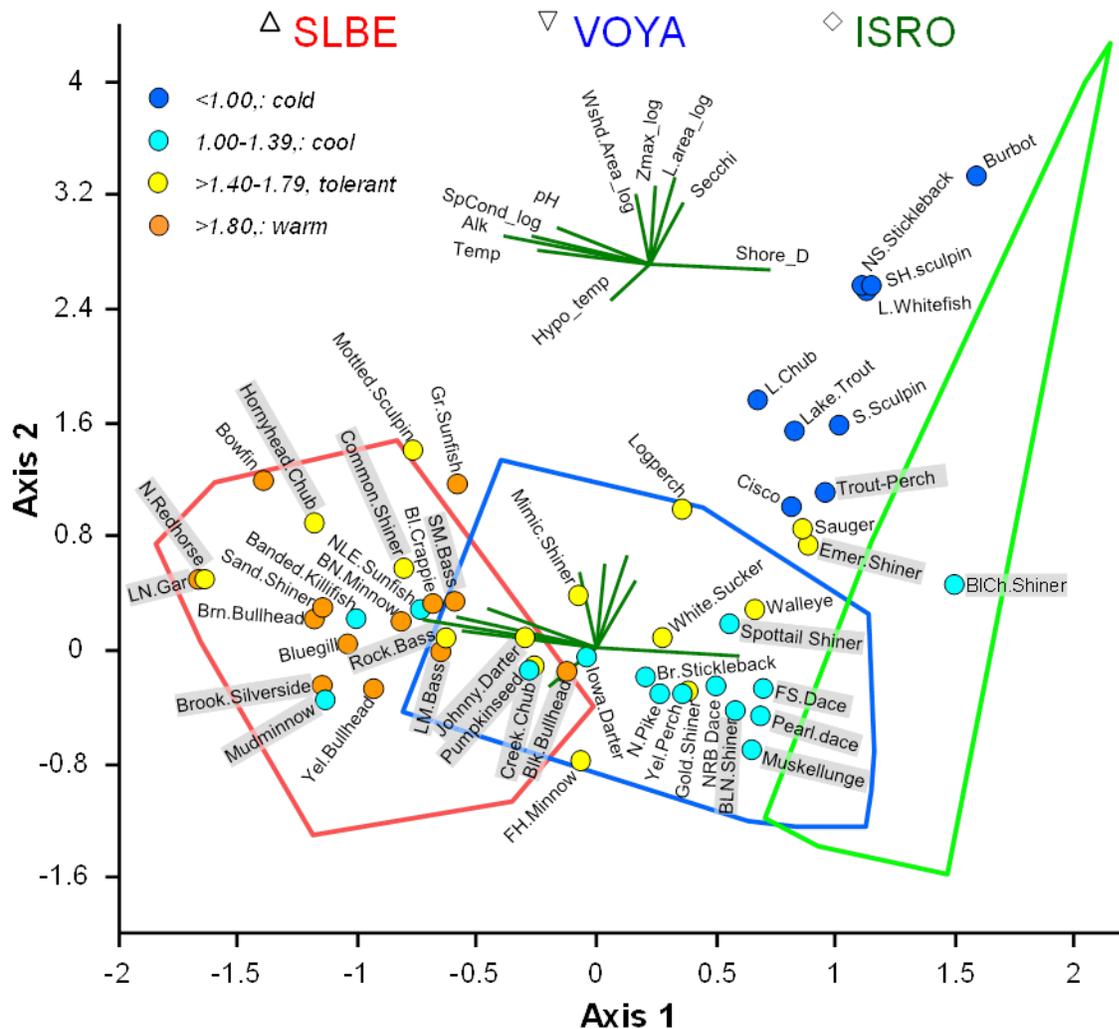


Figure 34. Global CCA plot for ISRO, VOYA, and SLBE lake communities showing positions of species mean scores in canonical space set by environmental variables and coded by species thermal classification. Polygons represent the area circumscribing the community scores for each region (not shown; see Figure 33).

Species presence/absence data across the three regions were organized with respect to the hypothetical ancestral source pool (see Table 2) (Figure 35). ISRO had the most primitive fauna since it is closest to the hypothetical source pool, followed by VOYA and finally by SLBE, with the most derived fauna. By sorting species presence/absence from the source pool and across regions, a pattern of descent becomes apparent; that is, a pattern of sequential shared and unique gains and losses of species which are summarized in an area cladogram (Figure 36) (sensu Gorman 1992). The cladogram is remarkably parsimonious and robust; the retention index was 1.0 (100% synapomorphy) and the consistency index was 1.0 (no homoplasy). To better understand the potential ecological basis for changes in community composition, the individual species gained or lost were coded by their thermal classification (see Table 2) (Figures 35 and 36). The fauna of ISRO retained

88% (29 of 33) of the species identified as the source pool and had no gains. The lost species consisted of three coldwater species and one coolwater species, all of which are shared with VOYA and SLBE (Figures 35 and 36). VOYA contained 31 species and retained 64% of the hypothetical source pool. Shared losses with SLBE included six coldwater and one coolwater species. Shared gains with SLBE included one warmwater, four thermally tolerant, and two coolwater species. VOYA had one unique loss (creek chub) and three unique gains (muskellunge, sauger, tadpole madtom), of which the first was classified as a coolwater species and the latter as thermally tolerant species. SLBE contained 36 species and retained 42% of the original hypothetical source fauna. Unique losses to SLBE included four coldwater, three coolwater, and four thermally tolerant species. Unique gains to SLBE included 12 warmwater, two thermally tolerant, and one coolwater species. The pattern of descent from the source pool to SLBE is characterized by a progressive loss of cold- and coolwater species and gain of warmwater and thermally tolerant species; this is reflected in the increasing mean thermal scores of the faunas from a low 0.85 for the hypothetical source pool to 2.06 for SLBE (Figure 36). Mean thermal scores of gained, lost, and retained species also reflect this trend from coldwater to warmwater communities.

To provide a better understanding of the contribution of species thermal characteristics to historical changes in communities across regions, which is shown in the area cladogram (Figure 36), ANOVA was used to compare species thermal scores among regions and the hypothetical source pool (Table 14A). As expected, there were highly significant differences in species thermal scores across regions and the source pool ($P < 0.0000$), with significant differences occurring between Source–VOYA, Source–SLBE, SLBE–ISRO, and SLBE–VOYA comparisons (Tukey's pairwise comparison; Table 14A). There were no significant differences between the Source–ISRO and the ISRO–VOYA comparisons. Next, differences in the thermal scores of species gained and lost in the area cladogram were compared with ANOVA and found significantly different (Figures 35 and 36, Table 14B). The average thermal score of species lost was 0.65 and consisted of 13 coldwater, five coolwater, and five thermally tolerant species. The average thermal score of species gained was 2.36 and consisted of four coolwater, eight thermally tolerant and 13 warmwater species. These results indicate that the thermal characteristics of the species losses and gains in the area cladogram have a significant ecological basis and suggest that warmer climatic conditions have driven changes in community composition from the source pool and ISRO to VOYA and SLBE. These results also show that the most significant branch in the area cladogram is between SLBE and the branch that includes ISRO and VOYA. The split between ISRO and VOYA is not significant, nor is the split between the source pool and ISRO.

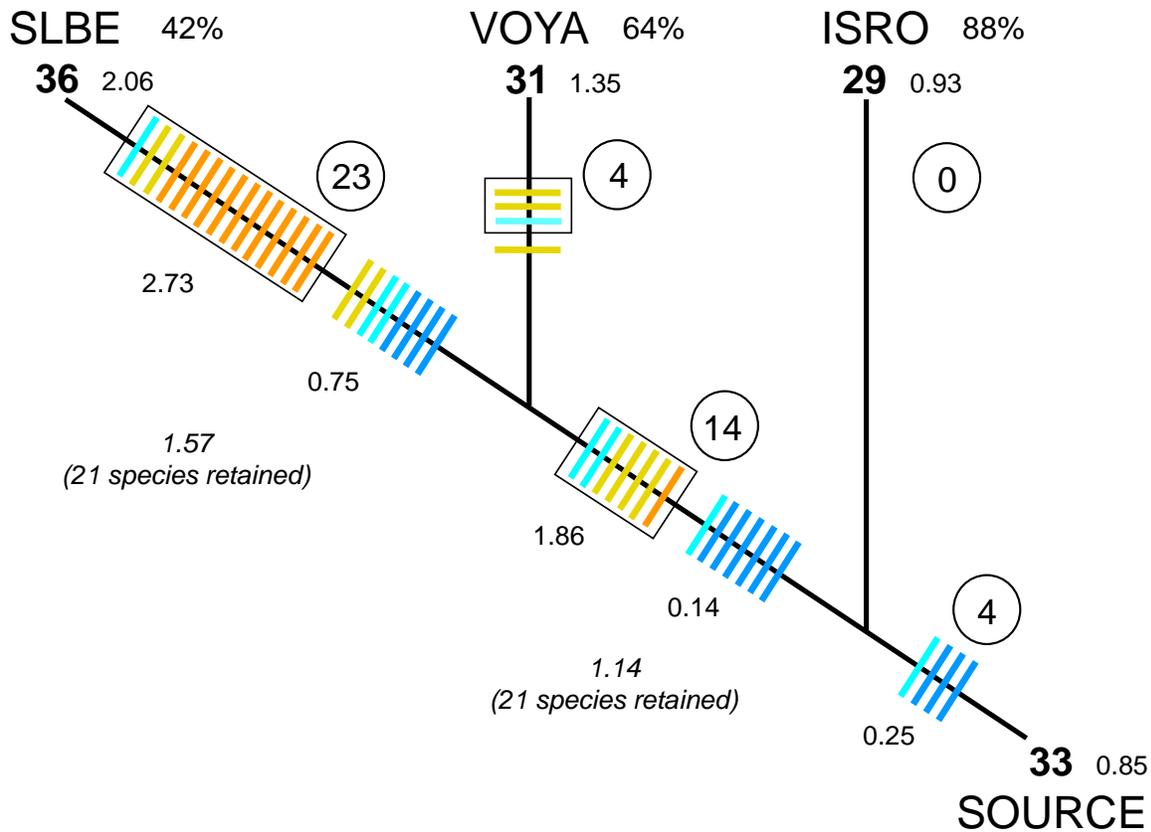


Figure 36. Area cladogram of ISRO, VOYA, and SLBE regional faunas. Characters for the cladogram are species (strikes on branches) and character states are species presence/absence (unboxed are species lost, boxed are species gained). Circled numbers represent the number of characters/steps that define each branch. Topology of the cladogram is the most parsimonious using the Branch and Bound algorithm and Fitch's Character Optimization Criteria to find the shortest tree (45 characters). The retention index is 1.0 (100% synapomorphy) and the consistency index was 1.0 (no homoplasy). Strikes are color-coded with species thermal scores: blue (cold), turquoise (cool), yellow (thermally tolerant), and orange (warm). The three regions draw from a common faunal source pool of 33 species with a mean thermal score of 0.85. Isle Royale retains 29 species, or 88% of the hypothetical post-glacial fauna, and has a mean thermal score of 0.93; VOYA has 31 species with a mean thermal score of 1.31 and retains 64% of the post-glacial fauna. SLBE has 36 species with a mean thermal score of 2.06 and retains 42% of the post-glacial fauna. VOYA and SLBE share seven losses, with a mean thermal score of 0.14, and seven gains, with a mean thermal score of 1.86. VOYA has one unique loss and three gains not shared with SLBE. SLBE has eight unique losses, with a mean thermal score of 0.75, and 15 unique gains, with a mean thermal score of 2.73. Numbers below groups of strikes represent mean thermal scores for the groups. Mean thermal scores of retained species are for species carried over from the previous branch (remaining species after losses but without new species). This cladogram reflects data portrayed in Figure 35.

Table 14. Comparison of fish faunas of ISRO, VOYA, SLBE and the hypothetical post-glacial source pool based on thermal scores of species and thermal scores of species lost and gained in area cladogram shown in Figures 33 and 34. Part A shows results of ANOVA testing for regional differences in species thermal scores. Part B shows results of ANOVA testing for differences in thermal scores of species lost and gained. Definitions of thermal scores and classification of communities are provided in Table 1. Assignments of thermal scores for species are listed in Table 2.

A. Differences in Species Thermal Scores Across Regions and Compared to Source Pool

SUMMARY

Groups	No. Species	Species Thermal Score		
		Sum	Average	Variance
SOURCE	33	28	0.8485	0.6326
ISRO	29	27	0.9310	0.6379
VOYA	31	42	1.3548	0.5699
SLBE	36	74	2.0556	0.6825

ANOVA, one-way

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	31.2354	3	10.4118	16.4556	4.4955E-09	2.6771
Within Groups	79.0902	125	0.6327			
Total	110.3256	128				

Omega ² :	0.2644	Welch F test in case of unequal variances:	F=15.39	df=68.78	P=9.234E-08
Levene's test for homogeneity of variances based on means:	0.9794	Shapiro-Wilk W:	0.9291		
Levene's test for homogeneity of variances based on medians:	0.9734	P(normal):	4.18E-06		

Tukey's pairwise comparisons Q \ Probability

Q \ P	SOURCE	ISRO	VOYA	SLBE
SOURCE	0	0.9759	0.0529	7.73E-06
ISRO	0.5875	0	0.1428	7.79E-06
VOYA	3.604	3.016	0	0.0024
SLBE	8.59	8.003	4.987	0

B. Differences in Thermal Scores of Species Lost and Gained

SUMMARY

Groups	No. Species	Species Thermal Score		
		Sum	Average	Variance
ALL LOSSES	20	10	0.5	0.5789
ALL GAINS	25	59	2.36	0.5733

Table 14 (continued). Comparison of fish faunas of ISRO, VOYA, SLBE and the hypothetical post-glacial source pool based on thermal scores of species and thermal scores of species lost and gained in area cladogram shown in Figures 33, 34. Part A shows results of ANOVA testing for regional differences in species thermal scores. Part B shows results of ANOVA testing for differences in thermal scores of species lost and gained. Definitions of thermal scores and classification of communities are provided in Table 1. Assignments of thermal scores for species are listed in Table 2.

ANOVA, one-way

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	38.44	1	38.44	66.7577	2.72E-10	4.067
Within Groups	24.76	43	0.5758			
Total	63.2	44				

Omega ² :	0.5315
Levene's test for homogeneity of variances based on means:	0.8822
Levene's test for homogeneity of variances based on medians:	0.5418
Welch F test in case of unequal variances:	F=66.68 df=40.77 P=4.092E-10
Shapiro-Wilk W:	0.8805
P(normal):	2.47E-04

Tukey's pairwise comparisons Q \ Probability

Q / P	LOSSES	GAINS
LOSSES	--	0.0001
GAINS	11.55	--

Assessment of Climate Change on Inland Lake Communities

Lakes of each region were classified as tiers 1–4 refuge lakes for coldwater fishes according to the MCCM criteria provided by Fang et al. (2012) (Tables 15–18). Plots of Zmax (maximum depth) vs. Secchi depth, and GR (geometry ratio) vs. Secchi depth allowed visualization of refuge (tiers 1 and 2) and non-refuge (tiers 3 and 4) lakes in ISRO, VOYA, and SLBE (Figures 37–39; data from Appendix III). To explore the relationship between the MCCM classification of the lakes depicted in these plots and the ecological characteristics of the fish communities, the lake scores were overlaid with color-coded community thermal classifications provided in Tables 3, 5, and 7, and lakes containing coldwater species cisco or lake trout were identified with blue text labels. The presence of specific coldwater and coolwater heritage species in refuge lakes was also considered. A summary of species affected by MCCM classification of inland lakes at ISRO, VOYA, and SLBE is provided in Table 15.

Table 15. Summary of climate change modeling results for inland lakes of ISRO, VOYA, and SLBE. Refuge lakes meet criteria for tier 1 and 2 refuge lakes according to the Minnesota Climate Change Model (MCCM; Jacobson et al. 2010, Fang et al. 2012). Thermal classification of species is defined in Tables 1 and 2. Asterisks denote species subject to loss under effects of climate change in the 21st century.

	Region		
	ISRO	VOYA	SLBE
No. of lakes	32	26	19
Refuge lakes (%)	7 (12%)	11 (42%)	2 (11%)
Coldwater heritage species	Cisco Lake Trout Slimy Sculpin Burbot Lake Whitefish Trout-perch Ninespine Stickleback Spoonhead Sculpin N. Lake Chub	Cisco Lake Trout Slimy Sculpin Burbot	
Coolwater heritage species	Pearl Dace N. Redbelly Dace Brook Stickleback Pumpkinseed Blackchin Shiner Iowa Darter	Pearl Dace N. Redbelly Dace Brook Stickleback N. Longear Sunfish Finescale Dace	Brook Stickleback*
Thermally tolerant heritage species	Mimic Shiner Logperch	Mimic Shiner Mottled Sculpin Tadpole Madtom Walleye Sauger	Mottled Sculpin
Non-refuge lakes (%)	25 (78%)	15 (58%)	17 (89%)
Coldwater heritage species	Trout-perch		
Coolwater heritage species	Pearl Dace Finescale Dace* N. Redbelly Dace Brook Stickleback Blackchin Shiner Iowa Darter Pumpkinseed	Pearl Dace Finescale Dace N. Redbelly Dace Brook Stickleback Muskellunge*	N. Redbelly Dace* Brook Stickleback* Blacknose Shiner* N. Longear Sunfish*
Thermally tolerant heritage species	Logperch Walleye	Logperch Mimic Shiner	Mimic Shiner

In ISRO, two lakes (Siskiwit and Sargent) were classified as tier 1 refuge lakes and both harbored coldwater fishes (Table 16, Figure 37). Five lakes (Amygdaloid, Angleworm, Desor, Mason, and Richie) were classified as tier 2 refuge lakes, but only Desor and Richie contained coldwater fishes. Of all the refuge lakes, only Siskiwit met criteria for adequate summer hypolimnetic DO and low temperature (8.8 ppm DO, 5°C near lake bottom; Appendix III). Angleworm and Richie had the warmest summer hypolimnetic temperatures (17.1°C and 13.4°C, respectively). Temperatures at lake bottom in the other refuge lakes ranged from 6.7°C in Sargent to 10.4°C in Desor, and hypolimnetic DOs were <0.40 ppm. Angleworm's relatively high hypolimnetic DO (7.9 ppm) in combination with a warm hypolimnion (17.1°C) indicate that this lake does not stratify in the summer. Taken together, only Siskiwit clearly meets all criteria as a refuge lake. With the exception of Angleworm, other tier 1 and tier 2 lakes may serve as refuge lakes if future assessments show that suitable oxythermal habitat is available at higher strata within the hypolimnion and nutrient loading is sufficiently low so that hypolimnetic oxygen levels remain ≥ 3 ppm DO (Jacobson et al. 2013). The most likely candidates are those refuge lakes presently containing coldwater fishes (Desor, Sargent, and Richie). However, a recent survey of Richie did not detect the presence of cisco (J. Glase, personal communication), suggesting this lake may not serve as a refuge lake. This leaves Siskiwit, Desor, and Sargent as the only candidate refuge lakes at ISRO.

Table 16. Heritage communities of ISRO lakes. LS = Lake Superior. Lake conn. = connection to Lake Superior; ? – unknown, i – intermittent, no – none. Heritage species have limited ISRO distribution and represent early post-glacial colonizers; all coldwater fishes are considered heritage species. Lakes with high heritage values are indicated in **bold font**. Tier represents a thermal classification of lakes based on climate models of Jacobson et al. (2010) and Fang et al. (2012): tier 1 and 2 represent lakes predicted to retain sufficient cold oxygenated habitat through 2100; tier 3 and 4 lakes are predicted to have insufficient oxygenated habitat to support cool- and coldwater fishes. Asterisks by lake names denote heritage communities subject to loss of species.

Lake	Lake area (ha)	Max depth (m)	Elev. Above LS	Approx		Lake conn	No. Spp	Heritage		Heritage species
				Tier	Age (y)			No. Spp	Value	
Epidote	1.3	3.96	5.8	3	667	?	2	0	low	
Scholts	2.3	1.52	20.8	4	2478	?	3	0	low	
John	3.3	5.49	12.8	3	1458	i	5	2	moderate	Pearl dace, Finescale dace
George	3.8	2.70	20.7	4	2467	?	2	0	low	
Dustin	4.4	6.10	14.8	3	1763	?	5	1	moderate	Walleye
Wagejo	6.1	2.19	45.7	4	5268	?	2	0	low	
Forbes	6.8	5.80	52.8	3	6020	i	3	1	moderate	Pearl dace
Patterson	10.1	3.60	6.8	3	748	i	2	0	low	
Ahmik	10.3	3.35	9.5	3	1034	i	2	0	low	
Amygdaloid	10.8	8.84	3.8	2	427	?	3	0	low	
Shesheeb	11.5	5.49	38.8	3	4472	?	4	0	low	
McDonald	14.8	4.00	29.8	3	3512	i	2	0	low	
Linklater	17.3	6.00	39.0	3	4446	?	4	0	low	
Eva	17.6	6.40	4.0	3	454	?	5	0	low	
Beaver	20.1	5.18	23.8	3	2836	i	4	0	low	
Otter	20.2	4.27	29.8	3	3552	i	4	0	low	
Mason	22.8	8.50	2.8	2	325	?	5	1	moderate	Pumpkinseed
Benson	24.1	3.80	56.7	3	6006	i	4	2	moderate	Finescale dace, Brook stickleback
Livermore	30.1	5.50	29.9	3	3524	?	3	0	low	
Lesage	45.0	6.40	40.2	3	4739	?	2	0	low	
Hatchet*	49.6	5.20	46.7	3	5756	i	7	4	high	Pearl dace, N. redbelly dace, Trout-perch, Brook stickleback
Angleworm	50.4	8.40	57.3	2	6606	?	3	0	low	
Harvey	55.4	4.00	49.1	3	5919	?	6	2	moderate	Pearl dace, Brook stickleback
Whittlesey	65.0	7.62	24.8	3	2955	?	8	3	high	Trout-perch, Logperch, Walleye

Table 16. Heritage communities of ISRO lakes. LS = Lake Superior. Lake conn. = connection to Lake Superior; ? – unknown, i – intermittent, no – none. Heritage species have limited ISRO distribution and represent early post-glacial colonizers; all coldwater fishes are considered heritage species. Lakes with high heritage values are indicated in bold font. Tier represents a thermal classification of lakes based on climate models of Jacobson et al. (2010) and Fang et al. (2012): tier 1 and 2 represent lakes predicted to retain sufficient cold oxygenated habitat through 2100; tier 3 and 4 lakes are predicted to have insufficient oxygenated habitat to support cool- and coldwater fishes. Asterisks by lake names denote heritage communities subject to loss of species. (continued)

Lake	Lake area (ha)	Max depth (m)	Elev. Above LS	Approx		Lake conn	No. Spp	Heritage		Heritage species
				Tier	Age (y)			No. Spp	Value	
Intermediate	70.8	6.70	22.8	3	2717	?	6	0	low	
Halloran	77.4	2.70	16.8	4	2236	no	4	0	low	
Chickenbone*	92.6	6.40	1.2	3	141	?	10	5	high	N. redbelly dace, Blackchin shiner, Pumpkinseed, Iowa darter, Walleye
Sargent	143.4	13.72	28.8	1	3319	?	11	5	high	Cisco, Blackchin shiner, Pumpkinseed, Iowa darter, Slimy sculpin
Feldtman	185.8	2.74	18.0	4	2452	?	3	0	low	
Richie	216.2	10.67	8.2	2	965	?	12	6	high	Cisco, Mimic shiner, Trout-perch, Brk. stickleback, Pumpkinseed, Slimy sculpin
Desor	427.8	14.02	77.1	2	10040	?	10	10	high	Cisco, L. whitefish, L. chub, Pearl dace, N. redbelly dace, Trout-perch, Brook stickleback, Ninespine stickleback, Spoonhead sculpin
Siskiwit	1635.2	46.00	17.8	1	2193	?	15	9	high	Cisco, L. whitefish, L. trout, Trout-perch, Burbot, Ninespine stickleback, Logperch, Slimy sculpin, Spoonhead sculpin

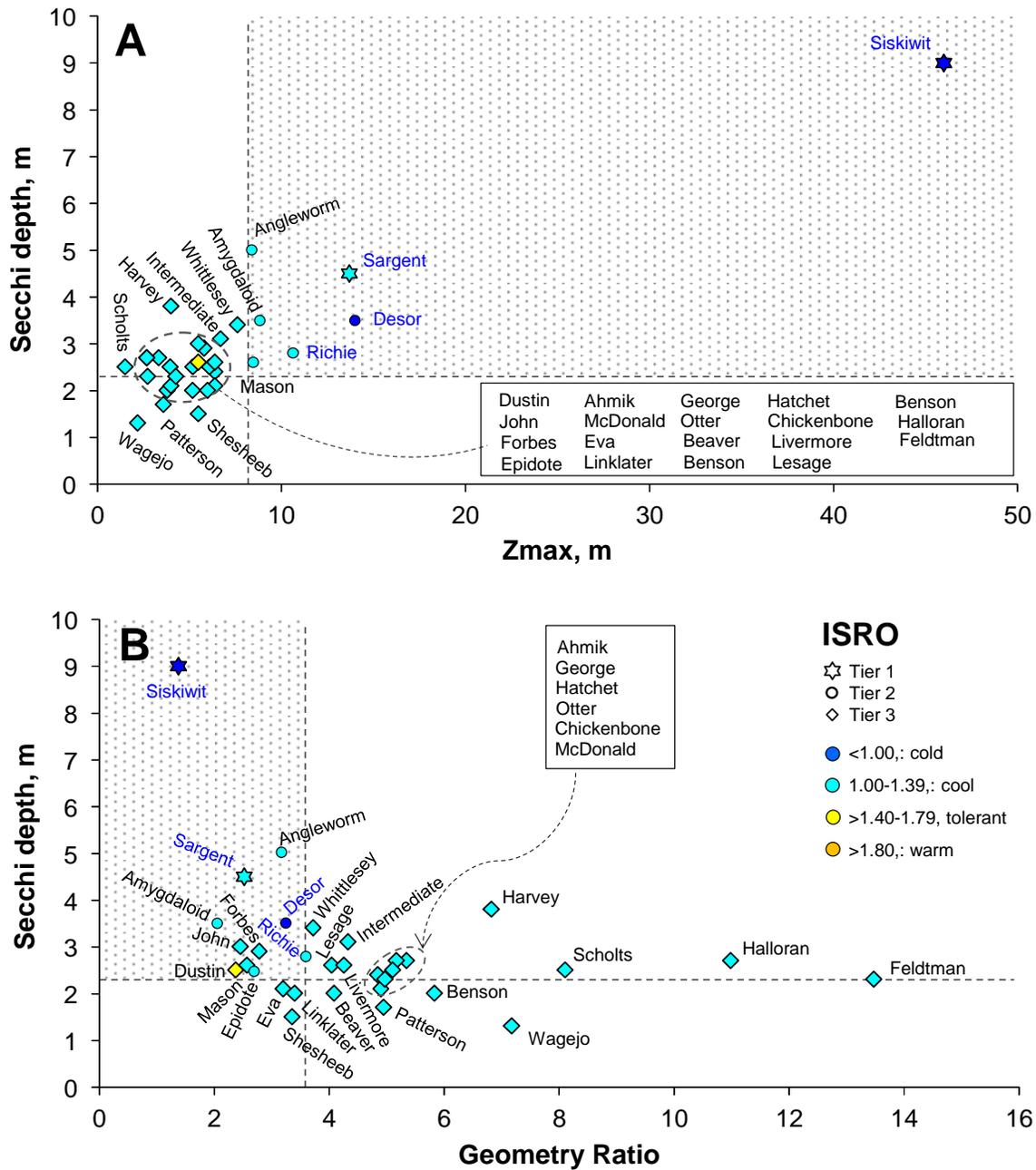


Figure 37. Classification of ISRO's inland lakes according to the Minnesota Climate Change Model (MCCM; Jacobson et al. 2012, Fang et al. 2012, Jiang et al. 2012). Tier 1 lakes are defined as having Secchi depths ≥ 3.2 m, Zmax (maximum depth) ≥ 13.7 , and geometry ratios ≤ 1.8 . Tier 2 lakes are defined as having Secchi depths ≥ 2.3 m, Zmax (maximum depth) ≥ 11.6 , and geometry ratios ≤ 2.7 . Tier 3 lakes have Secchi depths < 2.3 m, Zmax (maximum depth) < 11.6 , and geometry ratios > 2.7 . Lakes meeting two criteria for tiers 1 and 2 are located in the shaded quadrants of panels A and B. Fish communities are classified as cold, cool, cool-warm (tolerant), or warm as defined in Table 4. Lakes labeled with blue text contain coldwater species cisco or lake trout.

In VOYA, nine lakes were classified as tier 1 refuge lakes (Beast, Cruiser, Little Trout, Locator, Loiten, Mukooda, O'Leary, Quill, and Tooth), but coldwater fishes were present only in Cruiser, Little Trout, Locator, and Mukooda (Table 17, Figure 38). Of the tier 2 refuge lakes (Oslo and War Club), only War Club contained coldwater species. Summer hypolimnetic temperatures ranged from 4.4°C to 7.2°C in tier 1 lakes and 6.6°C to 7.7°C for tier 2 lakes (see Appendix III), indicating strong stratification predicted by MCCM criteria. However, only Cruiser had sufficient oxythermal habitat in the lower hypolimnion (5.5°C and 6.5 ppm DO) to provide suitable oxythermal habitat for coldwater fishes (≥ 3 ppm DO, $\leq 15^\circ\text{C}$; see Appendix III) (Jacobson et al. 2010). Despite low hypolimnion DO levels at lake bottom in Little Trout, Mukooda, Locator, and War Club, they support populations of cold water fishes (Table 17, Figure 38; see Appendix III) and may have suitable oxythermal habitat at higher strata within the hypolimnion. Taken together, only Cruiser was clearly identified as a tier 1 refuge lake. The other tier 1 and tier 2 lakes may serve as refuge lakes if future assessments demonstrate that suitable oxythermal habitat is available and nutrient loading is sufficiently low that hypolimnetic oxygen levels remain ≥ 3 ppm DO (Jacobson et al. 2013). The most likely candidate refuge lakes in VOYA are those containing coldwater fishes (Cruiser, Little Trout, Locator, Mukooda, and War Club).

In SLBE, only Narada met MCCM criteria as a refuge lake (tier 2) based on Zmax, GR, Secchi depth (Table 18, Figure 39), and summer hypolimnetic temperature (6.4°C; see Appendix III), but hypolimnetic DO was near anoxia (0.12 ppm; see Appendix III) and coldwater fishes were absent. Traverse met MCCM criteria as a tier 2 refuge lake, but the summer hypolimnetic temperature was too warm (15.2°C; see Appendix III), indicating weak summer stratification. Manitou and Loon met refuge lake criteria for Zmax, GR, and hypolimnetic temperature, but Secchi depths were too shallow (Table 18, Figure 39; see Appendix III), indicating that nutrient loading may be driving high productivity and biological oxygen demand (BOD) in these lakes. For the remaining lakes, maximum depths were too shallow, Secchi depths too shallow, or GR too large to meet MCCM criteria for refuge lakes. All stratified lakes (Deer, Loon, Manitou, and Narada) had very low hypolimnetic DOs (0.09–0.36 ppm; see Appendix III). Taken together, no lakes in SLBE harbor native coldwater species and none are likely to serve as refuge lakes in the future. However, reduction of nutrient inputs in Narada, Manitou, and Loon could improve the potential for these lakes to provide refuges for coldwater species in the future (Jacobson et al. 2013).

Table 17. Heritage communities of VOYA lakes. RNK = Rainy-Namakan-Kabetogama lakes. Lake conn. = connection to RNK lakes; ? – unknown, i – intermittent, no – none. Heritage species have limited VOYA distribution and represent early post-glacial colonizers; all coldwater fishes are considered heritage species. Lakes with high heritage values are indicated in **bold font**. Tier represents a thermal classification of lakes based on climate models of Jacobson et al. (2010) and Fang et al. (2012): tier 1 and 2 represent lakes predicted to retain sufficient cold oxygenated habitat through 2100; tier 3 lakes are predicted to have insufficient oxygenated habitat to support cool- and coldwater fishes. Asterisks by lake names denote heritage communities subject to loss of species.

Lake	Lake area (ha)	Max depth (m)	Elev. Above Rainy L (m)	Tier	Est. Age (y)	Lake Conn.	No. Spp.	Heritage		Heritage Species
								No. Spp.	Value	
Quarter Line	8.3	6.7	19.835	3	5544	i	4	0	low	
McDevitt	12.1	7.0	28.727	3	8030	?	2	0	low	
Agnes	13.0	5.5	10.435	3	2917	?	3	0	low	
Fishmouth	13.0	8.5	13.438	3	3756	?	5	1	moderate	Mimic shiner
Ryan	14.2	3.7	16.527	3	4620	i	6	0	low	
Wiyapka*	20.2	5.2	22.618	3	6322	i	7	4	high	Finescale dace, N. redbelly dace, Brook stickleback, Logperch
Little Shoepack	22.7	7.6	31.735	3	8871	?	7	2	moderate	Pearl dace, Muskellunge
Tooth	23.5	13.1	22.918	1	6406	i	4	0	low	
Jorgens	24.7	5.8	28.735	3	8032	?	3	0	low	
Weir	26.8	2.4	13.418	4	3751	i	4	1	moderate	Pearl dace
Brown	30.8	8.2	19.538	3	5461	?	4	0	low	
Beast	32.8	20.1	28.738	1	8033	i	10	4	high	Pearl dace, Finescale dace, N. redbelly dace, Brook stickleback
Quill	34.4	14.0	19.552	1	5465	?	6	0	low	
Ek	36.0	5.8	7.335	3	2050	?	4	0	low	
Loiten	36.6	14.9	22.652	1	6332	?	3	0	low	
War Club	36.8	12.2	10.452	2	2922	?	10	1	moderate	Cisco
Oslo	42.5	11.0	19.838	2	5545	?	4	0	low	
Net	43.7	3.7	9.518	3	2661	?	8	0	low	
Peary	45.3	4.6	4.338	3	1213	?	11	0	low	
Cruiser	46.5	27.7	40.935	1	11442	i	10	3	high	L. trout, Finescale dace, N. redbelly dace
Lucille	53.0	5.8	39.299	3	10985	i	6	1	moderate	N. redbelly dace
Locator	56.7	15.9	10.461	1	2924	?	9	1	moderate	Cisco
O'Leary	78.5	17.1	8.905	1	2489	?	9	1	moderate	Tadpole madtom
Little Trout	96.7	29.0	11.305	1	3160	i	13	6	high	Cisco, L. trout, Mimic shiner, Finescale dace, Walleye, Sauger
Shoepack*	123.8	7.3	25.652	3	7170	?	11	4	high	Pearl dace, Finescale dace, N. redbelly dace, Muskellunge
Mukooda	305.0	23.8	4.287	1	1198	i	15	7	high	Cisco, L. trout, Slimy sculpin, Mottled sculpin, Walleye, Burbot, N. longear sunfish

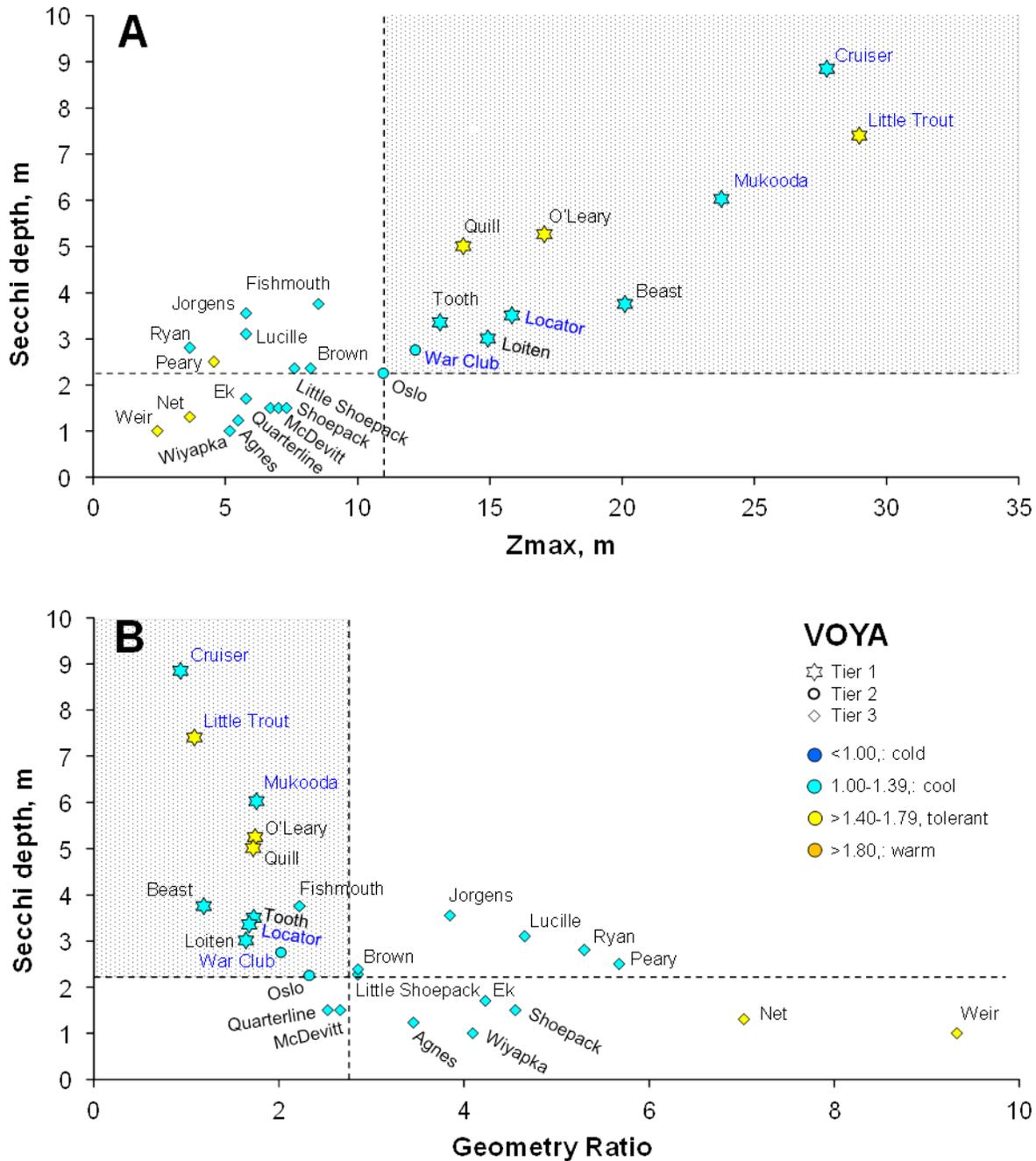


Figure 38. Classification of VOYA's inland lakes according to the Minnesota Climate Change Model (MCCM; Jacobson et al. 2012, Fang et al. 2012, Jiang et al. 2012). Tier 1 lakes are defined as having Secchi depths ≥ 3.2 m, Zmax (maximum depth) ≥ 13.7 , and geometry ratios ≤ 1.8 . Tier 2 lakes are defined as having Secchi depths ≥ 2.3 m, Zmax (maximum depth) ≥ 11.6 , and geometry ratios ≤ 2.7 . Tier 3 lakes have Secchi depths < 2.3 m, Zmax (maximum depth) < 11.6 , and geometry ratios > 2.7 . Lakes meeting two criteria for tiers 1 and 2 are located in the shaded quadrants of panels A and B. Fish communities are classified as cold, cool, cool-warm (tolerant), or warm as defined in Table 5. Lakes labeled with blue text contain coldwater species cisco or lake trout.

Table 18. Heritage communities of SLBE lakes. LM = Lake Michigan. Lake conn. = connection to Lake Michigan; ? – unknown, i – intermittent, no – none, yes – known perennial connections. Heritage species have limited SLBE distribution and represent early post-glacial colonizers. Tier represents a thermal classification of lakes based on climate models of Jacobson et al. (2010) and Fang et al. (2012): tier 1 and 2 represent lakes predicted to retain sufficient cold oxygenated habitat through 2100; tier 3 lakes are predicted to have insufficient oxygenated habitat to support cool- and coldwater fishes.

Lake	Lake Area (ha)	Max Depth (m)	Tier	Lake Conn.	Heritage			Heritage Species
					No. Spp.	No. Spp.	Value	
Hidden	0.6	1.0	4	no	5	2	moderate	N. redbelly dace, Brook stickleback
Deer	1.8	6.7	3	yes	10	1	moderate	Blacknose shiner
Day Mill	2.3	1.2	4	i	3	0	low	
Round	6.1	7.9	3	yes	13	1	moderate	Blacknose shiner
Tucker	6.9	3.7	3	yes	9	0	low	
Bass, South	10.9	7.9	3	i	16	1	moderate	N. longear sunfish
North Bar	12.1	9.5	3	yes	16	1	moderate	N. longear sunfish
Narada	12.6	11.9	2	yes	13	1	moderate	Brook stickleback
Mud	21.5	1.0	4	yes	12	0	low	
Fisher	21.9	4.6	3	yes	9	0	low	
Otter	25.9	6.4	3	yes	18	1	moderate	Blacknose shiner
Florence	31.6	7.9	3	i	4	0	low	
Loon	37.2	19.5	3	yes	22	0	low	
Bass, North	37.6	7.3	3	yes	12	1	low	Mimic shiner
Shell	41.3	4.0	3	i	12	1	low	Mimic shiner
School	71.2	4.7	3	i	11	1	low	Mimic shiner
Manitou	103.6	13.7	3	yes	5	0	low	Mottled sculpin
Long	131.9	6.1	3	i	13	0	low	
Little Traverse	261.0	16.5	2	yes	18	1	low	Mottled sculpin

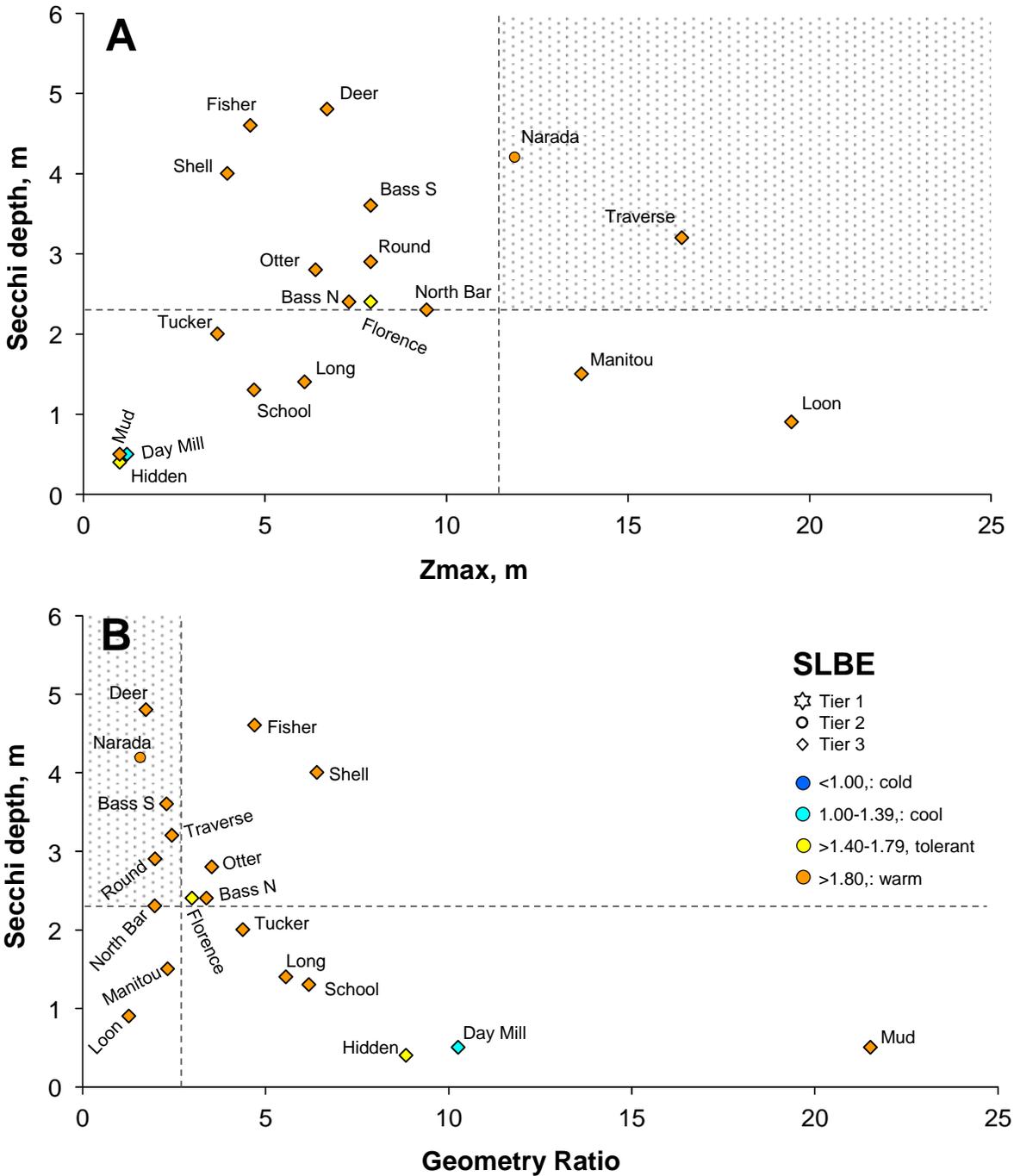


Figure 39. Classification of SLBE's inland lakes according to the Minnesota Climate Change Model (MCCM; Jacobson et al. 2012, Fang et al. 2012, Jiang et al. 2012). Tier 1 lakes are defined as having Secchi depths ≥ 3.2 m, Z_{max} (maximum depth) ≥ 13.7 , and geometry ratios ≤ 1.8 . Tier 2 lakes are defined as having Secchi depths ≥ 2.3 m, Z_{max} (maximum depth) ≥ 11.6 , and geometry ratios ≤ 2.7 . Tier 3 lakes have Secchi depths < 2.3 m, Z_{max} (maximum depth) < 11.6 , and geometry ratios > 2.7 . Lakes meeting two criteria for tiers 1 and 2 are located in the shaded quadrants, of panels A and B. Fish communities are classified as cold, cool, cool-warm (tolerant), or warm as defined in Table 6.

Assessment of Climate Change on Heritage Fishes and Heritage Communities

Heritage species have limited distributions and represent early post-glacial colonizers; all coldwater fishes were considered heritage species, as well as some coolwater and thermally tolerant species. We defined heritage communities as containing assemblages of three or more coldwater or coolwater heritage species. Lakes that met criteria for tier 1 or tier 2 refuge lakes were judged to be less susceptible to climate change and likely to provide refuges for their communities from the effects of predicted increases in temperature over the course of the 21st century. Non-refuge lakes (tier 3 and 4 lakes) were judged to be susceptible to climate warming and subject to changes in community composition through losses of coldwater and coolwater species and gains of thermally tolerant and warmwater species. We used the MCCM classification to assess the likelihood of non-refuge lakes to support heritage species and heritage communities with the onset of climate change (Tables 15–18; Figures 37–39). Of the three regions, VOYA contained the greatest number of refuge lakes (11), followed by ISRO (7), and SLBE (2). ISRO lakes harbored the greatest number of coldwater species (9) and other heritage species (10) (see Table 15). VOYA lakes harbored four coldwater species and 12 other heritage species. SLBE lakes harbored no coldwater species and six heritage species. We judged coldwater and coolwater heritage species in non-refuge lakes to be subject to loss with the onset of climate change. Thermally tolerant heritage species were judged to not be subject to loss.

ISRO contains seven refuge lakes (two are tier 1 and five are tier 2) and 25 non-refuge lakes (20 are tier 3 and five are tier 4) (see Tables 15 and 16). Of the seven refuge lakes, two did not contain heritage species (Amygdaloid and Angleworm), four contained a mix of heritage species (Sargent, Richie, Desor, and Siskiwit), and tier 2 lake Mason contained the coolwater heritage species pumpkinseed, but this species was present in other refuge lakes. Of the 20 tier 3 non-refuge lakes, 12 did not contain heritage species (Epidote, Patterson, Ahmik, Shesheeb, McDonald, Linklater, Eva, Beaver, Otter, Livermore, Lesage, and Intermediate), and eight contained heritage species (John, Dustin, Forbes, Benson, Hatchet, Harvey, Whittlesey, and Chickenbone). Heritage coldwater species burbot and trout-perch were judged subject to loss in tier 3 non-refuge lakes Hatchet, Harvey, and Whittlesey, but were also present in refuge lakes. Heritage coolwater species pearl dace, finescale dace, northern redbelly dace, blackchin shiner, Iowa darter, and pumpkinseed in tier 3 non-refuge lakes were judged subject to loss. However, all but finescale dace were also present in refuge lakes. Finescale dace was the only coolwater heritage species restricted to non-refuge lakes (Benson and John) and was judged subject to loss from ISRO. Thermally tolerant heritage species walleye and logperch found in tier 3 non-refuge lakes Dustin, Whittlesey, and Chickenbone were judged not susceptible to loss. The five tier 4 non-refuge lakes Feldtman, George, Halloran, Scholts, and Wajego did not contain heritage species (see Table 16 and Appendix VI).

VOYA contains 11 refuge lakes (nine are tier 1 and two are tier 2) and 15 non-refuge lakes (14 are tier 3 and one is tier 4) (see Tables 15 and 17). Of the 11 refuge lakes, four did not contain heritage species (Tooth, Quill, Loiten, and Oslo), three contained a single heritage species (War Club, Locator, and O'Leary), and four contained a mixture of heritage species (Beast, Cruiser, Little Trout, and Mukooda). The only heritage species restricted to a single refuge lake was tadpole madtom in O'Leary, but this species was classified as thermally tolerant and judged not susceptible to loss. Of the 14 tier-3 non-refuge lakes, nine did not contain heritage species (Agnes, Brown, Ek, Jorgens,

McDevitt, Net, Peary, Quarter Line, and Ryan) and four contained coolwater heritage species pearl dace, finescale dace, northern redbelly dace, brook stickleback, and muskellunge (Lucille, Little Shoepack, Shoepack, and Wiyapka). With the exception of muskellunge, these species also occurred in refuge lakes. The limitation of muskellunge to tier 3 non-refuge lakes Shoepack and Little Shoepack indicates that this species may be susceptible to loss from VOYA. Mimic shiner, a thermally tolerant heritage species, was present in tier 3 non-refuge lake Fishmouth and in refuge lake Little Trout and thus judged not subject to loss. Pearl dace, a coolwater heritage species, was present in non-refuge tier 4 lake Weir, other non-refuge lakes (Little Shoepack and Shoepack), and one refuge lake (Beast) and thus judged not subject to loss.

SLBE contains two tier 2 refuge lakes and 17 non-refuge lakes (14 are tier 3 and three are tier 4) (see Tables 15 and 18). The presence of coolwater heritage species brook stickleback in tier 2 refuge lake Narada was judged to be susceptible to loss because this species occurs in only one other lake—non-refuge tier 4 lake Hidden. Mottled sculpin, a thermally tolerant heritage species, was present only in tier 2 refuge lake Little Traverse, but was not judged to be subject to loss because, as previously discussed, the SLBE tier 2 lakes do not fully meet criteria for refuge lakes. Of the 14 tier-3 non-refuge lakes, seven did not contain heritage species (Tucker, Mud, Fisher, Florence, Loon, Manitou, and Long), while five contained coolwater heritage species blacknose shiner and northern longear sunfish that were judged susceptible to loss (Deer, Round, South Bass, North Bar, and Otter). The thermally tolerant heritage species mimic shiner occurred in tier 3 non-refuge lakes North Bass, Shell, and School and was judged not susceptible to loss. Tier 4 non-refuge lakes Day Mill and Mud did not contain heritage species, but tier 4 non-refuge lake Hidden contained coolwater heritage species northern redbelly dace and brook stickleback, which were judged subject to loss.

In summary, each region had one or more heritage species or communities that were judged subject to loss as a result of climate change in the 21st century (see Tables 15–18). At ISRO, the heritage coolwater species finescale dace was restricted to two non-refuge lakes and was judged subject to extirpation. In VOYA, the heritage coolwater species muskellunge was restricted to two non-refuge lakes and was judged subject to extirpation. In SLBE, heritage coolwater species brook stickleback, northern redbelly dace, northern longear sunfish, and blacknose shiner were judged subject to extirpation due to restricted distribution in non-refuge lakes or refuge lakes that do not fully meet criteria for refuge lakes. Of 32 lakes in ISRO, only four were classified as refuge lakes containing heritage communities: Sargent, Richie, Desor, and Siskiwit. The heritage communities in non-refuge lakes Hatchet and Chickenbone were judged susceptible to loss of coldwater and coolwater species (see Table 16). Of 26 lakes in VOYA, only four lakes were classified as refuge lakes containing heritage communities: Beast, Cruiser, Little Trout, and Mukooda. The heritage communities in non-refuge lakes Wiyapka and Shoepack were judged susceptible to loss of species (see Table 17). No SLBE lakes contained more than two heritage species, thus SLBE did not contain any heritage communities (see Table 18).

Discussion

It comes as no surprise that comparison of the fish communities in inland lakes at ISRO, VOYA, and SLBE revealed both faunal differences and similarities. Our thermal and faunal assemblage classifications provided independent metrics for assessing patterns of community composition and species distributions within and across regions. The correlation of these classifications with patterns of species distributions and community composition suggests that underlying ecological processes are driving the assembly and maintenance of inland lake communities. For example, we found lake communities composed of thermally tolerant and warmwater species had similar species compositions and were associated with similar physical and environmental conditions. Incorporation of Tonn's (1990) conceptual framework for fish community assembly (Figures 1 and 5) allowed us to identify source pools, dispersal potential, and filters that contribute to regional and local lake community composition. When placed within a context of geological history we were able to provide greater understanding of the underlying causes of concordant and discordant patterns of species distributions and community assembly in terms of ecology, history, and biogeography. Application of the MCCM climate change model by Jacobson et al. (2010, 2013), Fang et al. (2012), and Jiang et al. (2012) allowed us to evaluate the potential impact of future climate change on lake communities at ISRO, VOYA, and SLBE. We identified heritage species and heritage communities that are at risk of loss from climate change and suggest actions outlined by Jacobson et al. (2013) to reduce future losses.

Lake Size, Environmental Parameters, and Species Composition

Each region contained a wide range of lake sizes and depths. Predictably, lake environments and the habitats they delimit were found to be affected by lake size and depth, particularly summer hypolimnetic temperature. Species richness increased with lake size, though not for SLBE lakes. ISRO and SLBE provided a greater range of lake sizes (and thus habitats) than VOYA, as they had many lakes <20 ha in size that contained two or more fish species. This suggests that the environments of small lakes in VOYA are harsher than those in ISRO and SLBE. Alternatively, fish communities in smaller lakes of VOYA may have been extirpated shortly after these lakes were colonized during a warm dry period 8,000 BP, as indicated by climate reconstruction of sediment cores collected from VOYA lakes by Davis et al. (2000). Each region provided a range of thermal habitats, with smaller lakes being warmer and larger lakes providing both warmwater and coolwater habitats, depending on their depth and geomorphology. Small lakes had warm summer hypolimnetic temperatures ranging from 15°C to 25°C, while larger lakes were cooler, ranging from 5°C to 10°C. ISRO, and especially VOYA, stood out as having some lakes with cold ($\leq 5^\circ\text{C}$) hypolimnions. Though the ranges of thermal habitats appeared to be similar across regions, the species compositions were not. ISRO communities were dominated by coolwater species—31 of 32 communities were categorized as coolwater or coldwater. VOYA communities were also dominated by coolwater species—21 of 27 communities were categorized as coolwater and six as cool-warm. SLBE communities were dominated by a set of widespread warmwater and thermally tolerant species—16 of the 19 communities were classified as warmwater communities. Our results suggest that thermal tolerances of species and our thermal classification of lake communities and species may be more

reliable indicators of long-term environmental conditions than mid-summer measurements of physical parameters such as surface and hypolimnetic temperature and dissolved oxygen.

Regional Patterns of Community Composition

Patterns of regional community composition were first explored through analyses of similarity (ANOSIM, SIMPER, and Hierarchical Cluster Analysis). Overlays of classifications based on thermal attributes of species and faunal assemblages tested ecological factors underlying distribution patterns. Regional cluster analysis based on similarity of species composition showed no discernable relationship with thermal classification of communities, largely because of the limited range of thermal categories present in each region. For this same reason, regional cluster analysis based on inter-lake distances showed no discernable relationship to thermal classification of communities. Agreement between cluster analysis based on similarity of species composition and assemblage classification varied by region. Grouping of ISRO communities by cluster analysis and assemblage classification was largely concordant, less so for VOYA communities, and largely discordant for SLBE communities. The lack of concordance for SLBE communities was the result of community homogenization; six species occurred in 15 of 19 lakes, and four of these species represented the most widespread assemblage (4), which occurred in 11 lakes. Segregation of communities in SLBE was largely a matter of the presence of uncommon species and the absence of common species. Cluster analysis based on inter-lake distances was largely discordant with classification of communities by assemblage groups for ISRO and SLBE communities, but those in VOYA showed some concordance in groupings of two-to-five lakes. Finally, cluster analysis of ISRO and VOYA inland lakes based on relative lake age showed no apparent relationship with classification of communities by assemblage groups or thermal attributes.

DCA based on community composition of lakes in each region yielded results similar to those from the hierarchical cluster analysis. Overlaying community scores in DCA projections with thermal and assemblage classifications showed concordance with grouping of communities, particularly for those at ISRO. The addition of environmental variables in regional CCA community ordinations yielded clearer patterns of grouping and segregation of communities by thermal and assemblage classifications, particularly for ISRO and VOYA communities. Environmental variables correlated with grouping and segregation of communities by thermal and assemblage classifications included lake size, depth, and temperature. Plots of species scores in CCA projections with overlays of thermal scores showed concordance between our thermal classification and the distribution of species by environmental variables, particularly for ISRO and VOYA lakes, thus implicating temperature related environmental variables as being the principal drivers that determine composition of lake communities. In these multivariate projections, the homogenization of SLBE communities resulted in a weaker relationship between species composition and environmental variables and thermal and assemblage classifications.

Our regional analysis showed that the communities of ISRO, VOYA, and SLBE could be distinguished by differences in species composition. Overlays of thermal and assemblage classifications were helpful in interpreting grouping and segregation of communities in DCA and CCA. Principal factors affecting the grouping and segregation of communities and species in

multivariate projections were environmental variables, principally lake size, depth, and temperature, and biological variables, principally the presence of widespread species (northern pike, yellow perch, and largemouth bass) and coldwater species.

Global Patterns of Community Composition

Global (inter-regional) comparisons of inland lake communities were conducted with the same analytical tools as within region comparisons (ANOSIM, SIMPER, Hierarchical Cluster Analysis, DCA, and CCA). Cluster analysis based on similarity of species composition revealed grouping of communities that was mostly concordant with overlays of thermal and faunal assemblage classifications. The warmwater communities of SLBE formed a distinct branch, while those of ISRO and VOYA mixed on the same branches. Principal species contributing to clustering of communities into branches were northern pike, yellow perch, blacknose shiner, pumpkinseed, rock bass, largemouth bass, and bluntnose minnow. Global DCA projections of communities corroborated these results, showing that communities of SLBE were distinct from those of ISRO and VOYA, which displayed considerable overlap. An overlay of thermal classification onto community scores revealed a strong thermal gradient along Axis 1 that arrayed communities from warmwater (all in SLBE) to coldwater (all in ISRO). In the center of the gradient, the cool-warm and coolwater communities of VOYA and ISRO broadly overlapped. Overlaying community scores with assemblage classifications revealed grouping and segregation of communities by presence/absence of northern pike, yellow perch, largemouth bass, and coldwater species. This overlay revealed a complementary gradient along Axis 2 that separated communities based on the presence and absence of northern pike and yellow perch. A plot of species scores with a thermal classification overlay indicated that thermal attributes of species was the principal driver behind the dispersion of communities in DCA plots, but the presence and absence of northern pike and yellow perch was a secondary driver. For example, a group of species that scored low on Axis 2—particularly creek chub, fathead minnow, northern redbelly dace, brook stickleback, finescale dace, and pearl dace—were associated with the absence of northern pike. These species represent prey for northern pike and were only present in small lakes without northern pike. Also, these prey species were not present in larger lakes with more complex communities containing predators. The effects of predation by northern pike are likely more intense in small lakes, thus making coexistence with small minnow species unlikely. This is a good example of the biological effect of predation structuring local communities of small lakes (Jackson et al. 2001).

Ordination of lake communities across regions by environmental variables (global CCA) revealed a strong temperature gradient along Axis 1. Covariates of temperature were specific conductance, alkalinity, pH, and shoreline development. Axis 1 represented a gradient of warm hardwater lakes at SLBE to cool softwater lakes at VOYA and ISRO with greater shoreline development. As expected, an overlay of community thermal classification showed a gradient of warmwater to coldwater communities. An overlay of assemblage groups revealed loose clusters with considerable overlap. Axis 2 was partly explained by temperature and partly by community composition; communities that scored low on Axis 2 had fewer species and many lacked northern pike. Environmental variables associated with Axis 2 defined a gradient of lake size and depth; shallow lakes with few species scored low; larger, deeper, clearer lakes with more species scored high. Plots of mean species scores

with an overlay of species' thermal classifications were instructive in showing the relationship between community composition and environmental variables. Coldwater species scored relatively high on Axes 1 and 2, as they were largely found in larger, deeper, clearer lakes with cold hypolimnions. Many coolwater species clustered relatively high on Axis 1 and low on Axis 2, showing affiliation with smaller, shallower, and cooler lakes. Most warmwater species clustered relatively low on Axes 1 and intermediate on Axis 2, as they were more often found in warmer lakes of small to intermediate size. Thermally tolerant species were widely distributed along both axes, which suggests a wide thermal tolerance (Axis 1) and presence in a broad array of small-to-large and shallow-to-deep lakes (Axis 2).

Our regional and global analyses showed that each region presented a unique array of lake environments that are the product of regional climate, geology, and history. Regions with cooler climates (ISRO and VOYA) supported an array of coolwater and coldwater fishes, while SLBE had a warmer climate and supported an array of coolwater and warmwater fishes. The most common base assemblage found in lake communities across the three regions was northern pike and yellow perch, both coolwater species widely distributed in post-glacial landscapes in North America. Common adjuvants to this base assemblage were coolwater species blacknose shiner and pumpkinseed and thermally tolerant species golden shiner and white sucker. Several warmwater species were added to this base assemblage in SLBE communities: largemouth bass, bluegill, and bluntnose minnow. Communities across the three regions could be distinguished by species composition, thermal classification, and assemblage groups. Principal environmental variables responsible for the ordination of communities along environmental gradients were those associated with temperature, lake size, and depth. The patterns of species distribution and community composition we found in lakes across the three regions are consistent with Tonn's (1990) conceptual framework of community assembly. Regional filters determine the source pool of species available for colonization of inland lakes, and local filters act in concert to determine the ultimate composition of a lake community. Examples of filters include dispersal and access routes (e.g., water bodies, connecting streams, barriers), biological variables (e.g., predators, competitors, food base), and environmental variables, particularly climate and temperature-related variables.

Lake Environments as Determinants of Fish Community Composition

Within each region, the inland lakes present an array of environmental conditions within the scope of the regional climate and geography. For example, the climate at ISRO is strongly moderated by Lake Superior. Inland lake geomorphology is determined in part by the local geology (i.e., shallow soils atop basaltic rock cause lake volumes to be largely dependent on runoff). The remaining factors affecting environmental conditions are lake size and depth. Small, shallow lakes have warm anoxic hypolimnions in the summer and may be subject to winter kills. Larger, deeper lakes have cold, oxygenated hypolimnions year-round. As a result, there is a wide range of environmental conditions across the inland lakes of ISRO. Only fish that can withstand high summer temperatures and low oxygen levels will persist in smaller, shallower lakes, while large deep lakes can support a richer array of coldwater, coolwater, and thermally tolerant species.

VOYA is geologically similar to ISRO in having shallow soils atop igneous rock, but VOYA's regional climate is not moderated by a surrounding coldwater Great Lake; instead, the climate is northern continental with cold winters and warm summers. At VOYA, we might expect the environmental conditions of elevated temperatures and low oxygen during summer months to be more severe in smaller lakes. The impact of a more severe climate at VOYA may be the underlying cause for lakes <10 ha having fewer than two species present and only one lake <20 ha having two or more species present. A reconstruction of post-glacial climates from pollen cores by Davis et al. (2000) indicates that VOYA underwent an extended warm, dry period 6,000–9,000 BP. Possibly, this mid-Holocene warming resulted in the extirpation of fish from most lakes <20 ha in size. Large, deep lakes appear to be less affected by warming climates; although they retain conditions suitable for coldwater species, they also provide warm littoral habitats that support warmwater species. For example, large VOYA lakes Little Trout and Mukooda support diverse fish communities composed of coldwater, coolwater, and thermally tolerant species. Of all regions, VOYA contains the highest proportion (42%) of lakes >10 m deep with summer hypolimnion temperatures <10°C. Thus, because VOYA has more deep lakes and larger lakes than ISRO, the fauna in VOYA lakes is better buffered against climate change trending toward warmer conditions.

SLBE has both very different climatic and geological influences compared to ISRO and VOYA. The soils are dominated by glacial till and wind- and lake-transported sand deposits with a shallow water table. Because of the sandy soils, lakes of all sizes tend to be relatively shallow and have rounded shorelines. Although the climate is moderated by Lake Michigan, SLBE is more than 300 km south of ISRO and VOYA, resulting in warmer summers and winters. As a result of these influences, SLBE inland lakes are warmer in summer and support a mix of thermally tolerant and warmwater fishes. But the presence of two or more species in many lakes <10 ha contrasts sharply with the situation in VOYA. Possibly, the close proximity to Lake Michigan has moderated environmental conditions in small lakes, a hypothesis supported by reconstruction of post-glacial forests from pollen cores (Davis et al. 2000). Additionally, the high water table influenced by Lake Michigan reduces desiccation of small lakes and moderates summer hypolimnetic temperatures, thereby providing a refuge for fish during hot summers. Finally, most inland lakes in SLBE are interconnected permanently or intermittently by stream channels that communicate with Lake Michigan, which enhances dispersal and recolonization and decreases the likelihood of species extirpations.

Historical Ecology: Assembly of Regional Faunas

We recognized that similarities and differences in faunal compositions of the regions might have historical and physical explanations rather than those based purely on physiology and ecology. For example, some inter-regional differences may be related to differences in timing of and access to dispersal routes. ISRO is situated within Lake Superior, which serves as a barrier to warmwater fish dispersal. The effectiveness of Lake Superior as a barrier is demonstrated by the absence of warmwater species in coastal waters or inland lakes of ISRO. In contrast, warmwater species from the upper Mississippi refugia have been able to colonize the VOYA and SLBE regions. In VOYA, post-glacial dispersal through the streams and lakes of the Red River–Winnipeg–English drainage has apparently allowed later colonizers to reach the large lakes (Rainy, Kabetogama, and Namakan), but access to the smaller inland lakes has been thwarted. In SLBE, the juxtaposition and connections

with coastal waters of Lake Michigan has permitted extensive post-glacial colonization by warmwater species.

Application of our assemblage group classification revealed patterns within and across regions that have biogeographical implications. For example, all of the regional faunas shared a widespread assemblage consisting of northern pike and yellow perch. This coolwater assemblage is common in small inland lakes throughout the northern region of the Great Lakes drainages and adjacent post-glacial drainages. These two species have a Holarctic distribution in post-glacial streams and lakes (Scott and Crossman 1973, Crossman and McAllister 1986), and this assemblage was found in the majority of communities of small lakes (<20 ha) within ISRO, VOYA, and SLBE. Blacknose shiner was often an adjuvant to the northern pike–yellow perch assemblage in small- and intermediate-sized lakes (<30 ha). Other species shared across the regions included golden shiner, spottail shiner, mimic shiner, northern redbelly dace, fathead minnow, white sucker, brook stickleback, pumpkinseed, Iowa darter, and logperch. Together, these species represent the core post-glacial coolwater fish community that colonized small- and intermediate-sized inland lakes in the wake of the receding glaciers at the end of the Wisconsinan glaciation. Species with limited distributions across regions were associated with lake environments specific to a region. For example, the large, deep Siskiwit Lake on ISRO provided coldwater habitat that supported a complement of coldwater fishes found in nearby Lake Superior. In VOYA, the large deep lakes Little Trout and Mukooda provided coldwater habitat that supported cisco and lake trout populations. Neither these deep coldwater habitats nor their associated species were present in the SLBE lakes.

Some readers might question the absence of the central mudminnow from our post-glacial source pool. Although this species was absent during inland lakes surveys conducted at ISRO during 1929 by Walter Koelz (Hubbs and Lagler 1949) and in recent inland lake surveys conducted from 1995 to 1997 (Kallemeyn 2000), it was found in a survey of coastal waters conducted during 2001–2004 by Gorman and Moore (2009). However, it was absent in earlier surveys of coastal waters conducted in the 1920s to 1940s (Hubbs and Lagler 1949). The central mudminnow is listed as absent from waters of lakes Superior and Nipigon by Underhill (1986), and even though Crossman and McAllister (1986) report the central mudminnow as absent from most waters of the Hudson Bay drainage, it occurs in the Red, Winnipeg, and English river drainages that represent a vestige of the Lake Agassiz–Mississippian glacial refugia. To resolve these conflicting accounts, we propose that central mudminnow colonized Lake Superior at some time after the dispersal of our hypothetical faunal source pool. However, central mudminnows may have had earlier access to inland lakes at VOYA and SLBE because of its presence in the Mississippian glacial refugia (Crossman and McAllister 1986).

The next step in our analysis was to cast our results within a historical framework. The results of ANOSIM and SIMPER showed a pattern of shared and unique species across regions. Similarly, classification of communities by species mean thermal scores and assemblage groups were effective in distinguishing patterns of species groups across regions (see Table 14 and Figure 35). By comparing a list of species ordered by thermal classification and region to a hypothetical post-glacial source pool, patterns of shared, lost, and gained species became evident across the regions. When this

information was translated into an area cladogram, a historical-ecological tree of relationships among regional faunas emerged (see Figure 36). ISRO represents the closest regional fauna to the hypothetical post-glacial source pool, and SLBE represents the most derived fauna.

Historical changes in the inland lakes of the Great Lakes region may be interpreted as follows: A post-glacial fauna similar to that found currently in the inland lakes of ISRO colonized the newly formed inland lakes at the early Holocene, 9–12,000 BP. ISRO remained close to its original state because of its location within cold Lake Superior. As climates warmed, coldwater and coolwater species were lost and thermally tolerant, warmwater, and some coolwater species were gained through dispersal. SLBE has lost and gained more species than VOYA and now represents essentially a warmwater fauna with coolwater relicts. VOYA has retained more coolwater and coldwater species because it contains some deep lakes that provide coldwater habitats. In essence, this area cladogram represents a picture of fish community changes driven by global warming following the end of the Wisconsinan glaciation. The current phase of anthropogenic-induced global warming will likely have consequences that can be predicted by this area cladogram. All regions are likely to lose coldwater and coolwater species and the proportion of warmwater species will increase.

Roles of Post-glacial History and Biogeography in Determining Fish Community Composition of Inland Lakes

The earliest fish communities began to colonize inland lakes at ISRO, VOYA, and SLBE as they emerged or separated from the periglacial Laurentian lakes. These massive bodies of icemelt water provided habitats similar to that found in Lake Superior today and likely hosted a similar array of species that today inhabit the coastal waters of ISRO. Subsequent to initial colonization, climate change, warming aquatic habitats, and changing drainage patterns presented each region with new arrays of species. Also, these regions emerged from periglacial meltwater lakes at different times: SLBE, ca. 12,000 BP; ISRO and VOYA, ca. 10,000–11,000 BP. However, lakes continued to emerge in ISRO and VOYA because of isostatic rebound; recent examples from the past two millennia include Siskiwit and Chickenbone in ISRO and Mukooda and Peary in VOYA. The older communities within each region likely reflect greater successional change associated with warming post-glacial climates. Each region has a unique post-glacial history of geology and isostatic rebound, drainage patterns, and climate change which together determined what species successfully colonized and persisted in the inland lakes. The resulting regional faunas are a product of different patterns of colonization and dispersal from source pools, and of selection of species based on physiological tolerances and life histories. Thus, the present-day fish faunas of ISRO, VOYA, and SLBE are the product of their unique post-glacial histories.

ISRO represents the most primitive inland lake fauna; that is, it is closest in composition to the putative initial colonizing fauna, which is a subset of species presently found in the coastal waters of ISRO. Underhill (1986) suggested that the initial ISRO fauna was derived from Glacial Lake Duluth after further ice retreat and lowering of lake levels approximately 11,000 BP (early Lake Minong phase). Subsequent isolation of this fauna on a large island within Lake Superior is a contributing factor to its preserved state. However, coastal waters contain some more recent arrivals (central mudminnow, bluntnose minnow, rock bass, johnny darter and mottled sculpin) that were not likely

present in the early post-glacial era. But isolation within a large coldwater lake may have prevented more recent post-glacial colonizers of Lake Superior from reaching ISRO coastal waters, e.g., smallmouth bass, black bullhead, and northern redhorse (Hoff and Bronte 1999, Gorman and Moore 2009). Species present in the coastal waters of ISRO but not in the interior lakes include round whitefish, bluntnose minnow, longnose dace, blacknose dace, longnose sucker, rock bass, johnny darter, central mudminnow, and mottled sculpin (Kallemeyn 2000, Gorman et al. 2008, Gorman and Moore 2009). The timing of these species' arrival to ISRO may not have coincided with the timing of lake formation from emerging embayments, or these species were unable to thrive in newly isolated lake environments. Thus, only a subset of colonizing species from the glacial refugia was able to colonize the inland lake environments created by the retreating glaciers and isostatic rebound. These include the coldwater species listed in Table 2 and some cool and thermally tolerant species.

Huber (1973) hypothesized that inland lakes of ISRO were formed by embayments that were isolated from Lake Superior as a result of isostatic rebound starting from the southwest about 11,000 BP and moving to the northeast end of the island. Thus, ISRO inland lakes represent a progression of ages ordered by elevation, highest being oldest to lowest being youngest, owing to isostatic rebound. Because ISRO inland lakes would have been colonized by the coastal fauna that occurred at the time of separation, each lake represents a sample of the faunal source pool at the time of isolation. In a sense, each lake represents a repository or "Noah's Ark" for a particular time of isolation. However, as each lake had different sizes, depths, etc., they acted like filters (*sensu* Tonn 1990) to restrict the species that successfully colonized each lake. Yellow perch and northern pike were able to thrive in most of the inland lakes that support fish. Other species that were able to persist in many inland lakes were golden shiner, white sucker, and blacknose shiner. The process of lake community formation can be observed at ISRO, the most recent being Chickenbone—a shallow lake of moderate size that is a mere 1.2 m above an outflow connected to Lake Superior, and is estimated to be about ca. 140 years old (see Figure 17). Chickenbone Lake supports a mix of coolwater and thermally tolerant species but does not include coldwater species that are present in nearby coastal waters. Deeper lakes with cold hypolimnions (Siskiwit and Desor) support coldwater species, particularly lake trout, cisco, lake whitefish, ninespine stickleback, trout-perch, and spoonhead sculpin. Of these, Siskiwit is a young lake (ca. 2,200 yr) and Desor is one of the oldest (ca. 10,000 yr), based on rate of isostatic rebound and elevation above the current level of Lake Superior (Appendix IV-A).

VOYA represents an inland lake fauna very similar to ISRO, but because it is not isolated in a large lake, it has been more directly accessible to colonization by species from the Mississippian glacial refuge. Like ISRO, VOYA inland lakes represent a progression of ages ordered by elevation—highest being oldest to lowest being youngest—owing to isostatic rebound following deglaciation some 12,500 BP (Thorleifson 1996). The upland areas of VOYA likely began to emerge from the Rainy Arm of Lake Agassiz ca. 11,000 BP as an island archipelago and began to coalesce into larger islands by ca. 10,000 BP (Yang and Teller 2005). Given that VOYA inland lakes range in elevation up to 41 m above Rainy Lake, like ISRO, the highest elevation lakes were isolated first as isostatic rebound elevated the upland areas. By applying a model of isostatic rebound to lake elevations, we propose that VOYA inland lakes began to be isolated between 12,000 and 11,000 BP, with Cruiser

and Lucille being the oldest and Mukooda and Peary being the youngest and situated ca. 4 m above KNR (see Figure 22, Appendix IV-B).

Our model of estimating age by elevation and isostatic rebound rate is consistent with Breckenridge's (2013) post-glacial chronology for ISRO, and is concordant with Huber's (1973) post-glacial chronology of ISRO after incorporating new information from Breckenridge (2013). Our estimations of lake ages for VOYA are concordant with recent proposed models of post-glacial history and isostatic rebound for the Glacial Lake Agassiz basin (e.g., Yang and Teller 2005; Fisher 2003, 2005, 2007; Teller et al. 2002; Leverington et al. 2002; Leverington and Teller 2003). However, Winkler and Stanford (1998) suggest that all VOYA lakes were formed within a narrower time span following the retreat of Lake Agassiz about 9,900 BP, a chronology and post-glacial history not supported by the other more recent studies just mentioned.

The VOYA region had intermittent connections via Glacial Lake Agassiz with the periglacial and post-glacial Laurentian drainage basin and lost its final connection to Lake Superior through the Nipigon outlets after their closure ca. 8,800 BP (Appendix II). Crossman and McAllister (1986) suggest that more intimate connections were lost earlier, during the late Wisconsinan and before the formation of the early stages of Lake Agassiz ca. 13,000 BP, though more recent models of post-glacial chronology do not support this proposal. Once these connections were lost, VOYA inland lakes lost the potential for recolonization of coldwater species from the post-glacial Laurentian lakes, thus reducing that aspect of the regional fauna. On the other hand, VOYA lakes have been subject to several phases of dispersal and colonization from post-glacial refugia (Kallemeyn et al 2003). Continued connections with the shrinking Lake Agassiz and subsequent connections with the Red and English–Winnipeg river systems provided a rich source of potential colonizing species from the Mississippian glacial and post-glacial faunal source pool. And as the regional climate warmed, later successful colonizers from this source pool would include warmwater and thermally tolerant species.

Like ISRO, VOYA inland lakes became isolated over a protracted period of time, and because the regional source pool changed over time, each lake represents a sample of the faunal source pool at the time of isolation. As with ISRO, each VOYA lake represents a repository, or “Noah's Ark,” for a particular time of isolation. And as each lake had different sizes, depths, and environments, they acted like filters (*sensu* Tonn 1990) to restrict the species that successfully colonized each lake. For example, no lakes smaller than 12 ha are reported with fish by Kallemeyn et al. (2003), though smaller bodies of water exist either as marshes or beaver impoundments. The absence of fish in small lakes may have a historical explanation. Based on reconstruction of forest communities from pollen cores taken from inland lake sediments, Davis et al. (2000) showed that the climate of VOYA underwent significant warming 6,000–9,000 BP. We hypothesize that this warming may have been sufficient to eliminate coolwater species in small lakes and coldwater species in intermediate-sized lakes. This means there are no parallels to the simple communities of small ISRO lakes; smaller VOYA lakes are either fishless or have become bogs and marshes. Because VOYA was not surrounded by a large, cold Laurentian lake as was ISRO, the climate was not buffered, and changing environmental conditions, especially in small lakes, resulted in more constrictive filters that whittled down the community richness.

SLBE has potentially the oldest and most derived or divergent of the inland lake faunas from the putative post-glacial colonizing fauna. Crossman and McAllister (1986) estimated that the region became ice-free in the early Holocene, more than 12,800 BP. However, inland lake formation in SLBE is relatively complex and ongoing (Calver 1946, Drexler 1974, NPS 2005), and it is likely that most of the inland lakes formed after 4,000–3,000 BP (Larson and Schaetzl 2001). Following the final retreat of the Wisconsinan glaciation ca. 13,000 BP, elevation of periglacial Lake Michigan fluctuated over the next 10,000 years as a result of isostatic rebound and downcutting of the northern outlet. Initially, inland lake basins formed from embayments of periglacial Lake Algonquin, from kettle depressions, and from depressions behind large moraines. As the elevation of periglacial Lake Michigan dropped (Chippewa phase), subsequent dune formation, reworking of shorelines, and fluctuating lake levels created most of the inland lake basins now present in SLBE. Inland lake basins that have their origins in late Algonquin phase events (ca. 12,500 BP) include North Bass, School, and Lime lakes. Most lake basins formed following declining lake levels in the late Nipissing phase which ended ca. 4,000 BP (Thompson et al. 2011). Included are Little Traverse, South Bar, Long, Round, Rush, Platte, Mud, Loon, Otter, South Bass, and Deer lake basins. More recently formed lake basins (<3,000–2,000 BP) include North Bar, Shell, Hatt, Hidden, and Narada lakes.

The low elevation, high water table, and close proximity and connectedness of SLBE inland lakes by stream channels to Lake Michigan have facilitated colonization, recolonization, and movement of fishes among lakes. Species have had many opportunities for movement during cyclic periods of high lake levels in Lake Michigan, particularly during 1,500–2,000 BP (Arbogast and Loope 1999), and during periodic high rainfall and flooding events in lake drainages. Although environmental conditions affect lake composition, this is tempered by high levels of dispersal among lakes and the Lake Michigan source pool. Thus, there is only a weak species richness-lake size relationship, and homogenization of lake fish communities is evident, in contrast to the more isolated upland lakes of ISRO and VOYA. Increased connectedness to Lake Michigan has facilitated colonization by warmwater and thermally tolerant species as they expanded their distributions northward by traversing the coastal waters of Lake Michigan, ostensibly dispersing from the Mississippian refugia via the Chicago outlet during the Algonquin and Nipissing phases. Notable warmwater species that have colonized SLBE inland lakes include longnose gar, bowfin, sand shiner, brown bullhead, yellow bullhead, brook silverside, and largemouth bass.

Relative Contributions of History, Environment and Dispersal in Determining Inland Lake Community Composition: The ISRO Example

ISRO provides an unusual opportunity to assess the role of history versus local environmental conditions in determining species composition of inland lakes. (VOYA is a secondary example because its source pool was not as static or as restrictive as ISRO's Lake Superior source pool.)

ISRO lakes were created as a result of glacial retreat and isostatic rebound starting after 11,000 BP in the southwest end of the island (Huber 1973, Raymond et al. 1975, Bailey and Smith 1981, Flakne 2003, Breckenridge 2013). Although the time over which inland lakes of ISRO formed spanned more than 10,000 years, there appears to be no relationship between species composition and lake age (see Figure 16). We must assume that these lakes were originally colonized by fish from Lake Superior or

its precursor Lake Minong as embayments that were slowly cut off from the lake by isostatic rebound in a southwest-to-northeast direction (Huber 1973). The resulting species compositions of these newly formed lakes were determined principally by environmental conditions dictated by lake size and depth. Colonization of lakes after formation would be possible if outlets were sizeable and allowed upstream movement from Lake Superior. Species that may be capable of upstream movement and colonization include white sucker, brook stickleback, creek chub, redbelly dace, fathead minnow, golden shiner, and brook trout (Hubbs and Lagler 1949). However, more recent arrivals in the coastal waters of ISRO that are equally capable of upstream movement and colonization of inland lakes have not done so. Included are central mudminnow, bluntnose minnow, blacknose dace, longnose dace, longnose sucker, mottled sculpin, and johnny darter. Thus, upstream migration does not appear to have contributed to the present composition of inland lakes. If ISRO lakes were colonized by upstream movement of fish, colonization would have occurred during a limited time following isolation of a lake when an outlet stream was present. Lake Desor is a large deepwater lake containing coldwater species cisco, lake whitefish, lake chub, trout-perch, ninespine stickleback, and spoonhead sculpin. These species were isolated from the Lake Superior source pool as Lake Desor was separated from Lake Minong ca. 10,000 BP (Huber 1973, Raymond et al. 1975). The effect of this long isolation is reflected in the genetic uniqueness of Lake Desor's lake whitefish; they are significantly differentiated from Lake Superior and Lake Huron whitefish and show a distant sister relationship to the more recent derivative whitefish in Siskiwit Lake, which was isolated from Lake Superior some 2,200 years ago (see Figure 17) (Stott et al. 2004).

Assembly, Disassembly, and Reassembly of Inland Fish Communities of ISRO, VOYA, and SLBE: Integrating Roles of History, Dispersal, Filters, and Human Influences

Our study of the inland lake fish communities of ISRO, VOYA, and SLBE was guided by Tonn's (1990) conceptual framework for fish community assembly. Tonn's conceptual framework facilitates thinking about assembly of post-glacial fish communities of small lakes (<100 ha) and may also provide insights regarding the influences of global climate change anticipated in the 21st century. Like Tonn (1990), we found temperature, especially as expressed by local or regional climate, to be a primary determinant (filter) of fish community composition (assembly) of inland lakes. This is because temperature, as expressed by local climate and environmental conditions, is the primary determinant of the distribution and abundance of fish species in inland lakes (Magnuson et al. 1979, Coutant 1987). And because fish presence in a lake is determined by physiological limits for each species, fish integrate the effects of environmental temperature and serve as indicators of local climate. Tonn (1990) also observed that small inland lakes operated like islands; species richness is correlated with lake surface area and degree of isolation. This relationship was true for ISRO and VOYA but not SLBE, where we suspect that periodic interconnections among SLBE lakes and connections with Lake Michigan have resulted in homogenization of lake communities.

Tonn (1990) noted that the role of isolation and dispersal in maintaining or altering richness and composition of inland lake fish communities has not been adequately addressed (Magnuson et al. 1985). We attempted to address the relationship between inter-lake distance and relative age of the lake to community composition and found either no relationship or weak ones. Factors that appear to

be most important in determining species composition are the lake environment serving as a filter and the interplay with timing and dispersal from source pool and colonization potential of a lake. Thus, our analysis indicates that lake communities are largely a product of filtering of the local environment (temperature, oxygen, lake size) and history and physical access (dispersal from source pool and colonization potential). Lakes in ISRO are the clearest examples of this interpretation. Lakes were formed at different times over the past 11,000 years and most have had little opportunity for subsequent colonization. As such, each lake represents a repository of those fish able to colonize that lake at the time of formation, with little opportunity for future additions—only losses.

The post-glacial history of the inland lakes at VOYA parallels that of ISRO; VOYA lakes were isolated over a long period, beginning ca. 11,000 BP, as a result of differential elevation and ongoing isostatic rebound. But unlike ISRO, as VOYA lakes emerged, they could draw upon a richer and changing source pool to colonize lake habitats. So like ISRO, fish communities of VOYA lakes are a product of filtering by the local lake environment and the history of colonization, though for VOYA the faunal source pool evolved over time. Over the past century, this natural process has been disrupted by purposeful stocking of inland VOYA lakes with game fish, notably centrarchids (largemouth and smallmouth bass, bluegill, green sunfish, black crappie). Because baseline information on the status of inland VOYA lakes prior to the introduction of game fish is lacking, it is difficult to assess the impact of these perturbations, though our results suggest that the impacts thus far are not evident.

In contrast to the relative isolation and evolution of ISRO and VOYA lakes, SLBE lakes show a high degree of homogenization due to the high potential for dispersal between inland lakes and the Lake Michigan source pool. The high dispersal and recolonization potential of SLBE lakes diminishes the role of individual lake environments to act as filters.

Although Tonn's (1990) conceptual framework is primarily intended to understand assembly of inland lake fish communities, it has utility for identifying consequences of global warming on the composition of these communities. Because the time scale of anthropogenic-driven global climate warming is happening so quickly (<100 yr) relative to past natural climate warming (thousands of years), it represents a sharp perturbation of natural systems. Thus, we term the consequences of climate warming to inland lake communities as disassembly. Following on the heels of community disassembly will be community reassembly. For some areas, dispersal of fish into inland lakes following disassembly is highly unlikely (e.g., many VOYA and ISRO lakes), so that these communities will have permanent losses of species and the reassembled communities will be more simple. For many inland lakes of SLBE, dispersal is more likely, and reassembled communities are likely to reflect the changing composition of the regional Lake Michigan fauna. Again, reassembly will be determined by regional and local filters and by the actions of humans when they intervene and stock or move fish from place to place.

The mid-Holocene climate warming described in Davis et al. (2000) serves as an example of the effects of global warming. The mid-Holocene climate of VOYA favored warmwater and thermally tolerant species and disfavored cool- and coldwater species, and may have resulted in the depopulation of small lakes. It is likely that species were lost in small, shallow VOYA lakes with

little opportunity to recolonize. Climate change in ISRO was buffered by its location in Lake Superior, which allowed fish populations to persist in small lakes. So, after formation, ISRO lake communities may have been more stable because of an ameliorating climate. The effect of climate warming and possible species loss on SLBE lakes was countered by subsequent recolonization as a result of dispersal through stream connections between inland lakes and Lake Michigan. Thus, SLBE lake communities have had the opportunity to be reassembled repeatedly.

Across all regions, climate change resulted in shifts in distributional limits of species related to temperature tolerances. In the mid-Holocene, thermally tolerant species were able to colonize existing VOYA inland lakes that were accessible and to form reconstituted communities, or they colonized new lakes and became isolated due to isostatic rebound. Since 6,000 BP, the climate of the Great Lakes region has cooled, again shifting in favor of cool- and coldwater species, but barriers to dispersal and colonization that did not exist in the early Holocene have emerged. We hypothesize cycles of disassembly–reassembly may lead to loss of regional faunal diversity because changes in accessibility to faunal source pools restrict dispersal of species, and changes in lake environmental filters reduce colonization of species. The end result is reduced diversity of reassembled communities.

Changes in the potential for assembly–reassembly of inland lake communities during the Holocene suggest that the original post-glacial assembly was a unique process. The particular conditions following deglaciation and the available pool of colonizing species are not likely to be repeated until the next glaciation cycle. We also recognize that community assembly for inland lakes is not a one-time process, but one that operates in progressive steps. The first species that are able to colonize inland lakes are limited to those that can traverse periglacial lakes and their outlet streams and channels. Later, as drainages begin to form and the climate warms, other species are able to colonize lakes depending on their size and accessibility through outlet and interconnecting streams. Each lake has different accessibility to colonization and different thermal habitats that will determine the range of species able to colonize them. As climate continues to change or cycle, species may be lost and others will invade and may be able to colonize some inland lakes. In the case of ISRO and VOYA, many small lakes are perched in upland areas characterized by basaltic (ISRO) and granitic (VOYA) bedrock with either no outlet streams or highly intermittent small streams. Typically, many of these lakes are not accessible to future colonizations. SLBE lakes are located near the elevation of Lake Michigan and most are periodically connected to Lake Michigan and to each other by stream channels. Most of these lakes may be readily recolonized after climate-induced losses.

Assessment of the Effects of Anticipated Global Warming in the 21st Century

Kattenberg et al. (1996), Magnuson et al. (1997), and Kling et al. (2003) have predicted a 2°C–5°C increase in mean annual temperature for the Great Lakes region by 2090 as a result of global climate change. Summer surface temperatures of inland lakes are expected to increase 1°C–7°C, and inland lake levels are expected to decline as a result of warming and decreased rainfall. It is difficult to predict precise temperature changes for a specific lake because a number of factors determine lake temperature. The greatest impacts will be on small and shallow lakes; some small lakes may dry up and large shallow lakes may be substantially reduced in size. Fish communities will respond to

expected increased temperatures and loss of habitat. Impacts to coldwater and coolwater species are expected to be negative; impacts include reductions in abundance and distribution, and in some cases, regional extirpations. In contrast, the distribution and abundance of warmwater and thermally tolerant species are expected to increase, resulting in substantial changes in fish community compositions of some inland lakes. Direct mitigation of these expected impacts is not likely feasible, though restricting the introduction and distribution of warmwater species may be a good strategy for protecting remnant populations of cool and coldwater species. Davis et al. (2000) have suggested that the mid-Holocene climate change in the Great Lakes region was as warm as or warmer than the anticipated warming expected over the next century. However, the mid-Holocene warming was more gradual than the present situation and allowed for transition of communities, which minimized extinctions. Most of the warming from global climate change is expected to occur in a short time span (100 yr) and will likely result in many extinctions (Davis et al. 2000).

We used two approaches to assess the potential impact of 21st century climate change on the inland lakes of ISRO, VOYA, and SLBE. First, we applied the Minnesota Climate Change Model (Jacobson et al. 2010, 2013; Fang et al. 2012; Jiang et al. 2012) to the inland lakes and classified them as refuge and non-refuge lakes for coldwater species. Only tier 1 and tier 2 refuge lakes are likely to allow persistence of coldwater species through the end of the 21st century (Jacobson et al. 2010, 2013; Fang et al. 2012; Jiang et al. 2012). Tier 3 and tier 4 lakes are expected to undergo warming and lose coldwater and coolwater species but gain thermally tolerant and warmwater species as climate change progresses (Jacobson et al. 2010, 2013). In the second approach, we used the MCCM classification to identify inland lakes that would likely support heritage species and heritage communities in the face of 21st century climate change. Heritage species were defined as having limited distributions and representing early post-glacial colonizers; all coldwater fishes were considered heritage species, but some coolwater and thermally tolerant species were also considered heritage species. We defined heritage communities as containing assemblages of three or more coldwater or coolwater heritage species.

Across the three regions, the effect of climate warming on inland lakes is expected to result in thinning and warming of summer hypolimnia and increased frequency of winterkills, particularly in non-refuge lakes where coldwater and coolwater species are susceptible to loss. The combination of strong stratification, greater depth, and low productivity characteristic of refuge lakes should allow persistence of resident coldwater and coolwater species. The inland lake fish communities of ISRO are not expected to be as severely affected by climate change because ISRO's location within Lake Superior moderates its climate in contrast to the continental location of the inland lakes of VOYA (Magnuson et al 1997, Davis et al. 2000). Inland lakes of SLBE are already relatively warm compared to those of ISRO and VOYA, and although close proximity to Lake Michigan will likely ameliorate expected temperature increases (Davis et al. 2000), declining levels in Lake Michigan and declining water tables (Magnuson et al. 1997, Kling et al. 2003) are predicted to result in reductions in lake sizes, especially the smaller and shallower lakes.

Only five lakes in VOYA met MCCM criteria for tier 1 or tier 2 refuge lakes and contained heritage coldwater fishes (Cruiser, Little Trout, Locator, Mukooda, and War Club). Of these lakes, only

Cruiser clearly had sufficient oxythermal habitat at the lake bottom for coldwater fishes. The other VOYA candidate refuge lakes may have sufficient oxythermal habitat at higher strata in the hypolimnions but require additional measurement for verification. The long-term persistence of coldwater fishes in these lakes suggests that sufficient oxythermal habitat is present. Of the six candidate refuge lakes in VOYA, only Cruiser, Little Trout, and Mukooda contained heritage communities (three or more heritage species). Currently, populations of the coldwater heritage species lake trout in Cruiser are being maintained by natural reproduction and by stocking in Little Trout and Mukooda. The lake trout stock in Cruiser, one of the oldest inland VOYA lakes, may have been derived from colonization ca. 10,000 BP, the time when this lake was estimated to have become isolated. [*See Addendum at the beginning of this report.*]

In ISRO, only four lakes met the criteria as tier 1 and tier 2 refuge lakes and contained heritage coldwater fishes (Desor, Richie, Sargent, and Siskiwit), and of these only Siskiwit clearly had sufficient oxythermal habitat at the lake bottom. The other ISRO candidate refuge lakes may have sufficient oxythermal habitat at higher strata in the hypolimnion but require additional measurement for verification. As with VOYA, the presence of coldwater fishes in these ISRO candidate refuge lakes suggests that sufficient oxythermal habitat is present. However, recent surveys of one of these lakes (Richie) did not yield any cisco (J. Glase, personal communication), suggesting that this lake lacks sufficient oxythermal habitat and the coldwater species cisco may have disappeared due to early stages of climate warming. All four candidate refuge lakes in ISRO contained heritage communities. No lakes in SLBE met the criteria for refuge lakes and none contained coldwater fishes.

Each region contained one or more heritage species or communities in non-refuge lakes that were judged subject-to-loss as a result of climate change in the 21st century. Heritage coolwater species judged subject-to-loss and possible extirpation because of restricted distribution in one or two non-refuge lakes were represented by finescale dace in ISRO, muskellunge in VOYA, and brook stickleback, northern redbelly dace, northern longear sunfish, and blacknose shiner in SLBE. Non-refuge ISRO lakes Hatchet and Chickenbone contained heritage communities and were subject to losses of coolwater heritage species, but losses in these lakes would not result in extirpations because of the presence of their heritage species in refuge lakes. The heritage communities in non-refuge VOYA lakes Wiyapka and Shoepack were judged susceptible to loss of coolwater species, but losses in these lakes, with the exception of muskellunge in Shoepack, would be offset by species' presence in refuge lakes. Muskellunge is vulnerable to extirpation because of its presence in side-by-side non-refuge lakes Shoepack and Little Shoepack. No SLBE lakes contained more than two heritage species, thus SLBE did not contain any heritage communities. Of all the regions, SLBE is likely to suffer more losses and extirpations of heritage species as a result of climate change. However, it has the greatest potential for subsequent recovery because high interconnectedness among lakes and to Lake Michigan allows high rates of dispersal and colonization. But declining elevation of Lake Michigan and affected water tables with climate warming will likely cause SLBE lakes to become more isolated.

In each region, species most likely to be lost from smaller or shallower non-refuge lakes as a result of climate warming are northern pike, yellow perch, and blacknose shiner. These widespread coolwater species presently occur in the majority of lakes at ISRO and VOYA and are not considered heritage species. Climate warming will likely result in a reduction in the abundance and distribution of this assemblage in ISRO and VOYA lakes. In SLBE, this assemblage is present in only one lake (Otter), but one or more members of this assemblage (northern pike and yellow perch) are present in a majority of lakes. Climate change will likely hasten the displacement of these species by warmwater species largemouth bass, bluegill, and bluntnose minnow, which are already present in 13 of 19 SLBE lakes.

Expansion and invasion of warmwater and thermally tolerant species is another expected consequence of global climate change (Magnuson et al. 1997, Kling et al. 2003). Because ISRO is isolated within a large, cold Laurentian lake, colonization of coastal waters and inland lakes by warmwater and thermally tolerant species should be a rare event. The most likely avenue of colonization would be by accidental or purposeful introduction, but this, too, is unlikely because of the isolation of ISRO and its protection by the National Park Service. Thus, inland lake fish communities of ISRO are not expected to change substantially from expansion or invasion of warmwater and thermally tolerant species over the next century. VOYA presently has a number of warmwater species which were purposefully introduced into some inland lakes (e.g., smallmouth and largemouth bass) (Kallemeyn et al. 2003). As lake environments warm over the next century, conditions favorable to warmwater and thermally tolerant species will improve. Because of the connectedness of the large lakes of VOYA (KNR) to other large lakes and rivers in the Red River–Nelson River watershed, introductions and colonization of new species are expected to proliferate. Expansion of populations of warmwater species in KNR will increase the likelihood of accidental or purposeful introductions into the otherwise isolated inland lakes, resulting in a shift towards warmwater species dominated by largemouth bass and smallmouth bass, bluegill, and bluntnose minnow. As such, some inland lake fish communities of VOYA have the potential to become more like those found in SLBE, many of which are dominated by warmwater and thermally tolerant species, particularly largemouth bass, smallmouth bass, bluegill, and bluntnose minnow. Vigilance by natural resource managers can mitigate this outcome by stemming the proliferation of introduced species.

Because SLBE inland lakes already contain a full complement of warmwater and thermally tolerant species, no substantial changes in composition as a result of introductions or expansions are expected. However, most SLBE lakes are connected via stream channels to Lake Michigan and are subject to invasion by exotics. Already, SLBE lakes harbor a number of exotics that are present in Lake Michigan (see Table 2). In 2010, bighead carp was found in Lake Calumet, which is connected to Lake Michigan. Should this species spread throughout coastal waters of Lake Michigan, it will undoubtedly invade the larger inland lakes of SLBE that are connected via stream channels to Lake Michigan. SLBE lakes mostly likely to be affected include Loon, Otter, Fisher, and Little Traverse lakes. An interesting side note about the SLBE region: Round Lake is connected to Crystal Lake, which is where the State of Michigan introduced rainbow smelt in the early 1900s. Subsequently,

rainbow smelt escaped via the Betsie River outlet to Lake Michigan and then invaded all of the Great Lakes by the early 1930s.

Heritage Species and Communities

The heritage communities of each region are those communities that contain heritage species, defined as those species that likely colonized inland lakes during the early Holocene and/or and have limited distributions (see Tables 16–18). Communities in some of these lakes have been isolated for 2,000–10,000 years and represent unique natural resources. Protection of heritage communities is crucial to preserving regional biodiversity, especially in the face of pending global climate change over the next century. Many of these heritage communities and the unique populations they contain are likely to be as old as the estimated age of their formation; they are the result of the Wisconsin glacialiation, the final glacial period of the Pleistocene, which lasted ca. 100,000 years. A fish community is considered to have high heritage value when it contains three or more heritage species. Early Holocene colonizers with widespread distribution across ISRO, VOYA, and SLBE (e.g., northern pike, yellow perch, and blacknose shiner) are omitted from our exercise. Widespread post-glacial species are usually present in heritage communities and are therefore included by default.

Many of ISRO's inland lakes contain heritage species and communities and collectively represent a rich natural resource. In essence, each ISRO lake is like a genetic repository, capturing the genetic characteristics of each colonizing species at the time of lake formation, a time frame spanning centuries to more than 10,000 years. As discussed previously, the location of ISRO within Lake Superior has been buffered from periods of climate change in the mid-Holocene and should buffer the effects of future climate change, though our application of a modified MCCM to reflect that buffering suggests that there still may be losses in non-refuge lakes. Among those potential losses is the extirpation of the heritage coolwater species finescale dace, which is limited to two non-refuge lakes (John and Benson). Heritage coldwater species trout-perch is present in non-refuge lakes Hatchet and Whittlesey and thus subject to loss, though this species is present in refuge lakes. The remaining complement of ISRO heritage species are present in refuge lakes Desor, Richie, Sargent, and Siskiwit and are expected to persist through the period of climate warming. Communities in the oldest ISRO lakes represent unique natural resources. For example, Hatchet contains a heritage community estimated to be ca. 6,000 years old. The oldest ISRO fish community is contained in Lake Desor, which formed ca. 10,000 years ago from the time of Lake Minong, a precursor to Lake Superior. Thus, the fishes of Lake Desor represent relicts from the period before the formation of the upper Great Lakes. As mentioned previously, genetic studies have shown that lake whitefish in Lake Desor represent the ancestor to current lake whitefish populations in Lakes Superior and Huron (Stott et al. 2004). Other heritage species in Lake Desor are also likely to be similarly unique. Early stages of climate change may have already impacted refuge lake Richie; as noted in the previous section, recent surveys have failed to detect the presence of cisco, a heritage coldwater species that was found in previous surveys by Kallemeyn (2000) in the 1990s and Koelz (1929) in the 1920s.

Unlike ISRO, the continental climates in VOYA and SLBE have not buffered their lake communities from the effects of mid-Holocene climate change, and they are more vulnerable to the effects of future climate change. Like ISRO, the heritage coolwater and coldwater species of VOYA inland

lakes are likely to be genetically unique as most of these species were among the original colonizers >10,000 BP. Cruiser, the oldest VOYA lake, contains a community of 10 species that likely represents a genetic repository of post-glacial species from ca. 10,000 BP, the most notable being an endemic population of lake trout. Among the original colonizers of VOYA lakes is muskellunge in non-refuge Shoepack and Little Shoepack lakes, which represents a genetically unique population (Hanson et al. 1983, Fields et al. 1997, Frohnauer et al. 2007) that likely colonized these lakes 7,000–8,000 BP (see Figure 22). Also of interest are 19 species found in 10 VOYA lakes estimated to be >5,000 years old. Some coldwater, coolwater, and thermally tolerant species in VOYA lakes are likely to be more recent colonizers; examples of coldwater colonizers after 3,000 BP include cisco, lake trout, slimy sculpin, and burbot in lakes Little Trout, Locator, War Club, and Mukooda. The youngest and largest VOYA inland lake, Mukooda, was colonized ca. 1,200 BP and contains 15 native species, including the coldwater species just mentioned. As already mentioned, some VOYA lake communities have been despoiled by introductions, and losses due to global warming and further introductions and colonizations will likely change the character of many lakes toward warmwater communities. Fortunately, five VOYA lakes meet MCCM criteria as candidate refuge lakes (Cruiser, Little Trout, Locator, Mukooda, and War Club). Together, these lakes will likely retain a full complement of coolwater and coldwater fishes through the expected global warming over the next century. Thus, they represent the most valuable VOYA heritage communities for preservation of regional biodiversity.

Most populations of SLBE inland lake fishes are unlikely to be genetically unique because of the high degree of dispersal among lakes and the Lake Michigan source pool. Across the inland lakes of the upper Great Lakes, the dominance of the northern pike–yellow perch–blacknose dace assemblage will be diminished over the next century in favor of a largemouth bass–bluegill–bluntnose minnow assemblage. Many lakes at SLBE are already dominated by this same warmwater assemblage, and the presence of the northern pike–yellow perch–blacknose dace assemblage will likely be diminished further. No heritage communities exist in SLBE, though heritage coolwater species northern redbelly dace, brook stickleback, blacknose shiner, and northern longear sunfish occur, but mostly in smaller lakes. As previously discussed, these species are likely to disappear with the effects of climate change.

Recently, northern longear sunfish (*Lepomis peltastes*) (NLS) was elevated to full species status, separate from the central longear sunfish (*Lepomis megalotis*) (CLS) by Bailey et al. (2004). Extensive field sampling and genetic, morphological, and ecological evaluation of NLS in Minnesota supports the elevation to full species (Porterfield et al. 2008). NLS has a distribution that encompasses the post-glacial drainages of the Laurentian Great Lakes and overlaps considerably with the pumpkinseed (*Lepomis gibbosus*) (Scott and Crossman 1973, Lee et al. 1980, Trautman 1981). In Minnesota, NLS are small fish, requiring six growing seasons to reach 100 mm total length, and are restricted to clear, undisturbed lakes with vegetated shorelines (Porterfield et al. 2012). The lower peninsula of Michigan represents the center of the distributional range of NLS, where it is relatively common in clear, slow moving streams and clear lakes with vegetated shorelines (Bailey et al. 2004, Cook and Philipp 2009). However, the species has declined in the eastern, southern, and western portions of its range (Ontario and Quebec: Scott and Crossman 1973; Ohio: Trautman 1981;

Wisconsin: Becker 1983; New York: Smith 1985, Wells and Haynes 2007) and is rare in Minnesota (Porterfield et al. 2012). NLS were found in one VOYA lake (Mukooda) and two SLBE lakes (South Bass and North Bar). Given the restricted distribution of NLS and its sensitivity to habitat degradation (Porterfield et al. 2008, 2012), this species should be considered a heritage species and protected from overstocking with the larger-bodied CLS.

Conclusion

It is our hope that the information provided in this report will be useful in developing plans to conserve inland lake fish communities at ISRO, VOYA, and SLBE for the benefit of future generations. We caution that the success of preservation may be limited by the extent of climate change in the coming decades and centuries. Of concern is that climate change appears to be progressing faster than earlier model predictions, due largely to rapid world-wide economic development and sharp increases in carbon output since 2000 (Intergovernmental Panel on Climate Change 2014). Nevertheless, the preservation of heritage communities in the inland lakes of ISRO, VOYA, and SLBE for future generations will demonstrate the conviction, foresight, and wise stewardship of the current human generation.

Recommendations

Future Research and Monitoring

Our predictions for the persistence of heritage species and their communities in refuge lakes is predicated on climate warming being limited to $\leq 5^{\circ}\text{C}$ before 2090 and that conservation measures will be adopted to reduce anthropogenic habitat loss and nutrient loading and prevent introductions of non-indigenous species into inland lakes. In gathering environmental and biological data for this report it became very apparent that there are no regular monitoring programs for the inland lakes of ISRO, VOYA, and SLBE. Datasets for inland lake limnology and biological communities are often incomplete and there is little standardization for collection of data across the regions. This situation is not conducive to understanding the impacts of climate change, developing management and conservation plans to mitigate the effects of climate change, and evaluating the efficacy of management and conservation plans. To rectify this situation, we propose the following recommendations for research and monitoring of the inland lakes at ISRO, VOYA, and SLBE.

1. Though most of the inland lake fish communities of the three regions have been surveyed at least partially over the past 10–20 years, coordinated, timely, contemporary, and complete inventories are needed to establish a baseline for a long-term monitoring program to assess changes as climate change ensues. As for contemporary baselines, the most recent inventories of inland lakes were conducted in 2003–2006 at SLBE (Fessel 2007), 1995–1997 at ISRO (Kallemeyn 2000), and over more than a quarter-century (1975–2001) at VOYA (Kallemeyn et al. 2003). At a minimum, inland lakes need to be re-inventoried every 5-to-10 years. Sampling should strive to determine species richness (presence/absence) but not quantitative abundance. Thus, multiple sampling gears should be deployed to increase the likelihood of capturing all species present. Relative abundance indices can be generated based on frequency of presence across replicates of each sampling gear.
2. Fish communities in the connecting streams and rivers of inland lakes and in the coastal waters of large regional lakes should be surveyed every 5-to-10 years in conjunction with surveys of inland lakes. Complementary surveys of coastal waters and connecting streams serve to characterize the state of potential faunal source pools for inland lakes and provide advance information on changes in large systems as climate warming progresses. Coastal waters and embayments of ISRO represent the Lake Superior source pool for ISRO inland lakes. Coastal waters and embayments of Rainy, Namakan, and Kabetogama lakes represent the faunal source pool for VOYA inland lakes. Coastal waters and tributary streams of SLBE represent the Lake Michigan faunal source pool for SLBE inland lakes. Though natural dispersal from these potential source pools is lessened by the effects of climate change, the close proximity of adjacent water bodies increases the likelihood of anthropogenic introductions. Like inventories of inland lakes, surveys of coastal waters, embayments, and streams should focus on assessing species richness (presence/absence) and relative abundance (frequency of presence across replicates of each gear type).

3. Limnological surveys of inland lakes should be conducted during mid-summer in conjunction with community inventories to monitor changes in the environmental parameters as climate change ensues. Surveys should be conducted on all inland lakes every 5-to-10 years and annually on refuge lakes and a subset of non-refuge lakes. The annual surveys on selected lakes should consist of seasonal water column profiles of temperature and dissolved oxygen over a range of depths, and profiles should be conducted both day and night over a period of days. Assessment of summer nitrogen and phosphorus levels will more accurately establish the trophic status of each lake and the potential for biological oxygen demand (BOD) to deplete oxythermal habitat (TDO3) in summer and winter months. These measurements are required to estimate the amount of oxythermal habitat in each lake during seasons where TDO3 is at a minimum. Information from these surveys will be invaluable for modeling climate change (discussed below).
4. Development of climate models specific for each region is needed to better understand how future climate change in ISRO, VOYA, and SLBE will impact inland lake systems. Information from these models should be invaluable for formulating conservation measures and watershed management plans to protect regional biodiversity. Good examples of models that predict the effect of climate change include those for Minnesota inland lakes (Jacobson et al. 2010, 2013; Sharma et al. 2011; Fang et al. 2010, 2012). We have applied their models for Minnesota lakes to inland lakes of VOYA, ISRO, and SLBE with slight modification. However, our applications have not been validated by region-specific models.
5. Genetic characterization of heritage species in inland lakes is needed to better understand the uniqueness of these populations, their inter-relationships, and relationships to metapopulations. Deduced evolutionary relationships among populations and metapopulations will provide understanding of the timing of post-glacial isolation and subsequent evolution. Genetic characterization will provide support for conservation and protection of populations of heritage species to maintain biodiversity in the face of expected global warming and extirpation of populations.
6. Additional information on post-glacial history of each region is desirable to provide a more complete understanding of the changes that have occurred since the formation of each lake. For example, research to study sediment profiles of lakes can provide estimates of the lake ages and estimate of the times of community and climate change (e.g., Davis et al. 2000, Flakne 2003). The position of ISRO well inside the Lake Superior basin provides an excellent vantage to study post-glacial history since the close of the Wisconsinan, particularly the chronology of the Marquette advance and retreat. As noted by Huber (1973), additional field work on glacial geology in ISRO is needed as many investigators in the 20th century have relied on second-hand information, principally from field work conducted in the 1920s by Stanley (1932). Recent modeling of the glacial history of ISRO by Breckenridge (2013) has greatly improved understanding of post-Valders ice sheet advance that exited the Laurentian drainage ca. 9,000 BP. This work complements recent studies in the Thunder Bay region by Loope (2006) and Boyd et al. (2012) and in the Lake of the Woods–VOYA–

Boundary Waters region by Yang and Teller (2005). These studies used DEM (Digital Elevation Model) technology, which inputs high-resolution imagery from the SRTM (Shuttle Radar Topography Mission) and can reveal subtleties of complex glacial topographies. Though this remote sensing technology has provided new insights into glacial and post-glacial history, there is a great need for ground truthing and verification of glacial features by carbon-14 aging of organic material entrained in strandlines, particularly those at ISRO (A. Breckenridge, personal communication).

7. Field surveys/ground truthing of elevations of lake basins and outlets, connecting streams, and intermittent streams are needed to better understand the relative isolation of inland lakes from potential source pools for colonization/recolonization. VOYA and ISRO have DEMs based on SRTM and high-resolution LiDAR data. When imported into ArcView GIS, these data provide a good benchmark for designing follow-up field surveys. We have used low-resolution DEM data in GIS to estimate elevations of outlets and connecting channels of inland lakes.

Management and Conservation

Direct mitigation of the effects of climate change on inland lake environments is not likely feasible, though a number of management and conservation actions can potentially limit the effects of climate change on inland lake communities. Below we list management and conservation recommendations that are intended to reduce the loss of heritage species and heritage communities over the next century.

1. Protection of indigenous faunas from stocking, transfers, and invasions. Northern longear sunfish (*Lepomis peltastes*) are likely present in VOYA and SLBE, and these stocks should be protected from stocking of central longear sunfish (*Lepomis megalotis*). Stocking of native species, particularly lake trout, brook trout, and muskellunge, should not include stocks not indigenous to the area. Use of live bait for fishing should be discouraged, as this is a common avenue of interlake stock transfers and introduction of non-indigenous species and diseases.
2. Protection of lakes with coldwater species from loss of cold oxythermal habitat (TDO3). Lakes containing cisco, lake whitefish, and lake trout are subject to loss of oxythermal habitat with the onset of climate warming in the 21st century. Climate modeling of Minnesota inland lakes by Jacobson et al. (2010, 2013), Sharma et al. (2011), Fang et al. (2010, 2012) suggests that if these lakes remain oligotrophic, sufficient cold oxythermal habitat in hypolimnions will remain throughout the 21st century. The key to retaining oligotrophic conditions in inland lakes is the protection of lake watersheds from habitat disturbance and nutrient loading (Jacobson et al. 2010, 2013). We suggest developing watershed management plans for all lakes, especially refuge lakes, to address reduction of nutrient loading, siltation, and protection of watershed cover. Watershed plans should address the impact of land use practices and disturbances that increase erosion, siltation, and nutrient loading (e.g., trails, roads, human settlements, camping sites, latrines, and forest clearing). Ideally, watersheds should be maintained in a pristine natural state by minimizing human disturbance. Efficacy of

watershed management plans can be evaluated by long-term monitoring programs described in above in our recommendations for future research and monitoring.

3. Transfer heritage species at risk of loss from non-refuge lakes to refuge lakes. Heritage species finescale dace in ISRO and muskellunge in VOYA are restricted to two non-refuge lakes and are in jeopardy of extirpation. Consideration should be given to stock transfers of these species to refuge lakes to reduce the likelihood of extirpation. Transfers of heritage species northern redbelly dace, northern longear sunfish, and blacknose shiner in SLBE may not be effective because no lakes in SLBE currently meet criteria for refuge lakes. However, if a watershed management plan is developed and implemented for Narada and Little Traverse lakes and results in the creation of sufficient oxythermal habitat, stock transfers might be beneficial.
4. Management of fish stocks in each region should give priority to native fishes. In VOYA, there are a number of inland lakes with introduced game fish, particularly smallmouth bass and largemouth bass, which have the potential to result in the extirpation of native fishes in those lakes with the onset of climate change. Similar examples exist for SLBE lakes. We recommend cessation of stocking of game fishes in all inland lakes, and the development or modification of fishery management plans to enhance native fishes.

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Appendix I. Post-glacial History of Upper Great Lakes Region

Chronology of Ice Retreat and Connections Between Lake Agassiz, Upper Mississippi drainage, Lake Superior, and the VOYA and ISRO Regions

The uplands of the Voyageurs National Park region were covered by the Red River–Hudson Bay lobe of the Wisconsin-Laurentian Ice Sheet (LIS) until ca. 13,000 BP (years before present; ages reported in calendar years)¹ and then was subsequently inundated by Lake Agassiz until ca. 12,700 BP when the uplands emerged due to isostatic rebound and shifting position of Lake Agassiz northward and westward (Thorleifson 1996) and possible rapid draining through eastern outlets (Clayton 1983, Teller 1985, Thorleifson 1996, Leverington and Teller 2003), or through a northwest outlet to the Arctic Sea via the Mackenzie River (Minning et al. 1994, Teller et al. 2005, Teller and Boyd 2006, Fisher et al. 2006, Lowell et al. 2009, Murton et al. 2010). A readvance of the LIS ca. 11,400 BP (Marquette advance) blocked eastern outlets; Lake Agassiz rose and inundated most of the VOYA–Lake of the Woods region (Thorleifson 1996). When the Marquette advance began to retreat ca. 10,500 BP, eastern outlets reopened, Lake Agassiz fell, and the VOYA uplands began to reemerge as an archipelago and coalesced into larger islands by ca. 10,000 BP (Yang and Teller 2005). Over the course of deglaciation and subsequent inundation and dewatering, the VOYA region was colonized by fishes present in the proglacial lakes and rivers that formed at the margins of the LIS², and colonization of the higher elevation inland lakes likely occurred ca. 11,000–10,000 BP. Fishes of the Mississippian refuge had access to the VOYA–Lake of the Woods region during several phases of Lake Agassiz following initial deglaciation ca. 13,000 BP to final dewatering of VOYA highlands ca. 10,000 BP

Cass and Lockhart Phases, ca. 13,200–12,200 BP

As the LIS retreated northward, marginal Lake Agassiz formed (ca. 13,000–14,000 BP) and overflowed south into the Minnesota River (glacial Warren River) (Figure 4 in Clayton 1983, Figure 7c in Fenton et al. 1983; Fisher 2005, Dyke 2004). At the same time, marginal Lake Koochiching (a proglacial lake) formed in the area of VOYA and was filled with water flowing north from lower

¹ Throughout the literature on Quaternary science, age estimates of <65,000 BP are largely based on ¹⁴C dating methods and underestimate age in calendar years. Most of the literature reports ages in years based on ¹⁴C estimates unless otherwise noted. Readers will find much variation in estimates of calendar years but greater agreement in estimates of ¹⁴C years in the literature. Dyke (2004) provides a detailed revision of late and post-Wisconsinan glaciation based on improved radiocarbon dating with the advent of Accelerator Mass Spectrometry. Thus, many of the estimated ¹⁴C dates from publications predating the early 2000s are judged to be 500–2000 years older than revised estimates (Dyke 2004). Readers should be aware that the chronology of post-Wisconsinan glaciation will continue to be revised as new technologies and field studies yield more accurate estimates of the time of the retreat of ice sheets, isostatic rebound, and glacial lake outflows. For example, Breckenridge (2103) provides a revised chronology of the retreat of the Marquette advance over Lake Superior based on Digital Elevation Models (DEM) and LiDAR data.

² Appendix II provides a timetable for this account of the post-glacial history of VOYA.

Lake Agassiz through the McIntosh River outlet (Figure 4 in Clayton 1983, Figure 7c in Fenton et al. 1983). Lake Koochiching drained through the Prairie River outlet into Lake Upham-Aitkin during ca. 13,200–13,000 BP (Clayton 1983, Hobbs 1983), then through various outlets into the upper St. Louis River, then to the western tip of the Superior Lobe, and then through the St. Croix River to the Mississippi River. This sequence of connections and outlets provided early access for fishes from the upper Mississippian Refuge to proto-lakes and drainages of the Minnesota–Ontario border region. The fish communities of these proto-lakes and drainages served as the local source pool for fishes that would colonize the future inland lakes of VOYA, the Boundary Waters, the Rainy Lake system, and Lake of the Woods. After ca. 12,300 BP the McIntosh spillway was abandoned and the connection from lower Lake Koochiching to the St. Louis River ended (Figure 5 in Clayton 1983). Lake Koochiching merged with Lake Agassiz and became the Rainy Arm. During this period, the principal outlet for Lake Agassiz shifted to the south through the Minnesota River, and the highest uplands of the VOYA region first became dewatered due to isostatic rebound. Some researchers proposed a new eastern outlet may have formed through the Rainy Arm to the Kaministikwia River to Thunder Bay–Lake Superior following isostatic rebound that diminished flow through the southern outlet (Teller and Thorleifson 1983; Teller 1985; Leverington et al. 2000, 2002; Teller et al. 2002; Leverington and Teller 2003). Toward the end of the Lockhart phase (late Herman stage, after ca. 12,300 BP), these authors proposed that an outburst from this eastern outlet to Lake Superior resulted in a sharp drop in Lake Agassiz and triggered the start of the low Moorhead phase. However, this hypothesis has been challenged by a number of researchers for lack of sufficient evidence (Minning et al. 1994, Teller et al. 2005, Teller and Boyd 2006, Fisher et al. 2006, Lowell et al. 2009), and more recent evidence supports a northwest outburst through a Mackenzie River outlet to the Arctic Sea, which is hypothesized to have triggered the Younger-Dryas “mini-ice age” (Murton et al. 2010). Regardless of whether there was an outburst to Lake Superior, even a low-discharge eastern outlet would have allowed access for fishes of the St. Croix drainage and Lake Superior region to the VOYA–Rainy Lake–Lake of the Woods region.

Moorhead Phase, ca. 12,200–11,200 BP

Following a catastrophic release through east or northwest outlets, Lake Agassiz reached its smallest size since ca. 13,400 BP, the southern outlet to the Minnesota River was halted, and the higher uplands of VOYA were first dewatered as a result of isostatic rebound and the sharp drop in Lake Agassiz (Thorleifson 1996). The Younger-Dryas cold period (ca. 13,000–11,500 BP) largely coincided with the low water Moorhead Phase (Teller and Leverington 2004). The larger inland lakes of VOYA (proto-lakes Rainy, Kebetogama, and Namakan) remained contiguous with the Rainy Arm of Lake Agassiz. During this phase, the Rainy Arm may have developed an early eastern outlet through pro-glacial channels and lakes along the retreating face of the LIS to proto-Lake Nipigon, which then flowed out to Lake Superior (Clayton 1983). It was about this time that Isle Royale (southwest end) first emerged from Lake Superior but was soon reglaciated by a rapid readvance of the Laurentian Ice Sheet.

Emerson Phase, ca. 11,200–10,700 BP

The LIS advanced rapidly across the Nipigon and Superior basins ca. 11,200 BP (Marquette Phase, Superior Lobe) (Figure 7 in Clayton, 1983). Isle Royale was once again covered in ice. Eastern

outlets of Lake Agassiz through lakes Nipigon and Superior were blocked by ice, and after ca. 10,700 BP, the level of Lake Agassiz rose and expanded sufficiently to resume drainage south through the Minnesota River outlet (Teller et al. 2002; Fisher 2003, 2005). The resumption of the southern outlet was the result of rapid isostatic rebound along the northern margins of the basin that tilted the lake southward. As the level of Lake Agassiz rose, the Rainy Arm and the VOYA region were re-inundated. Modeling results that utilized sub-areal data collected by the space shuttle (Shuttle Radar Topography Mission) indicate that the VOYA highlands began to emerge ca. 11,000 BP and the emergent uplands approached modern margins by ca. 10,000 BP (Yang and Teller 2005).

Nipigon Phase, ca. 10,700–8,800 BP

The Nipigon Phase corresponds roughly with the Minong Phase of Lake Superior (Farrand 1969), though it slightly predates the opening of the Nipigon outlets (Teller and Thorleifson 1983). As the Superior lobe of the Marquette advance of the LIS retreated, the Lake Nipigon outlets once again reopened ca. 10,700 BP, resulting in a stepped decline in Lake Agassiz as water exited through a succession of outlets (Clayton 1983, Teller and Thorleifson 1983, Thorleifson 1996, Leverington and Teller 2003) and resulted in punctuated catastrophic flooding into the Lake Superior basin (Clayton 1983, Larson and Schaetzl 2001). The rise in Lake Superior resulted in flood waters flowing out through the Portage and Brule rivers and into the St. Croix River in the west, and across the middle Upper Peninsula through the Huron Mountain–Au Train spillway in the east (Clayton 1983). Subsequently, water levels rose in lakes Michigan and Huron and exited via the Chicago outlet in southwest Lake Michigan. The Lake Huron outlet via the Ottawa River (Ojibway–Barlow) to the Champlain Sea was supplemented by the Port Huron outlet of southern Lake Huron. The stepped lowering of Lake Agassiz during the Nipigon phase resulted in the abandonment of the Minnesota River outlet around ca. 10,500 BP (Fisher 2003, 2005), retraction of the Rainy Arm, and the formation of the proto VOYA lakes and drainage system by ca. 10,000 BP (Yang and Teller 2005).

By about 10,500 BP, the rapidly retreating LIS in the Lake Superior basin reached the southwest end of ISRO, paused in the vicinity of Lake Desor, and then rapidly retreated, deglaciating the remainder of the island by ca. 9,600 BP (Farrand 1969; Huber 1973; Saarnisto 1974, 1975; Boyd et al. 2012). However, Breckenridge (2013) provides a revised chronology based on a new analysis of strand lines utilizing DEM. The southwest end of ISRO was deglaciating ca. 11,000 BP, Lily Lake was isolated ca. 10,700 BP, and the island was fully deglaciating by ca. 10,500 BP. There appears to have been a ca. 50-year pause in the region of Lily Lake at ca. 10,800 BP. Lake Desor was isolated from Lake Minong during this interval, likely after 10,500 BP when lake levels dropped. After 10,500 BP, the LIS retreated rapidly in a northeasterly direction, deglaciating the Lake Superior basin by ca. 10,000 BP (Farrand 1969; Saarnisto 1974, 1975; Barnett 1992; Larson and Schaetzl 2001; Breckenridge 2013).

Ojibway Phase, ca. 8,800–8,400 BP

By ca. 8,800 BP, the retreating ice sheet and subsequent rebound in the Lake Nipigon basin shifted the outflow of Lake Agassiz north, disconnecting the Nipigon outlet and connecting eastward with the Ojibway–Barlow channel to the Champlain Sea. Around 8,400 BP the final Fidler stage of Lake

Agassiz emptied catastrophically northeast into the emerging Hudson Bay (Klassen 1983, Leverington et al. 2002, Teller et al. 2002, Dyke 2004).

Appendix II. Annotated Chronology of the Glacial History of the Laurentian Drainage.

“C¹⁴ yr” refers to estimation of age in years before present (BP) based on C¹⁴ aging. “Cal yr” refers to estimation of calibrated or corrected age in calendar years before present (BP). Readers should note some disparity in age estimates; these are reflections of changes in radiocarbon dating after the early 2000s (Dyke 2004).

C ¹⁴ yr (BP)	Cal yr (BP)	Event	References
18000–16000	21400–19100	Readvance of the Laurentian Ice Sheet (LIS); covers Great Lakes	Larson and Schaetzl (2001), Dyke (2004)
15500	18500	LIS retreats partially; marginal L Milwaukee forms in lower Michigan basin; marginal L Leverett present in Erie basin	Dyke and Prest (1987), Larson and Schaetzl (2001), Dyke (2004)
15000–14500	17900–17350	LIS readvances over Great Lakes	Larson and Schaetzl (2001), Dyke (2004)
14000–12500	16800–14400	L Chicago reforms in lower Michigan basin; L Maumee present in Erie basin	Larson and Schaetzl (2001), Dyke (2004)
12000	14100	Early L Algonquin forms in Huron basin, LIS retreats from S end of Ontario basin	Larson and Schaetzl (2001), Dyke (2004)
11500	13345	LIS readvances partially over Michigan and Huron basins, leaves no prominent end moraines, rapidly retreats	Hansel et al. (1985), Colman et al. (1994a, 1994b), Larson and Schaetzl (2001), Dyke (2004)
11700–11500	13200–13000	Early L Agassiz (Cass phase) forms at the margins of the retreating LIS in the Minnesota R basin. L Agassiz outlets include S to Mississippi R and N through McIntosh R to L Koochiching to L Upham–Aitkin and then S to the St Louis R and finally to the St. Croix R. Beginning of Holocene	Clayton (1983), Fenton et al. (1983), Hobbs (1983), Teller 1985, Thorleifson (1996), Larson and Schaetzl (2001), Leverington and Teller (2003), Fisher (2005), Hill (2007), Dyke (2004) suggests Cass phase of L Agassiz began earlier, ca. 12000 C ¹⁴ BP, ca. 14100 BP,
11600–10900	13000–12200	L Agassiz Lockhart phase, Alice and Trail stages, coalesces with L Koochiching (now the Rainy Arm), VOYA region deglaciated, L Agassiz Herman stages, S outlet, MacIntosh spillway abandoned, outlet through Rainy Arm to Kaministikwia R–Thunder Bay–L Superior develops,	Clayton (1983), Teller and Thorleifson (1983, 1987), Teller (1985), Thorleifson (1996), Leverington et al. (2000), Larson and Schaetzl (2001), Teller et al. (2002), Leverington and Teller (2003), Teller and Leverington (2004)
10900	12200	L Agassiz enters last Herman stage of Lockhart phase, outflow switches from S (Miss. R) to E (L Superior).	Clayton (1983), Teller 1985, Thorleifson (1996), Leverington, et al. (2000), Teller et al. (2002), Teller and Leverington (2004), Fisher (2005), Dyke (2004) suggests a more recent timing (ca. 10500 C ¹⁴ BP, ca. 12650 BP).

Appendix II (continued). Annotated chronology of the glacial history of the Laurentian drainage.

C¹⁴ yr (BP)	Cal yr (BP)	Event	References
10900	12250	L Agassiz outlet and/or outburst E to Lake Superior through Thunder Bay, previously S to Miss. R. Leverington et al. (2000), Teller et al. (2002), and Teller and Leverington (2004) suggest the rapid drawdown of L Agassiz at end of Lockhart phase (late Herman stage) was due to outburst E into L Superior (possible Younger Dryas trigger?)	Clayton and Moran (1982), Teller and Thorleifson (1983, 1987), Teller (1985), Leverington et al. (2000), Teller et al. (2002), Leverington and Teller (2003), Teller and Leverington (2004) also show a NW outlet ca. 11700 BP.
ca. 11000	ca. 13000	L Agassiz falls rapidly due to outburst, enters Moorhead phase, beginning of the Younger Dryas cold period.	Clayton (1983), Teller 1985, Thorleifson (1996), Larson and Schaetzl (2001), Teller and Leverington (2004), Lowell et al. (2005), Teller et al. (2005), Teller and Boyd (2006), Murton et al. (2010)
11000–10500	12750–12300	LIS retreats from S shore of L. Superior, Au Train outlet to L Michigan basin begins, L Algonquin approaches maximum and falls shortly thereafter, basins of some SLBE lake are formed, SW ISRO ice free for first time, but only for ca. 250 years.	Clayton (1983), Attig et al. (1985), Thorleifson (1996), Fenton et al. (2003), Larson and Schaetzl (2001), Leverington and Teller (2003), Lineback et al. (1979), Dyke (2004)
10800	12100	L Agassiz outburst E through Thunder Bay outlet to L Superior questioned, Thunder Bay under LIS, no outlet E to Superior?	Minning et al. (1994), Teller et al. (2005), Teller and Boyd (2006), Fisher et al. (2006), Lowell et al. (2009), Lowell and Fisher (2009), Carlson, et al. (2009), Murton et al. (2010)
10900	12100	L Agassiz southern Mississippi outlet first disrupted	Fisher (2003, 2005)
ca. 10700–10300	ca. 12100–11600	L Agassiz–Early Moorhead phases, outflow E (L Superior) – alternate timing	Leverington, et al. (2002), Leverington and Teller (2003)
10500–9500	12650–10750	Lake Algonquin drops with opening of Ottawa River outlets, rapid drop in lake level and outflow to St. Lawrence–Champlain Sea	Eschmann and Karrow (1985), Finamore (1985), Kaszycki (1985), Larsen (1987), Lewis and Anderson (1989, 1992), Lewis et al. (1994), Larson and Schaetzl (2001), Dyke (2004)
10200	11500	Outburst from Glacial Lake Algonquin into Champlain Sea (same as Cronin et al 2008)	Katz et al. (2011)
10100	11700	L Agassiz Emerson phase, Norcross stage, outflow switches from E (L Superior) to S (Miss. R) to NW (Mackenzie R)	Leverington, et al. (2000, 2002), Teller (2001), Teller et al. (2002), Leverington and Teller (2003), Teller and Leverington (2004)
10100	11400	Outburst from Glacial Lake Algonquin into Champlain Sea (same as Katz et al. 2011)	Cronin et al. (2008)
ca. 10000	ca. 11300	Evidence for L Agassiz Younger Dryas outburst through NW outlet to the Mackenzie River and then to the Arctic Sea	Murton et al. (2010) estimates 10000 C ¹⁴ BP, 11300 BP as the approx. date for L Agassiz outburst to the NW, consistent with Dyke (2004) maps.
ca. 10000	ca. 11500	End of Younger Dryas	Teller and Leverington (2004), Teller et al. (2005) Teller and Boyd (2006)

Appendix II (continued). Annotated chronology of the glacial history of the Laurentian drainage.

C¹⁴ yr (BP)	Cal yr (BP)	Event	References
10000	11220–11550	Marquette LIS advances (Valders Stade of the Wisconsinan Glaciation), covers Thunder Bay region blocking possible E outlet, Rainy Arm expands and inundates VOYA region.	Farrand (1969), Huber (1973), Saarnisto (1974, 1975), Clayton and Moran (1982), Attig et al. (1985), Farrand and Drexler (1985), Teller and Thorleifson (1983, 1987), Thorleifson (1996), Dyke (2004), Teller et al. (2005)
10000	11200	Marquette LIS advances S of Superior watershed, leaves prominent end moraine, Au Train outlet L Michigan basin ends	Lineback et al. (1979), Farrand and Drexler (1985), Dyke and Prest (1987), Lowell et al. (1999), Larson and Schaetzl (2001), Dyke (2004)
10000	11500	Marquette LIS advance reaches south shore, Superior split into lakes Duluth and Minong	Saarnisto (1974, 1975), Drexler et al. (1983), Dyke and Prest (1987), Dyke (2004), Boyd et al. (2012),
10000	11500	L Superior moraines laid down by Marquette LIS advance	Drexler et al. (1983), Lowell et al. (1999), Derouin et al. (2007), Hill (2007), Breckenridge (2013)
10000	11500	L Superior level controlled by end moraine Nadoway Pt–Gross Cap	Farrand and Drexler (1985), Yu et al. (2010)
11000–10000	12650–10500	Lake of the Woods basin emerges, VOYA uplands emerge as an archipelago 10500–11000 BP (Yang and Teller 2005), other estimates: ca. 10500 BP (Thorleifson 1996), ca. 11500 BP (Clayton 1983, Dyke and Prest 1987), ca. 10500 C ¹⁴ BP, ca. 12650 BP (Dyke 2004)	Clayton (1983), Dyke and Prest (1987), Thorleifson (1996), Dyke (2004), Yang and Teller (2005)
9900	11100	L Agassiz Emerson phase, Tintah–Norcross stages, outflow switches from NW (Mackenzie R) to S (Miss. R) back to NW	Clayton and Moran (1982), Clayton (1983), Leverington et al. (2002), Teller (2001), Teller et al. (2002)
9650	11000	L Minong outlet via Au Train outlet to L Michigan basin	Farrand (1969), Saarnisto (1975)
9600	11050–10950–	Rainy Arm of L Agassiz retreats, VOYA uplands begin to re-emerge	Dyke (2004)
9500	10700	L Agassiz NW outlet ended, S outflow through Minnesota R resumes (though Teller et al. (2002) suggest earlier outflows)	Fisher (2003, 2005, 2007), Teller (2001), Teller et al. (2002), note different chronologies between Fisher and Teller.
9500	10700	L Agassiz (Nipigon phase) outflow through Nipigon basin begins, Nipigon Phase corresponds roughly with the beginning of the Minong Phase of L Superior	Clayton (1983), Teller and Thorleifson (1983, 1987), Teller (1987), Dyke and Prest (1987), Teller and Mahnic (1988), Larson and Schaetzl (2001), Farrand (1969), Boyd et al. (2012)
9400	10500	L Agassiz Emerson phase, Upper Campbell stage, outflow switches from NW (Mackenzie R) to E (L Nipigon–L Superior)	Leverington, et al. (2002), Teller (2001), Teller et al. (2002)
9400	10500	L Agassiz S outlet to Mississippi R outlet abandoned, no further connection	Fisher (2003, 2005)
9400	10400	L Agassiz outlet through L Nipigon begins, Nipigon phase starts, Clayton (1983) estimates ca. 10,700 BP (different timing)	Clayton (1983), Leverington and Teller (2003), Dyke (2004) suggests slightly different dates: ca. 9500–9000 C ¹⁴ BP, ca. 10700–10200 BP
9300	10400	L Agassiz Nipigon phase, Lower Campbell stage, outflow is E (L. Superior)	Thorleifson (1996), Leverington, et al. (2002), Teller (2001), Teller et al. (2002)

Appendix II (continued). Annotated chronology of the glacial history of the Laurentian drainage.

C¹⁴ yr (BP)	Cal yr (BP)	Event	References
9600–9300	10500–11000	Marquette LIS retreats from Keweenaw Peninsula, reaches SW ISRO and Thunder Bay, Lake Duluth merges with Lake Minong, ISRO deglaciated by 11000 BP (Dyke 2004) vs. 10500 BP (Breckenridge 2013), ISRO Lily Lake isolated 10700 BP (Flakne 2003, Breckenridge 2013)	Saarnisto (1974, 1975), Boyd et al. (2012), Breckenridge (2013), Dyke (2004) presents older dates,
9300	10500	L Agassiz outflow to L Nipigon basin to L Superior, uplands of VOYA region dewatered for second time.	Teller and Thorleifson (1983, 1987), Teller and Mahnic (1988), Leverington and Teller (2003), Breckenridge et al. (2004, 2012), Dyke (2004), Yang and Teller (2005)
9200	10300	L Agassiz Nipigon phase, McCauleyville stage, outflow is E (L. Superior)	Leverington, et al. (2002), Teller et al. (2002)
9000	10100	L Superior late Minong phase, Beaver Bay stage, sharp drop in elevation, L Desor is isolated from L Superior	Farrand (1969), Huber (1973), Saarnisto (1974, 1975), Raymond et al. (1975)
9000–8400	10000–9000	Lakes Superior, Huron, Michigan drain via Ottawa R to Lampsillis L, upper St Lawrence lowlands	Dyke and Prest (1987), Dyke (2004) suggests older dates (ca. 9500–9000 C ¹⁴ BP, ca. 10700–10200 BP)
8900	10000	Rainy arm of L Agassiz retreats, Lakes Rainy, Namakan, Kabetogama isolated from L Agassiz, VOYA archipelago coalesces into larger islands	Dyke and Prest (1987), Yang and Teller (2005), Dyke (2004) suggests slightly older dating (ca. 9000 C ¹⁴ BP, ca. 10200 BP)
8900–8600	10000–9600	L Agassiz Nipigon phase, Hillsboro stage, outflow E to L Superior, Marquette LIS retreats toward N rim of L Superior basin	Farrand (1969), Saarnisto (1974, 1975), Barnett (1992), Larson and Schaetzl (2001), Leverington, et al. (2002), Teller et al. (2002)
8600–8400	9600–9400	ISRO deglaciated ca. 9500 BP, L Superior basin deglaciated, L Minong occupies Superior basin, last Minong shorelines develop ca. 9400 BP, Breckenridge (2013) proposes earlier chronology.	Farrand (1969), Huber (1973), Saarnisto (1974, 1975), Dyke (2004) suggests older deglaciation of ISRO: (ca. 9600 C ¹⁴ BP, ca. 10950 BP)
8500	9500	L Agassiz Nipigon phase, Burnside stage, outflow is E (L. Superior)	Leverington, et al. (2002), Teller et al. (2002)
8500	9500	L Agassiz (Nipigon phase) outflow through Nipigon basin ends (this chronology is different from Leverington and Teller (2003))	Clayton (1983), Teller and Thorleifson (1983, 1987), Teller (1987), Teller and Mahnic (1988), Larson and Schaetzl (2001), Dyke (2004)
8400–8000	9400–9000	L Superior (Minong phase) controlled by end moraine at Nadoway Pt – Gross Cap (eastern L Superior), fails and triggers catastrophic drop, regression, L Superior Houghton low water phase begins	Farrand (1969), Farrand and Drexler (1985), Boyd et al. (2012), Yu et al. (2010), Breckenridge (2013)
8200	9100	L Agassiz Nipigon phase, Pas stage, outflow is E (L Superior)	Leverington, et al. (2002), Thorleifson (1996), Teller et al. (2002)
8100	9000	Lake of the Woods fully isolated from L Agassiz,	Yang and Teller (2005), Dyke (2004) suggests older dating (ca. 9000 C ¹⁴ BP, ca. 10200 BP)

Appendix II (continued). Annotated chronology of the glacial history of the Laurentian drainage.

C¹⁴ yr (BP)	Cal yr (BP)	Event	References
8100	9100	Abrupt failure of end moraine in eastern L Superior, compare to Yu et al. (2010), end of Minong phase, beginning of Houghton phase	Loope et al. (2010)
8000	8800	L Agassiz outlet through L Nipigon ends, Nipigon phase–Pas stage ends, Ojibway phase–Gimli stage begins	Leverington and Teller (2003), Dyke (2004) suggests older dates (ca. 8500 C ¹⁴ BP, ca. 9500 BP)
7700	8400	L Agassiz Ojibway–Kinojevis–Fidler stage, outflow switches from L Superior farther E to Ottawa R	Leverington, et al. (2002), Teller et al. (2002)
7700	8600	L Agassiz Ojibway–Kinojevis–Fidler stage, outflow switches from L Superior farther E to Ottawa R	Leverington, et al. (2002)
7700	8400	Largest outburst from Hudson Bay, L Agassiz shrinks by 80%	Teller et al. (2002), Barber et al. (1999)
<7700	<8600	L Agassiz Ojibway–Fidler stage, final stage of Lake Agassiz, outflow switches from E (Ottawa R) to N (Hudson Bay)	Klassen (1983), Leverington, et al. (2002), Teller et al. (2002), Dyke (2004) suggest this switch occurred 7700–7600 C ¹⁴ BP (8450–8400 BP).
5500	6100	Outlets through Chicago R and Port Huron (S end of Huron)	Eschmann and Karrow 1985, Hansel et al. (1985), Farrand and Drexler (1985)
5500	6100	Nipissing Great Lakes forms, N. Bay outlet to Ontario R. closes due to isostatic rebound	Larson and Schaetzl (2001)
4100–4000	4600–4400	Nipissing II high–water phase	Arbogast and Loope (1999), Arbogast (2000), Loope and Arbogast (2000), Thompson et al. (2011), Boyd et al. (2012),
4500–3500	5000–4000	Nipissing high stand associated with bluff cutting and creation of large perched dunes that formed SLBE lake basins	Arbogast and Loope (1999), Arbogast (2000), Loope and Arbogast (2000), Larson and Schaetzl (2001), Thompson et al. (2011), Johnston et al. (2012)
<4000	<4400	Erosion of S Lake Huron outlet, lowering of Lake Nipissing levels, Nipissing Phase II ends	Arbogast and Loope (1999), Arbogast (2000), Loope and Arbogast (2000), Thompson et al. (2011), Boyd et al. (2012), Johnston et al. (2012)
3500	4000	Port Huron outlet down cuts, Chicago outlet abandoned, Michigan and Huron basins drop, end of Nipissing phase	Eschmann and Karrow (1985), Hansel et al. (1985), Thompson and Baedke (1997), Baedke and Thompson (2000), Larson and Schaetzl (2001)
<3000	<3500	Post–Nipissing formation of most SLBE inland lakes	Drexler (1974)
2200–1200	2300–1300	Rebound at Sault Ste Marie separates Superior from Huron and Michigan, Boyd et al. (2012) suggest more recent dating.	Farrand (1969), Farrand and Drexler (1985), Larson and Schaetzl (2001), Johnston et al. (2007), Boyd et al. (2012)
ca. 900	1060	Rebound at Sault Ste Marie separates Superior from Huron and Michigan	Johnston et al. (2012)

Appendix III. Morphometry and Limnology of 77 Inland Lakes at ISRO, VOYA, and SLBE.

Regn	Lake	Lake code	Spp rich.	Therm score	Lk Area (ha)	Wshd Area (ha)	LA / WA	Shore D	Zmax (m)	GR	Alk	Surf Temp (°C)	DO (ppm)	Hypo temp (°C)	Hypo DO (ppm)	Sp Cond	pH	Secchi (m)	Deg Day
ISRO	Ahmik	AHM	2	1.00	10.3	35.4	0.29	2.1	3.4	5.3	47.5	16.8	9.50	16.7	9.44	91.5	7.7	2.7	54
ISRO	Amygdaloid	AMY	3	1.00	10.8	26.1	0.41	2.7	8.8	2.1	32.5	17.7	6.49	8.1	0.30	64.5	7.7	3.5	54
ISRO	Angleworm	ANG	3	1.33	50.4	495.6	0.10	3.0	8.4	3.2	20.8	20.0	9.07	17.1	7.92	50.7	7.4	5.0	54
ISRO	Beaver	BEA	4	1.25	20.1	258.3	0.08	1.9	5.2	4.1	45.7	20.2	6.06	10.8	3.16	93.9	7.7	2.0	54
ISRO	Benson	BEN	4	1.00	24.1	83.0	0.29	1.8	3.8	5.8	29.0	20.7	9.45	20.6	9.46	57.4	7.6	2.0	54
ISRO	Chickenbone	CHI	10	1.20	92.6	1556.4	0.06	2.6	6.4	4.8	41.1	22.5	9.14	20.9	7.64	79.3	7.8	2.4	54
ISRO	Desor	DES	10	0.50	427.8	1436.7	0.30	1.8	14.0	3.2	46.7	20.2	6.19	10.4	0.26	88.1	7.9	3.5	54
ISRO	Dustin	DUS	5	1.40	4.4	497.8	0.01	1.7	6.1	2.4	28.2	19.8	5.96	10.6	0.37	56.8	7.7	2.5	54
ISRO	Epidote	EPI	2	1.00	1.3	55.8	0.02	1.2	4.0	2.7	34.0	17.0	5.83	14.9	3.59	68.3	7.4	2.5	54
ISRO	Eva	EVA	5	1.20	17.6	231.1	0.08	1.6	6.4	3.2	45.0	20.5	9.31	18.7	4.45	91.1	7.8	2.1	54
ISRO	Feldtmann	FEL	3	1.33	185.8	886.6	0.21	1.4	2.7	13.5	23.8	21.6	6.33	19.8	6.36	58.4	7.4	2.3	54
ISRO	Forbes	FOR	3	1.00	6.8	40.8	0.17	3.0	5.8	2.8	32.5	23.5	8.59	18.9	8.72	66.5	7.6	2.9	54
ISRO	George	GEO	2	1.00	3.8	18.1	0.21	2.0	2.7	5.2	52.3	20.1	6.05	19.6	6.04	91.6	7.9	2.7	54
ISRO	Halloran	HAL	7	1.25	77.4	230.7	0.34	1.4	2.7	11.0	22.5	20.5	6.18	20.1	6.11	50.7	7.4	2.7	54
ISRO	Harvey	HAR	4	1.33	55.4	292.8	0.19	1.7	4.0	6.8	39.2	24.2	9.95	24.0	9.85	66.0	8.9	3.8	54
ISRO	Hatchet	HAT	6	1.29	49.6	502.2	0.10	1.7	5.2	5.1	38.5	23.4	8.78	23.3	8.67	75.5	7.7	2.5	54
ISRO	Intermediate	INT	6	1.33	70.8	481.7	0.15	2.2	6.7	4.3	25.7	24.0	8.71	22.0	2.92	55.3	7.4	3.1	54
ISRO	John	JOH	5	1.20	3.3	126.4	0.03	1.8	5.5	2.5	53.5	18.5	6.65	9.3	0.92	99.5	7.8	3.0	54
ISRO	Lesage	LES	2	1.00	45.0	933.0	0.05	2.4	6.4	4.0	30.5	23.6	8.54	21.3	5.35	61.7	7.6	2.6	54
ISRO	Linklater	LIN	4	1.25	17.3	99.4	0.17	2.4	6.0	3.4	46.3	21.3	8.92	13.2	0.47	99.5	7.5	2.0	54
ISRO	Livermore	LIV	3	1.00	30.1	168.8	0.18	2.0	5.5	4.3	40.2	21.3	8.05	21.5	8.01	79.9	7.8	2.6	54
ISRO	Mason	MAS	5	1.20	22.8	492.8	0.05	2.3	8.5	2.6	26.3	20.3	9.06	8.1	0.22	58.6	7.5	2.6	54
ISRO	McDonald	MCD	2	1.00	14.8	104.9	0.14	1.8	4.0	4.9	44.1	21.5	5.88	19.5	5.38	88.7	7.7	2.1	54
ISRO	Otter	OTT	4	1.00	20.2	96.3	0.21	1.8	4.3	5.0	32.6	23.2	6.78	18.1	6.74	69.8	7.6	2.3	54
ISRO	Patterson	PAT	2	1.00	10.1	43.3	0.23	1.8	3.6	5.0	48.4	17.3	8.17	17.2	8.02	93.1	7.6	1.7	54
ISRO	Richie	RIC	12	1.00	216.2	2080.2	0.10	2.4	10.7	3.6	32.5	23.5	8.40	13.4	0.20	68.2	7.5	2.8	54
ISRO	Sargent	SAR	11	1.00	143.4	1089.3	0.13	3.6	13.7	2.5	39.7	20.3	8.89	6.7	0.39	84.5	7.7	4.5	54
ISRO	Scholts	SCH	3	1.00	2.3	469.3	0.00	2.1	1.5	8.1	34.2	20.4	5.62	20.4	5.62	68.2	7.7	2.5	54
ISRO	Shesheeb	SHE	4	1.25	11.5	155.1	0.07	1.9	5.5	3.4	45.1	21.0	7.63	13.5	4.01	96.7	7.5	1.5	54

Appendix III (continued). Morphometry and Limnology of 77 Inland Lakes at ISRO, VOYA, and SLBE.

Regn	Lake	Lake code	Spp rich.	Therm score	Lk Area (ha)	Wshd Area (ha)	LA / WA	Shore D	Zmax (m)	GR	Alk	Surf Temp (°C)	DO (ppm)	Hypo temp (°C)	Hypo DO (ppm)	Sp Cond	pH	Secchi (m)	Deg Day
ISRO	Siskiwit	SIS	15	0.67	1635.2	7287.1	0.22	2.2	46.0	1.4	30.1	19.5	7.90	5.0	8.80	65.0	7.9	9.0	54
ISRO	Wagejo	WAG	2	1.00	6.1	58.2	0.10	1.4	2.2	7.2	30.5	19.9	8.13	19.8	8.21	68.4	7.3	1.3	54
ISRO	Whittlesey	WHI	8	1.25	65.0	450.5	0.14	2.4	7.6	3.7	27.2	21.5	9.80	16.0	3.75	54.1	7.8	3.4	54
VOYA	Agnes	AGN	4	1.75	13.0	744.0	0.02	1.8	5.5	3.5	7.0	23.7	6.62	15.7	0.65	18.0	6.3	1.2	224
VOYA	Beast	BST	11	1.45	32.8	224.0	0.15	2.0	20.1	1.2	6.0	26.1	7.64	4.5	0.29	23.0	6.8	3.8	224
VOYA	Brown	BRN	4	1.25	30.8	645.0	0.05	2.1	8.2	2.9	5.0	26.2	7.77	8.3	0.40	13.0	7.1	2.4	224
VOYA	Cruiser	CRU	10	1.30	46.5	161.0	0.29	2.0	27.7	0.9	7.0	24.4	7.91	5.5	6.46	12.0	6.6	8.9	224
VOYA	Ek	EK	5	1.60	36.0	257.0	0.14	1.6	5.8	4.2	11.0	24.3	7.74	16.5	0.70	29.0	6.9	1.7	224
VOYA	Fishmouth	FSH	4	1.25	13.0	33.0	0.39	1.5	8.5	2.2	6.0	26.2	8.26	8.4	1.35	21.0	7.6	3.8	224
VOYA	Jorgens	JOR	4	1.50	24.7	172.0	0.14	1.8	5.8	3.8	12.0	26.2	7.53	19.6	0.64	24.0	6.5	3.6	224
VOYA	Lit. Shoepack	LSH	7	1.29	22.7	148.0	0.15	1.8	7.6	2.9	8.2	25.4	7.44	17.2	1.34	15.0	6.7	2.4	224
VOYA	Lit. Trout	LTR	14	1.57	96.7	253.0	0.38	1.8	29.0	1.1	11.0	25.2	8.06	4.4	1.05	27.0	7.7	7.4	224
VOYA	Locator	LOC	10	1.40	56.7	1231.0	0.05	2.5	15.9	1.7	6.0	25.7	7.80	6.0	2.59	16.0	6.4	3.5	224
VOYA	Loiten	LOI	4	1.75	36.6	289.0	0.13	1.6	14.9	1.6	8.2	24.9	7.74	5.5	1.58	24.0	6.9	3.0	224
VOYA	Lucille	LUC	7	1.43	53.0	156.0	0.34	1.6	5.8	4.7	8.2	25.2	7.70	22.3	9.67	22.0	7.1	3.1	224
VOYA	McDevitt	MDV	2	1.00	12.1	134.0	0.09	1.7	7.0	2.7	6.7	22.5	6.70	15.8	0.22	20.0	6.5	1.5	224
VOYA	Mukooda	MUK	20	1.90	305.0	754.0	0.40	1.3	23.8	1.8	16.0	28.1	8.19	7.2	0.69	44.0	7.3	6.0	224
VOYA	Net	NET	9	1.78	43.7	403.0	0.11	2.1	3.7	7.0	12.0	28.9	7.52	24.8	7.49	37.0	6.3	1.3	224
VOYA	O'Leary	OLE	8	1.88	78.5	275.0	0.29	1.2	17.1	1.7	28.0	24.2	8.05	6.1	0.32	55.0	8.0	5.3	224
VOYA	Oslo	OSL	4	1.25	42.5	493.0	0.09	2.4	11.0	2.3	6.0	26.4	7.38	6.6	2.16	13.0	7.5	2.3	224
VOYA	Peary	PEA	11	1.73	45.3	852.0	0.05	1.4	4.6	5.7	8.0	26.3	8.21	23.5	5.43	25.0	6.9	2.5	224
VOYA	Quarter Line	QUA	5	1.60	8.3	26.0	0.32	1.6	6.7	2.5	8.0	23.0	6.81	7.8	0.28	23.0	6.8	1.5	224
VOYA	Quill	QUI	7	1.71	34.4	554.0	0.06	1.9	14.0	1.7	6.0	25.4	7.77	5.1	2.68	23.0	7.2	5.0	224
VOYA	Ryan	RYA	6	1.17	14.2	99.0	0.14	1.7	3.7	5.3	5.0	25.9	7.59	23.3	4.45	25.0	7.0	2.8	224
VOYA	Shoepack	SHO	11	1.36	123.8	1992.0	0.06	2.4	7.3	4.6	6.0	24.5	7.30	22.1	0.80	12.0	6.2	1.5	224
VOYA	Tooth	TOO	4	1.00	23.5	172.0	0.14	1.8	13.1	1.7	8.0	24.5	7.65	5.1	0.76	29.0	7.1	3.4	224
VOYA	War Club	WAR	11	1.36	36.8	835.0	0.04	1.9	12.2	2.0	4.0	25.7	7.62	7.7	1.02	27.0	7.1	2.8	224
VOYA	Weir	WEI	4	1.50	26.8	781.0	0.03	1.7	2.4	9.3	7.3	22.5	5.70	19.1	0.92	20.0	6.4	1.0	224
VOYA	Wiyapka	WIY	7	1.29	20.2	269.0	0.08	1.3	5.2	4.1	9.5	22.5	6.90	15.0	0.30	32.0	6.7	1.0	224
SLBE	Bass South	BAS	16	2.07	10.9	74.5	0.15	1.3	7.9	2.3	128.0	24.8	9.12	18.8	14.55	304.0	8.7	3.6	448

Appendix III (continued). Morphometry and Limnology of 77 Inland Lakes at ISRO, VOYA, and SLBE.

Regn	Lake	Lake code	Spp rich.	Therm score	Lk Area (ha)	Wshd Area (ha)	LA / WA	Shore D	Zmax (m)	GR	Alk	Surf Temp (°C)	DO (ppm)	Hypo temp (°C)	Hypo DO (ppm)	Sp Cond	pH	Secchi (m)	Deg Day
SLBE	Bass North	BAN	12	2.08	37.6	1820.3	0.02	1.3	7.3	3.4	96.0	24.2	8.80	23.6	8.36	225.0	9.1	2.4	448
SLBE	Day Mill	DAY	3	1.00	2.3	119.3	0.02	1.2	1.2	10.3	186.0	23.8	0.95	23.8	0.95	385.0	7.3	0.5	448
SLBE	Deer	DEE	10	2.10	1.8	47.3	0.04	1.3	6.7	1.7	146.0	24.0	8.37	12.6	0.36	309.0	8.2	4.8	448
SLBE	Fisher	FIS	9	2.00	21.9	11146.8	0.00	1.6	4.6	4.7	128.0	24.2	9.20	24.2	9.35	268.0	8.6	4.6	448
SLBE	Florence	FLO	4	1.50	31.6	557.5	0.06	1.5	7.9	3.0	82.0	24.5	7.72	24.2	3.71	112.0	7.3	2.4	448
SLBE	Hidden	HID	5	1.60	0.6	55.1	0.01	1.2	1.0	8.8	98.0	23.6	7.86	23.6	7.86	209.0	8.6	0.4	448
SLBE	Long	LON	13	2.08	131.9	382.1	0.35	1.5	6.1	5.6	100.0	23.4	9.25	23.4	9.19	212.0	9.1	1.4	448
SLBE	Loon	LOO	22	2.20	37.2	3280.7	0.01	1.4	19.5	1.3	142.0	25.1	8.23	7.8	0.09	305.0	8.5	0.9	448
SLBE	Manitou	MAN	5	2.40	103.6	914.0	0.11	1.4	13.7	2.3	114.0	24.1	8.75	8.0	0.11	261.0	8.8	1.5	448
SLBE	Mud	MUD	12	2.00	21.5	60.5	0.35	1.2	1.0	21.5	146.0	28.6	6.16	28.6	6.16	398.0	8.6	0.5	448
SLBE	Narada	NAR	13	1.92	12.6	640.0	0.02	0.9	11.9	1.6	130.0	24.1	8.18	6.4	0.12	268.0	8.1	4.2	448
SLBE	North Bar	NBA	16	2.20	12.1	260.2	0.05	2.0	9.5	2.0	144.0	26.2	8.77	14.6	1.87	325.0	8.3	2.3	448
SLBE	Otter	OTR	18	2.06	25.9	240.5	0.11	1.3	6.4	3.5	134.0	24.8	9.01	24.6	8.43	299.0	8.5	2.8	448
SLBE	Round	ROU	13	2.15	6.1	26.0	0.23	1.2	7.9	2.0	186.0	25.9	8.24	20.9	1.07	329.0	8.7	2.9	448
SLBE	School	SCL	11	2.09	71.2	1681.4	0.04	1.2	4.7	6.2	98.0	26.6	9.21	21.3	1.20	233.0	8.5	1.3	448
SLBE	Shell	SHL	12	2.08	41.3	177.9	0.23	1.5	4.0	6.4	104.0	26.1	8.98	25.5	8.44	225.0	8.7	4.0	448
SLBE	Lit. Traverse	TRA	18	2.17	261.0	5015.2	0.05	1.3	16.5	2.4	128.0	23.7	8.60	15.2	2.75	354.0	8.3	3.2	448
SLBE	Tucker	TUC	9	2.00	6.9	157.2	0.04	1.3	3.7	4.4	128.0	26.7	8.77	25.1	8.54	281.0	8.4	2.0	448

Appendix IV. Elevations and Estimated Ages of Inland Lakes at ISRO and VOYA.

A. Elevations and estimated rebound rates and ages of inland lakes at ISRO.

Lake	Lake Code	Lake Area (ha)	Lake Elevation (m)	Elevation Above LS (m)	Elevation Minong Plane (m)	Estimated Rebound Rate (m/100 yr)	Estimate Age (yr) ¹	Estimated Age (yr) ²
Ahmik	AHM	10.3	192.7	9.5	41.0	0.90	1050	1034
Amygdaloid	AMY	10.8	187.0	3.8	38.0	0.87	434	427
Angleworm	ANG	50.4	240.5	57.3	36.0	0.85	6744	6606
Beaver	BEA	20.1	207.0	23.8	33.0	0.82	2910	2836
Benson	BEN	24.1	239.9	56.7	44.0	0.94	6059	6006
Chickenbone	CHI	92.6	184.4	1.2	34.0	0.83	145	141
Desor	DES	427.8	260.3	77.1	25.0	0.73	10542	10040
Dustin	DUS	4.4	198.0	14.8	33.0	0.82	1809	1763
Epidote	EPI	1.3	189.0	5.8	36.0	0.85	681	667
Eva	EVA	17.6	187.2	4.0	37.0	0.86	463	454
Feldtman	FEL	185.8	201.2	18.0	22.5	0.70	2553	2452
Forbes	FOR	6.8	236.0	52.8	37.0	0.86	6136	6020
George	GEO	3.8	203.9	20.7	33.0	0.82	2531	2467
Halloran	HAL	77.4	200.0	16.8	23.5	0.72	2347	2236
Harvey	HAR	55.4	232.3	49.1	32.0	0.81	6086	5919
Hatchet	HAT	49.6	229.9	46.7	30.0	0.78	5947	5756
Intermediate	INT	70.8	206.0	22.8	33.0	0.82	2788	2717
John	JOH	3.3	196.0	12.8	37.0	0.86	1486	1458
Lesage	LES	45	223.4	40.2	34.0	0.83	4853	4739
Linklater	LIN	17.3	222.2	39.0	37.0	0.86	4532	4446
Livermore	LIV	30.1	213.1	29.9	34.0	0.83	3609	3524
Mason	MAS	22.8	186.0	2.8	35.0	0.84	332	325
McDonald	MCD	14.8	213.0	29.8	34.0	0.83	3597	3512
Otter	OTT	20.2	213.0	29.8	33.0	0.82	3645	3552
Patterson	PAT	10.1	190.0	6.8	40.0	0.89	760	748
Richie	RIC	216.2	191.4	8.2	34.0	0.83	988	965
Sargent	SAR	143.4	212.0	28.8	36.0	0.85	3388	3319
Scholts	SCH	2.3	204.0	20.8	33.0	0.82	2543	2478
Shesheeb	SHE	11.5	222.0	38.8	36.0	0.85	4566	4472
Siskiwit	SIS	1635.2	201.0	17.8	30.0	0.78	2266	2193
Wagejo	WAG	6.1	228.9	45.7	36.0	0.85	5378	5268
Whittlesey	WHI	65	208.0	24.8	33.0	0.82	3033	2955
Lily	LIL	1.5	301.0	117.8	23.3	0.71	16522	15724
Ojibway	OJB	3.4	256.0	72.8	38.0	0.87	8357	8213

¹ These estimates assume a constant rate of rebound.

² These estimates assume a faster rate of rebound for 2,000 yr after deglaciation, slower rate after 2,000 yr.

B. Elevations and estimated ages of inland lakes at VOYA. Ages of all lakes were estimated using elevation above Rainy Lake and Brevik's (1994) rebound rate of 0.35775 m/100 yr.

Lake	Lake code	L Area (ha)	Elevation (m)	Elevation >Rainy (m)	Est. age (yr)
Agnes	AGN	13	348.44	10.44	2917
Beast	BST	32.8	366.74	28.74	8033
Brown	BRN	30.8	357.54	19.54	5461
Cruiser	CRU	46.5	378.94	40.94	11442
Ek	EK	36	345.34	7.33	2050
Fishmouth	FSH	13	351.44	13.44	3756
Jorgens	JOR	24.7	366.74	28.74	8032
Little Shoepack	LSH	22.7	369.74	31.74	8871
Little Trout	LTR	96.7	349.31	11.31	3160
Locator	LOC	56.7	348.46	10.46	2924
Loiten	LOI	36.6	360.65	22.65	6332
Lucille	LUC	53	377.30	39.30	10985
McDevitt	MDV	12.1	366.73	28.73	8030
Mukooda	MUK	305	342.29	4.29	1198
Net (Nett)	NET	43.7	347.52	9.52	2661
O'Leary	OLE	78.5	346.91	8.90	2489
Oslo	OSL	42.5	357.84	19.84	5545
Peary	PEA	45.3	342.34	4.34	1213
Quarter Line	QUA	8.3	357.84	19.84	5544
Quill	QUI	34.4	357.55	19.55	5465
Ryan	RYA	14.2	354.53	16.53	4620
Shoepack	SHO	123.8	363.65	25.65	7170
Tooth	TOO	23.5	360.92	22.92	6406
War Club	WAR	36.8	348.45	10.45	2922
Weir	WEI	26.8	351.42	13.42	3751
Wiyapka	WIY	20.2	360.62	22.62	6322
Kabetogama	--	--	339.33	1.32	--
Namakan	--	--	339.22	1.22	--
Rainy	--	--	338.04	0.00	--

Appendix V. Species Recorded From Inland Lakes at ISRO, VOYA, and SLBE.

X–Species present; L—at or near distributional limit; I—introduced to the region; i—introduced into inland lakes. Note that species classified as thermally tolerant or cool-warm receive the same thermal score. * Reported by Koelz (1929) and Hubbs and Lagler (1949). † Not reported as present in waters of Lake Superior by Bailey and Smith (1981).

Common Name	Genus	Species	Abbrev.	Species Code	Thermal Classif.	Thermal Score	ISRO	VOYA	SLBE
Sea lamprey	<i>Petromyzon</i>	<i>marinus</i>	Pmar	SEL	cold	0			I
Longnose gar	<i>Lepisosteus</i>	<i>osseus</i>	Loss	LNG	warm	3			L
Bowfin	<i>Amia</i>	<i>calva</i>	Acal	BOW	warm	3			X
Alewife	<i>Alosa</i>	<i>pseudoharengus</i>	Apse	ALE	cold	0			I
Coho	<i>Oncorhynchus</i>	<i>kisutch</i>	Okis	COH	cold	0			I
Chinook	<i>Oncorhynchus</i>	<i>tschawytscha</i>	Otsc	CHI	cold	0			I
Rainbow trout	<i>Oncorhynchus</i>	<i>mykiss</i>	Omyk	RBT	cold	0	coastal, i		
Brook trout	<i>Salvelinus</i>	<i>fontinalis</i>	Sfon	BKT	cold	0	X*		
Lake trout	<i>Salvelinus</i>	<i>namaycush</i>	Snam	LKT	cold	0	X	X	
Cisco	<i>Coregonus</i>	<i>artedi</i>	Cart	CIS	cold	0	X	X	
Lake whitefish	<i>Coregonus</i>	<i>clupeaformis</i>	Cclu	LWF	cold	0	X		
Round whitefish	<i>Prosopium</i>	<i>cylindraceum</i>	Pcyl	RWF	cold	0	coastal		
Central mudminnow	<i>Umbra</i>	<i>limi</i>	Ulim	CMM	cool	1	coastal †	X	X
Northern pike	<i>Esox</i>	<i>lucius</i>	Eluc	NPK	cool	1	X	X	X
Muskellunge	<i>Esox</i>	<i>masquinongy</i>	Emas	MUS	cool	1		X	
Common carp	<i>Cyprinus</i>	<i>carpio</i>	Ccar	CMC	warm	3			I
Rainbow smelt	<i>Osmerus</i>	<i>mordax</i>	Omor	RBS	cold	0	coastal, i		
Northern redbelly dace	<i>Phoxinus</i>	<i>eos</i>	Peos	NRD	cool	1	X	X	L
Finescale dace	<i>Phoxinus</i>	<i>neogaeus</i>	Pneo	FSD	cool	1	X	X	
Northern lake chub	<i>Couesius</i>	<i>plumbeus</i>	Cplu	NLC	cold	0	X		
Longnose dace	<i>Rhinichthys</i>	<i>cataractae</i>	Rcat	LND	cold	0	coastal		
Blacknose dace	<i>Rhinichthys</i>	<i>atratus</i>	Ratr	BND	cool	1	coastal †		
Pearl dace	<i>Margariscus</i>	<i>margarita</i>	Mmar	PLD	cool	1	X	X	
Creek chub	<i>Semotilus</i>	<i>atromaculatus</i>	Satr	CKC	thrm. tolerant	2	X		X
Golden shiner	<i>Notemigonus</i>	<i>crysoleucas</i>	Ncry	GDS	thrm. tolerant	2	X	X	X
Emerald shiner	<i>Notropis</i>	<i>atherinoides</i>	Nath	EMS	thrm. tolerant	2	X	X	
Blackchin shiner	<i>Notropis</i>	<i>heterodon</i>	Nhtn	BCS	cool	1	X		

Appendix V (continued). Species Recorded From Inland Lakes at ISRO, VOYA, and SLBE.

X—Species present; L—at or near distributional limit; I—introduced to the region; i—introduced into inland lakes. Note that species classified as thermally tolerant or cool-warm receive the same thermal score. * Reported by Koelz (1929) and Hubbs and Lagler (1949). † Not reported as present in waters of Lake Superior by Bailey and Smith (1991).

Common Name	Genus	Species	Abbrev.	Species Code	Thermal Classif.	Thermal Score	ISRO	VOYA	SLBE
Blacknose shiner	<i>Notropis</i>	<i>heterolepis</i>	Nhet	BNS	cool	1	X	X	X
Spottail shiner	<i>Notropis</i>	<i>hudsonius</i>	Nhud	STS	cool	1	X	X	X
Sand shiner	<i>Notropis</i>	<i>stramineus</i>	Nstr	SDS	warm	3			X
Mimic shiner	<i>Notropis</i>	<i>volucellus</i>	Nvol	MMS	thrm. tolerant	2	X	X	X
Common shiner	<i>Luxilus</i>	<i>cornutus</i>	Lcor	CMS	cool-warm	2		L	X
Hornyhead chub	<i>Nocomis</i>	<i>bigguttatus</i>	Nbig	HHC	cool-warm	2			X
Fathead minnow	<i>Pimephales</i>	<i>promelas</i>	Ppro	FHM	thrm. tolerant	2	X	X	X
Bluntnose minnow	<i>Pimephales</i>	<i>notatus</i>	Pnot	BNM	warm	3	coastal †	X	X
White sucker	<i>Catostomus</i>	<i>commersoni</i>	Ccom	WHS	thrm. tolerant	2	X	X	X
Longnose sucker	<i>Catostomus</i>	<i>catostomus</i>	Ccat	LNS	cold	0	coastal		
Northern redhorse	<i>Moxostoma</i>	<i>macrolepidotum</i>	Mmac	NRH	thrm. tolerant	2			X
Black bullhead	<i>Ameiurus</i>	<i>melas</i>	Amel	BLB	warm	3		L, i	X
Brown bullhead	<i>Ameiurus</i>	<i>nebulosus</i>	Aneb	BRB	warm	3		L, i	X
Yellow bullhead	<i>Ameiurus</i>	<i>natalis</i>	Anat	YLB	warm	3			X
Tadpole madtom	<i>Noturus</i>	<i>gyrinus</i>	Ngyr	TPM	thrm. tolerant	2		L	
Banded killifish	<i>Fundulus</i>	<i>diaphanus</i>	Fdia	BKF	cool	1			X
Brook silverside	<i>Labidesthes</i>	<i>sicculus</i>	Lsic	BSS	warm	3			X
Burbot	<i>Lota</i>	<i>lota</i>	Llot	BUR	cold	0	X	X	
Brook stickleback	<i>Culaea</i>	<i>inconstans</i>	Cinc	BSB	cool	1	X	X	X
Ninespine stickleback	<i>Pungitius</i>	<i>pungitius</i>	Ppun	NSB	cold	0	X		
Trout-perch	<i>Percopsis</i>	<i>omiscomaycus</i>	Pomi	TRP	cold	0	X		
Rock bass	<i>Ambloplites</i>	<i>rupestris</i>	Arup	RKB	cool-warm	2		X	X
Green sunfish	<i>Lepomis</i>	<i>cyanellus</i>	Lcya	GSF	warm	3		X, i	X
Pumpkinseed	<i>Lepomis</i>	<i>gibbosus</i>	Lgib	PKS	cool	1	X*	X	X
Bluegill	<i>Lepomis</i>	<i>macrochirus</i>	Lmac	BGL	warm	3		X, i	X
Northern longear sunfish	<i>Lepomis</i>	<i>peltastes</i>	Lpel	NLS	cool	1		L	X
Smallmouth bass	<i>Micropterus</i>	<i>dolomieu</i>	Mdol	SMB	warm	3		X, i	X
Largemouth bass	<i>Micropterus</i>	<i>salmoides</i>	Msal	LMB	warm	3		L, i	X
Black crappie	<i>Pomoxis</i>	<i>nigromaculatus</i>	Pnig	BLC	warm	3		X, i	X

Appendix V (continued). Species Recorded From Inland Lakes at ISRO, VOYA, and SLBE.

X—Species present; L—at or near distributional limit; I—introduced to the region; i—introduced into inland lakes. Note that species classified as thermally tolerant or cool-warm receive the same thermal score. * Reported by Koelz (1929) and Hubbs and Lagler (1949). † Not reported as present in waters of Lake Superior by Bailey and Smith (1991).

Common Name	Genus	Species	Abbrev.	Species Code	Thermal Classif.	Thermal Score	ISRO	VOYA	SLBE
Yellow perch	<i>Perca</i>	<i>flavescens</i>	Pfla	YLP	cool	1	X	X	X
Sauger	<i>Sander</i>	<i>canadense</i>	Scan	SAU	thrm. tolerant	2		X	
Walleye	<i>Sander</i>	<i>vitreum</i>	Svit	WLE	thrm. tolerant	2	X	X	
Logperch	<i>Percina</i>	<i>caprodes</i>	Pcap	LGP	thrm. tolerant	2	X	X	X
Iowa darter	<i>Etheostoma</i>	<i>exile</i>	Eexi	IOD	cool	1	X	X	X
Johnny darter	<i>Etheostoma</i>	<i>nigrum</i>	Enig	JOD	thrm. tolerant	2	coastal	X	X
Slimy sculpin	<i>Cottus</i>	<i>cognatus</i>	Ccog	SLS	cold	0	X	X	
Spoonhead sculpin	<i>Cottus</i>	<i>ricei</i>	Cric	SPS	cold	0	X		
Mottled sculpin	<i>Cottus</i>	<i>bairdi</i>	Cbai	MTS	cool-warm	2	coastal	X	X

Appendix VI. Species Records for the 32 Inland Lakes at ISRO with Two or More Species.

Lake and species codes are listed in Appendices III and V, respectively. Not listed is brook trout (*Salvelinus fontinalis*) which was found in two inland lakes (DES, HAT) by Koelz (1929) and reported in Hubbs and Lagler (1949).

Lake	Species																								Species Richness				
	CIS	LWF	LKT	NPK	NLC	PLD	GDS	EMS	BCS	BNS	STS	MMS	NRD	FSD	FHM	CKC	WHS	TRP	BUR	BKS	NSS	PKS	IOD	YLP		LGP	WAL	SLS	SPS
AHM	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
AMY	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
ANG	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	3
BEA	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
BEN	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	4
CHI	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	10
DES	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	10
DUS	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	5
EPI	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
EVA	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5
FEL	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	3
FOR	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
GEO	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
HAL	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
HAR	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	6
HAT	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	7
INT	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	6
JOH	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	5
LES	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
LIN	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
LIV	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
MAS	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	5
MCD	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
OTT	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
PAT	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2

Appendix VI (continued). Species Records for the 32 Inland Lakes at ISRO with Two or More Species.

Lake	Species																								Species Richness				
	CIS	LWF	LKT	NPK	NLC	PLD	GDS	EMS	BCS	BNS	STS	MMS	NRD	FSD	FHM	CKC	WHS	TRP	BUR	BKS	NSS	PKS	IOD	YLP		LGP	WAL	SLS	SPS
RIC	1	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0	1	0	12
SAR	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	11
SCH	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
SHE	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
SIS	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	1	1	15
WAG	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
WHI	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	8
Occurrences	4	2	1	26	1	5	9	1	2	20	9	1	3	2	2	1	13	5	1	5	2	4	2	30	2	3	3	2	29

Appendix VII (continued). Species records for the 26 inland lakes at VOYA with two or more species.

Lake	Species																										Species Richness																			
	NPK	GDS	BNS	STS	MMS	NRD	FHM	CKC	WHS	BKS	PKS	IOD	YLP	LGP	SEL	LNG	BOW	ALE	CHI	COH	CMM	BNM	CMC	CMS	HHC	SDS		NRH	BLB	BRB	YLB	BKF	BSS	MTS	BLC	BLG	GSF	LMB	NLS	RKB	SMB	JOD				
BAS	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	16
BAN	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	12		
DAY	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
DEE	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	10	
FIS	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	10	
FLO	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	
HID	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	5	
LON	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	14	
LOO	1	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	0	1	1	1	22	
MAN	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	7
MUD	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	12	
NAR	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	13	
NBA	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	16	
OTR	1	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	18	
ROU	0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	14	
SCL	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	11	
SHL	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	12	
TRA	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	1	0	0	0	1	0	1	1	1	0	0	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	1	20	
TUC	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	10		
Occurrences	15	3	3	3	3	1	2	1	9	2	15	10	15	2	1	1	2	4	1	2	6	15	2	3	3	8	1	1	8	3	9	1	2	4	15	1	15	2	13	11	10	36				

Appendix IX. Distances (km) Between Lakes at ISRO.

	AHM	AMY	ANG	BEA	BEN	CHI	DES	DUS	EPI	EVA	FEL	FOR	GEO	HAL	HAR	HAT
AHM		52.2	107.5	56.1	69.7	52.7	85.9	102.3	93.6	25.6	122.1	70.4	101.3	146.0	65.4	68.0
AMY	52.2		158.1	13.2	120.3	9.7	42.9	149.4	144.2	27.2	79.2	121.0	150.3	113.7	22.4	25.0
ANG	107.5	158.1		154.4	42.8	158.5	140.7	17.6	14.0	131.4	90.4	38.7	16.7	61.3	148.6	150.2
BEA	56.1	13.2	154.4		124.2	13.6	30.5	137.0	145.6	31.1	66.8	124.9	138.0	101.4	10.1	12.7
BEN	69.7	120.3	42.8	124.2		120.7	153.9	37.6	28.9	93.6	110.4	5.7	36.6	81.2	133.4	136.1
CHI	52.7	9.7	158.5	13.6	120.7		43.3	149.8	144.6	27.6	79.6	121.4	120.7	114.1	22.8	25.5
DES	85.9	42.9	140.7	30.5	153.9	43.3		123.3	131.9	60.8	53.1	154.6	124.2	87.7	24.7	26.3
DUS	102.3	149.4	17.6	137.0	37.6	149.8	123.3		8.8	126.2	73.0	33.6	1.2	43.9	131.2	134.2
EPI	93.6	144.2	14.0	145.6	28.9	144.6	131.9	8.8		117.5	81.6	24.9	7.8	52.5	139.7	141.3
EVA	25.6	27.2	131.4	31.1	93.6	27.6	60.8	126.2	117.5		97.1	94.3	125.2	131.6	40.3	43.0
FEL	122.1	79.2	90.4	66.8	110.4	79.6	53.1	73.0	81.6	97.1		106.3	74.0	37.4	61.0	62.6
FOR	70.4	121.0	38.7	124.9	5.7	121.4	154.6	33.6	24.9	94.3	106.3		32.6	77.2	134.1	136.8
GEO	101.3	150.3	16.7	138.0	36.6	120.7	124.2	1.2	7.8	125.2	74.0	32.6		44.9	132.1	133.7
HAL	146.0	113.7	61.3	101.4	81.2	114.1	87.7	43.9	52.5	131.6	37.4	77.2	44.9		95.5	97.1
HAR	65.4	22.4	148.6	10.1	133.4	22.8	24.7	131.2	139.7	40.3	61.0	134.1	132.1	95.5		6.9
HAT	68.0	25.0	150.2	12.7	136.1	25.5	26.3	134.2	141.3	43.0	62.6	136.8	133.7	97.1	6.9	
INT	119.8	147.2	35.1	135.6	55.1	147.6	121.1	17.7	26.3	143.7	70.9	51.0	18.7	41.8	129.0	130.6
JOH	90.2	140.8	18.0	144.4	25.5	141.2	135.9	11.9	4.1	114.1	85.6	21.5	10.9	56.5	143.7	145.3
LES	104.6	155.2	2.8	151.6	39.9	155.6	137.9	14.8	11.1	128.5	87.6	35.9	13.8	58.5	145.7	147.3
LIN	52.6	9.6	158.4	13.5	120.7	9.3	43.3	149.7	144.6	27.6	79.5	121.4	150.7	114.1	22.8	25.4
LIV	55.3	12.3	161.1	16.2	123.3	0.1	45.9	152.4	147.2	30.2	82.2	124.0	153.3	116.7	25.4	28.1
MAS	98.0	157.2	12.4	144.9	33.2	149.0	131.2	8.1	4.5	121.9	80.9	29.2	7.2	51.8	139.1	140.7
MCD	58.3	15.3	156.6	1.0	126.4	15.8	32.7	139.2	147.8	33.3	69.0	127.1	140.2	103.5	12.3	14.9
OTT	58.7	15.8	153.4	3.4	126.8	16.2	29.6	136.0	144.6	33.7	65.8	127.5	137.0	100.4	9.1	11.7
PAT	0.4	53.5	108.7	57.4	71.0	53.9	87.1	103.6	94.9	26.8	123.4	71.7	102.6	147.2	66.6	69.3
RIC	100.2	150.7	6.7	147.1	35.4	151.2	133.4	10.3	6.7	124.1	83.1	31.4	9.3	54.0	141.3	142.9
SAR	53.3	10.3	159.1	14.2	121.4	4.3	43.9	150.4	145.3	28.3	80.2	122.1	151.4	114.8	23.5	26.1
SCH	101.6	150.6	17.0	138.3	36.9	121.0	124.5	1.5	8.1	125.6	74.3	32.9	0.1	45.2	132.4	134.0
SHE	52.0	9.0	157.8	12.9	120.0	8.6	42.6	149.1	143.9	26.9	78.9	120.7	150.0	113.4	22.1	24.7
SIS	112.7	140.1	28.0	128.5	48.0	140.5	114.1	10.6	19.2	136.6	63.8	43.9	11.6	34.7	121.9	123.5
WAG	55.9	13.0	161.7	16.8	124.0	6.9	46.6	153.0	147.9	30.9	82.8	124.7	154.0	117.4	26.1	28.7
WHI	102.8	149.8	18.1	137.5	38.1	150.3	123.7	0.3	9.3	126.7	73.5	34.0	0.4	44.4	131.7	135.4

Appendix IX (continued). Distances (km) Between Lakes at ISRO.

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	INT	JOH	LES	LIN	LIV	MAS	MCD	OTT	PAT	RIC	SAR	SCH	SHE	SIS	WAG	WHI
AHM	119.8	90.2	104.6	52.6	55.3	98.0	58.3	58.7	0.4	100.2	53.3	101.6	52.0	112.7	55.9	102.8
AMY	147.2	140.8	155.2	9.6	12.3	157.2	15.3	15.8	53.5	150.7	10.3	150.6	9.0	140.1	13.0	149.8
ANG	35.1	18.0	2.8	158.4	161.1	12.4	156.6	153.4	108.7	6.7	159.1	17.0	157.8	28.0	161.7	18.1
BEA	135.6	144.4	151.6	13.5	16.2	144.9	1.0	3.4	57.4	147.1	14.2	138.3	12.9	128.5	16.8	137.5
BEN	55.1	25.5	39.9	120.7	123.3	33.2	126.4	126.8	71.0	35.4	121.4	36.9	120.0	48.0	124.0	38.1
CHI	147.6	141.2	155.6	9.3	0.1	149.0	15.8	16.2	53.9	151.2	4.3	121.0	8.6	140.5	6.9	150.3
DES	121.1	135.9	137.9	43.3	45.9	131.2	32.7	29.6	87.1	133.4	43.9	124.5	42.6	114.1	46.6	123.7
DUS	17.7	11.9	14.8	149.7	152.4	8.1	139.2	136.0	103.6	10.3	150.4	1.5	149.1	10.6	153.0	0.3
EPI	26.3	4.1	11.1	144.6	147.2	4.5	147.8	144.6	94.9	6.7	145.3	8.1	143.9	19.2	147.9	9.3
EVA	143.7	114.1	128.5	27.6	30.2	121.9	33.3	33.7	26.8	124.1	28.3	125.6	26.9	136.6	30.9	126.7
FEL	70.9	85.6	87.6	79.5	82.2	80.9	69.0	65.8	123.4	83.1	80.2	74.3	78.9	63.8	82.8	73.5
FOR	51.0	21.5	35.9	121.4	124.0	29.2	127.1	127.5	71.7	31.4	122.1	32.9	120.7	43.9	124.7	34.0
GEO	18.7	10.9	13.8	150.7	153.3	7.2	140.2	137.0	102.6	9.3	151.4	0.1	150.0	11.6	154.0	0.4
HAL	41.8	56.5	58.5	114.1	116.7	51.8	103.5	100.4	147.2	54.0	114.8	45.2	113.4	34.7	117.4	44.4
HAR	129.0	143.7	145.7	22.8	25.4	139.1	12.3	9.1	66.6	141.3	23.5	132.4	22.1	121.9	26.1	131.7
HAT	130.6	145.3	147.3	25.4	28.1	140.7	14.9	11.7	69.3	142.9	26.1	134.0	24.7	123.5	28.7	135.4
INT		30.3	32.3	147.6	150.2	25.6	137.1	133.9	121.0	27.8	148.3	19.0	146.9	1.6	150.9	18.2
JOH	30.3		15.2	141.2	143.8	8.5	146.9	147.3	91.5	10.7	141.9	11.2	140.5	23.2	144.5	12.6
LES	32.3	15.2		155.6	158.3	8.1	153.8	150.6	105.9	2.4	156.3	13.9	154.9	25.2	158.9	15.3
LIN	147.6	141.2	155.6		11.8	148.9	15.7	16.1	53.9	151.1	9.8	121.0	0.2	140.5	12.4	150.2
LIV	150.2	143.8	158.3	11.8		151.6	18.4	18.8	56.5	153.8	6.8	123.6	11.1	143.1	9.4	147.7
MAS	25.6	8.5	8.1	148.9	151.6		147.1	143.9	99.2	3.5	149.6	7.5	148.3	18.5	152.2	6.8
MCD	137.1	146.9	153.8	15.7	18.4	147.1		0.9	59.6	149.3	16.4	140.5	15.1	130.0	19.0	139.7
OTT	133.9	147.3	150.6	16.1	18.8	143.9	0.9		60.0	146.1	16.8	137.3	15.5	126.8	19.4	136.5
PAT	121.0	91.5	105.9	53.9	56.5	99.2	59.6	60.0		101.4	54.6	102.9	53.2	113.9	57.2	104.1
RIC	27.8	10.7	2.4	151.1	153.8	3.5	149.3	146.1	101.4		151.8	9.6	150.4	20.7	154.4	10.8
SAR	148.3	141.9	156.3	9.8	6.8	149.6	16.4	16.8	54.6	151.8		121.7	9.1	141.2	0.5	150.9
SCH	19.0	11.2	13.9	121.0	123.6	7.5	140.5	137.3	102.9	9.6	121.7		120.3	11.9	124.3	0.1
SHE	146.9	140.5	154.9	0.2	11.1	148.3	15.1	15.5	53.2	150.4	9.1	120.3		139.8	11.7	149.5
SIS	1.6	23.2	25.2	140.5	143.1	18.5	130.0	126.8	113.9	20.7	141.2	11.9	139.8		143.8	11.1
WAG	150.9	144.5	158.9	12.4	9.4	152.2	19.0	19.4	57.2	154.4	0.5	124.3	11.7	143.8		153.5
WHI	18.2	12.6	15.3	150.2	147.7	6.8	139.7	136.5	104.1	10.8	150.9	0.1	149.5	11.1	153.5	

Appendix X. Distances (km) Between Lakes at VOYA.

	AGN	BST	BRN	CRU	EK	FSH	JOR	LSH	LTR	LOC	LOI	LUC	MDV
AGN		27.9	77.4	31.6	48.7	80.4	50.6	96.0	58.4	137.8	144.6	67.9	30.3
BST	27.9		51.2	6.5	65.8	54.1	67.6	69.7	56.7	145.6	152.4	66.2	4.0
BRN	77.4	51.2		56.0	115.4	8.4	117.2	24.0	106.0	99.8	106.7	115.8	49.9
CRU	31.6	6.5	56.0		69.5	58.9	71.3	74.5	61.6	150.4	157.3	71.1	8.9
EK	48.7	65.8	115.4	69.5		118.3	2.9	133.9	96.3	90.1	96.9	105.8	68.2
FSH	80.4	54.1	8.4	58.9	118.3		120.1	18.1	109.2	94.0	100.9	118.7	52.9
JOR	50.6	67.6	117.2	71.3	2.9	120.1		135.7	98.1	90.9	97.8	107.6	70.0
LSH	96.0	69.7	24.0	74.5	133.9	18.1	135.7		125.4	92.8	100.0	134.3	68.5
LTR	58.4	56.7	106.0	61.6	96.3	109.2	98.1	125.4		185.3	192.2	12.7	59.1
LOC	137.8	145.6	99.8	150.4	90.1	94.0	90.9	92.8	185.3		4.7	194.8	144.3
LOI	144.6	152.4	106.7	157.3	96.9	100.9	97.8	100.0	192.2	4.7		201.7	151.2
LUC	67.9	66.2	115.8	71.1	105.8	118.7	107.6	134.3	12.7	194.8	201.7		68.6
MDV	30.3	4.0	49.9	8.9	68.2	52.9	70.0	68.5	59.1	144.3	151.2	68.6	
MUK	56.6	55.0	104.5	59.8	94.6	107.5	96.4	123.1	6.1	183.6	190.4	17.6	57.4
NET	16.0	18.6	71.5	26.7	54.0	74.4	55.8	89.0	75.0	143.0	149.8	85.9	24.3
OLE	29.3	27.7	77.2	32.5	67.3	80.2	69.1	95.8	29.9	156.3	163.1	39.4	30.1
OSL	78.7	52.4	0.2	57.2	116.6	9.6	118.4	25.2	107.2	101.1	107.9	117.0	51.2
PEA	75.1	48.8	2.7	53.6	113.0	6.0	114.9	21.6	103.6	97.5	104.3	113.4	47.6
QUA	50.2	67.3	116.8	71.0	2.5	119.8	1.5	135.4	97.7	90.6	97.4	107.2	69.7
QUI	142.6	150.4	104.7	155.3	94.9	98.8	95.8	97.6	190.2	2.7	0.8	199.7	149.2
RYA	65.8	39.5	12.6	44.4	103.7	15.5	105.5	31.2	94.6	107.0	113.9	104.1	38.3
SHO	93.1	66.9	21.1	71.7	131.1	15.3	132.9	0.3	122.5	95.6	102.5	131.5	65.6
TOO	15.3	19.2	68.7	24.0	53.2	71.7	55.0	87.3	72.2	142.2	149.1	81.7	21.6
WAR	139.9	147.8	102.0	152.6	92.2	96.2	93.1	94.9	187.5	0.1	279.0	197.0	146.5
WEI	26.7	1.6	51.2	3.6	64.7	54.1	66.5	69.7	56.7	145.6	152.4	66.2	68.9
WIY	14.3	20.2	69.7	25.0	52.2	72.7	54.0	88.3	73.2	141.2	148.1	82.7	22.6

Appendix X (continued). Distances (km) Between Lakes at VOYA.

	MUK	NET	OLE	OSL	PEA	QUA	QUI	RYA	SHO	TOO	WAR	WEI	WIY
AGN	56.6	16.0	29.3	78.7	75.1	50.2	142.6	65.8	93.1	15.3	139.9	26.7	14.3
BST	55.0	18.6	27.7	52.4	48.8	67.3	150.4	39.5	66.9	19.2	147.8	1.6	20.2
BRN	104.5	71.5	77.2	0.2	2.7	116.8	104.7	12.6	21.1	68.7	102.0	51.2	69.7
CRU	59.8	26.7	32.5	57.2	53.6	71.0	155.3	44.4	71.7	24.0	152.6	3.6	25.0
EK	94.6	54.0	67.3	116.6	113.0	2.5	94.9	103.7	131.1	53.2	92.2	64.7	52.2
FSH	107.5	74.4	80.2	9.6	6.0	119.8	98.8	15.5	15.3	71.7	96.2	54.1	72.7
JOR	96.4	55.8	69.1	118.4	114.9	1.5	95.8	105.5	132.9	55.0	93.1	66.5	54.0
LSH	123.1	89.0	95.8	25.2	21.6	135.4	97.6	31.2	0.3	87.3	94.9	69.7	88.3
LTR	6.1	75.0	29.9	107.2	103.6	97.7	190.2	94.6	122.5	72.2	187.5	56.7	73.2
LOC	183.6	143.0	156.3	101.1	97.5	90.6	2.7	107.0	95.6	142.2	0.1	145.6	141.2
LOI	190.4	149.8	163.1	107.9	104.3	97.4	0.8	113.9	102.5	149.1	279.0	152.4	148.1
LUC	17.6	85.9	39.4	117.0	113.4	107.2	199.7	104.1	131.5	81.7	197.0	66.2	82.7
MDV	57.4	24.3	30.1	51.2	47.6	69.7	149.2	38.3	65.6	21.6	146.5	68.9	22.6
MUK		73.3	28.1	105.8	102.2	96.0	188.4	92.9	120.2	70.5	185.8	55.0	71.5
NET	73.3		45.9	72.7	69.1	55.4	147.8	59.8	82.3	4.1	145.1	21.9	9.5
OLE	28.1	45.9		78.5	74.9	68.7	161.1	65.6	92.9	43.2	158.5	27.7	44.2
OSL	105.8	72.7	78.5		2.7	118.1	105.9	13.9	22.4	70.0	103.3	52.4	71.0
PEA	102.2	69.1	74.9	2.7		114.5	102.3	10.3	18.8	66.4	99.7	48.8	67.4
QUA	96.0	55.4	68.7	118.1	114.5		95.4	105.1	132.5	54.7	92.7	66.1	53.7
QUI	188.4	147.8	161.1	105.9	102.3	95.4		111.9	100.5	147.1	0.8	150.4	146.1
RYA	92.9	59.8	65.6	13.9	10.3	105.1	111.9		28.3	57.1	109.2	39.5	58.1
SHO	120.2	82.3	92.9	22.4	18.8	132.5	100.5	28.3		84.4	97.8	66.8	85.4
TOO	70.5	4.1	43.2	70.0	66.4	54.7	147.1	57.1	84.4		144.4	19.2	8.7
WAR	185.8	145.1	158.5	103.3	99.7	92.7	0.8	109.2	97.8	144.4		147.8	143.4
WEI	55.0	21.9	27.7	52.4	48.8	66.1	150.4	39.5	66.8	19.2	147.8		20.2
WIY	71.5	9.5	44.2	71.0	67.4	53.7	146.1	58.1	85.4	8.7	143.4	20.2	

Appendix XI. Distances (km) Between Lakes at SLBE.

	BAS	BAN	DAY	DEE	FIS	FLO	HID	LON	LOO	MAN	MUD	NAR	NBA	OTR	ROU	SCL	SHL	TRA	TUC
BAS		44.5	35.3	45.0	24.6	31.8	6.4	62.1	53.4	23.7	54.8	1.9	31.1	43.7	85.7	0.1	2.0	2.5	25.2
BAN	44.5		51.0	0.0	40.3	55.9	38.6	25.7	17.0	31.2	18.4	44.5	13.4	0.4	49.3	45.6	43.5	46.3	40.9
DAY	35.3	51.0		51.5	9.6	51.9	29.4	13.5	59.9	36.5	61.3	35.3	37.6	50.2	92.2	36.3	34.2	37.0	10.9
DEE	45.0	0.0	51.5		40.7	56.4	39.1	26.2	17.5	31.7	18.9	45.0	13.9	0.9	49.8	46.1	44.0	46.8	41.4
FIS	24.6	40.3	9.6	40.7		41.2	18.6	57.8	49.1	25.8	50.6	24.6	26.9	39.5	81.4	25.7	23.5	26.3	0.4
FLO	31.8	55.9	51.9	56.4	41.2		26.3	68.6	59.9	30.2	61.3	31.8	50.6	55.1	90.0	32.9	30.8	33.6	41.8
HID	6.4	38.6	29.4	39.1	18.6	26.3		56.2	47.5	18.6	48.9	8.3	25.2	37.8	79.8	7.5	5.4	10.0	19.3
LON	62.1	25.7	13.5	26.2	57.8	68.6	56.2		8.0	43.9	7.6	62.1	31.0	24.9	50.6	62.1	61.1	63.8	58.5
LOO	53.4	17.0	59.9	17.5	49.1	59.9	47.5	8.0		35.2	0.8	53.4	22.3	16.2	41.9	54.5	52.4	55.1	49.8
MAN	23.7	31.2	36.5	31.7	25.8	30.2	18.6	43.9	35.2		36.7	23.8	18.5	30.4	63.7	24.8	22.7	25.5	26.4
MUD	54.8	18.4	61.3	18.9	50.6	61.3	48.9	7.6	0.8	36.7		54.8	23.7	17.6	43.3	55.9	53.8	56.5	51.2
NAR	1.9	44.5	35.3	45.0	24.6	31.8	8.3	62.1	53.4	23.8	54.8		31.2	44.5	85.7	3.0	20.6	3.6	25.3
NBA	31.1	13.4	37.6	13.9	26.9	50.6	25.2	31.0	22.3	18.5	23.7	31.2		12.6	54.6	32.2	30.1	32.9	27.6
OTR	43.7	0.4	50.2	0.9	39.5	55.1	37.8	24.9	16.2	30.4	17.6	44.5	12.6		48.5	44.8	42.7	45.5	40.1
ROU	85.7	49.3	92.2	49.8	81.4	90.0	79.8	50.6	41.9	63.7	43.3	85.7	54.6	48.5		86.8	84.7	87.4	82.1
SCL	0.1	45.6	36.3	46.1	25.7	32.9	7.5	62.1	54.5	24.8	55.9	3.0	32.2	44.8	86.8		3.1	3.6	26.3
SHL	2.0	43.5	34.2	44.0	23.5	30.8	5.4	61.1	52.4	22.7	53.8	20.6	30.1	42.7	84.7	3.1		3.8	24.2
TRA	2.5	46.3	37.0	46.8	26.3	33.6	10.0	63.8	55.1	25.5	56.5	3.6	32.9	45.5	87.4	3.6	3.8		27.0
TUC	25.2	40.9	10.9	41.4	0.4	41.8	19.3	58.5	49.8	26.4	51.2	25.3	27.6	40.1	82.1	26.3	24.2	27.0	

Appendix XII. Detrended Correspondence Analysis (DCA) Community Scores, Species Scores, and Eigenvalues for 32 ISRO Inland Lake Communities with Two or More Species.

Results are shown for an 18-segment model which has the fewest segments for the level of variance explained.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Eigenvalues	Variance Explained	
Ahmik	0.00	0.98	Cisco	2.25	-0.66	Axis 1	0.587	49%
Amygdaloid	0.47	0.62	L.Whitefish	3.74	-1.03	Axis 2	0.315	75%
Angleworm	0.66	1.44	Lake.Trout	2.51	-0.59	Axis 3	0.153	87%
Beaver	0.11	0.91	N.Pike	-0.55	0.50	Axis 4	0.108	96%
Benson	1.59	1.49	L.Chub	5.02	-1.47	Axis 5	0.000	100%
Chickenbone	1.35	1.13	Pearl.dace	2.65	3.11			
Desor	3.15	0.65	Gold.Shiner	-0.79	0.09			
Dustin	0.94	1.64	Emer.Shiner	2.51	-0.59			
Epidote	0.00	0.98	Blackchin.Shiner	1.45	0.25			
Eva	0.37	0.70	Blacknose.Shiner	1.25	1.58			
Feldtmann	0.66	1.44	Spottail.Shiner	1.41	-0.11			
Forbes	1.48	2.05	Mimic.Shiner	1.85	-0.25			
George	0.00	0.98	NR.Dace	3.18	2.76			
Halloran	0.11	0.91	FS.Dace	1.94	-0.03			
Harvey	2.09	2.56	FH.Minnow	3.49	3.89			
Hatchet	3.04	2.80	Creek.Chub	4.82	4.05			
Intermediate	0.64	0.98	White.Sucker	1.98	2.36			
John	1.67	1.70	Trout-Perch	2.58	0.47			
Lesage	0.00	0.98	Burbot	2.51	-0.59			
Linklater	0.11	0.91	Br.Stickleback	2.61	2.97			
Livermore	0.42	1.18	NS.Stickleback	3.74	-1.03			
Mason	0.36	0.73	Pumpkinseed	1.33	0.01			
McDonald	0.00	0.98	Iowa.Darter	1.45	0.25			
Otter	0.66	0.86	Yel.Perch	0.55	1.46			
Patterson	0.00	0.98	Logperch	2.11	-0.34			
Richie	1.37	0.67	Walleye	1.46	2.28			
Sargent	1.12	0.49	Slimy.Sculpin	1.97	-0.39			
Scholts	0.42	1.18	Spnhead.sculpin	3.74	-1.03			
Shesheeb	0.11	0.91	Sum of Scores	62.75	17.91			
Siskiwit	2.15	0.00						
Wagejo	0.00	0.98						
Whittlesey	1.35	1.03						
Sum of Scores	26.40	35.83						

Appendix XIII. Canonical Correspondence Analysis (CCA) Community Scores, Species Scores, Environmental Variable Loadings, and Eigenvalues for 32 ISRO Inland Lake Communities with Two or More Species.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Environ. Variable	Axis 1	Axis 2	Eigenvalues	Variance Explained	
Ahmik	-0.610	0.403	Cisco	1.629	-1.562	L.area_log	0.777	-0.352	Axis 1	0.4273	43%
Amygdaloid	-0.365	0.181	L.Whitefish	2.908	0.513	Wshd.Area_log	0.672	-0.456	Axis 2	0.2343	66%
Angleworm	-0.366	0.220	Lake.Trout	3.820	2.112	Shore_D	0.140	-0.478	Axis 3	0.1418	80%
Beaver	-0.495	0.020	N.Pike	-0.576	0.312	Zmax_log	0.803	-0.359	Axis 4	0.0599	86%
Benson	-0.460	0.604	L.Chub	1.996	-1.086	Hypo_temp	-0.457	0.382	Axis 5	0.0390	90%
Chickenbone	-0.281	-0.964	Pearl.dace	-0.407	1.178	Secchi	0.729	-0.026	Axis 6	0.0000	90%
Desor	1.350	-0.001	Gold.Shiner	-0.287	-0.852						
Dustin	-0.448	0.037	Emer.Shiner	3.820	2.112						
Epidote	-0.610	0.403	Blackchin.Shiner	-0.390	-3.199						
Eva	-0.371	-0.036	Blacknose.Shiner	-0.473	0.127						
Feldtmann	-0.366	0.220	Spottail.Shiner	0.125	-0.262						
Forbes	-0.508	0.600	Mimic.Shiner	0.587	-2.729						
George	-0.610	0.403	NR.Dace	0.178	-0.381						
Halloran	-0.495	0.020	FS.Dace	-0.858	1.305						
Harvey	-0.299	0.754	FH.Minnow	-0.528	2.381						
Hatchet	0.008	0.754	Creek.Chub	-0.568	1.796						
Intermediate	-0.289	-0.054	White.Sucker	0.121	-0.145						
John	-0.452	0.592	Trout-Perch	1.123	-0.040						
LeSage	-0.610	0.403	Burbot	3.820	2.112						
Linklater	-0.495	0.020	Br.Stickleback	0.134	0.492						
Livermore	-0.564	0.311	NS.Stickleback	2.908	0.513						
Mason	-0.415	-0.540	Pumpkinseed	-0.098	-2.782						
McDonald	-0.610	0.403	Iowa.Darter	-0.390	-3.199						
Otter	-0.392	0.168	Yel.Perch	-0.643	0.493						
Patterson	-0.610	0.403	Logperch	1.800	0.909						
Richie	0.262	-0.722	Walleye	-0.667	-0.601						
Sargent	0.048	-1.163	Slimy.Sculpin	1.507	-1.720						
Scholts	-0.564	0.311	Spnhd.sculpin	2.908	0.513						
Shesheeb	-0.495	0.020									
Siskiwit	1.653	0.399									
Wagejo	-0.610	0.403									
Whittlesey	0.101	0.099									

Appendix XIV. Detrended Correspondence Analysis (DCA) Community Scores, Species Scores, and Eigenvalues for 26 VOYA Inland Lake Communities with Two or More Species.

Results are shown for a 10-segment model which has the fewest segments for the level of variance explained.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Eigenvalues	Variance Explained	
Agnes	1.013	1.612	Cisco	-0.413	-0.321	Axis 1	0.477	47%
Beast	2.614	0.579	Lake Trout	0.670	-0.956	Axis 2	0.315	80%
Brown	1.193	1.350	N. Pike	0.742	1.040	Axis 3	0.202	99%
Cruiser	2.001	0.543	Pearl dace	2.963	1.219			
Ek	0.810	1.402	Golden Shiner	1.667	1.884			
Fishmouth	0.884	1.022	Emer. Shiner	2.623	0.008			
Jorgens	1.354	0.916	Blacknose Shiner	1.567	2.304			
Little.Shoepack	2.030	1.206	Spottail Shiner	-0.076	2.958			
Little.Trout	0.810	0.040	Mimic Shiner	0.037	-0.620			
Locator	0.569	1.638	NR Dace	3.514	0.179			
Loiten	0.062	2.133	FS Dace	3.373	-0.315			
Lucille	1.731	0.996	FH Minnow	3.378	0.530			
McDevitt	0.685	1.476	White Sucker	1.833	0.142			
Mukooda	0.000	0.000	Brk. Stickleback	4.628	0.417			
Net	1.254	1.216	Pumpkinseed	0.035	2.512			
O'Leary	0.996	0.986	NLE Sunfish	-1.727	-1.283			
Oslo	1.193	1.350	Iowa Darter	2.693	-0.205			
Peary	1.238	1.108	Yellow Perch	0.628	1.913			
Quarter Line	1.151	1.785	Logperch	5.631	0.510			
Quill	0.338	2.338	Walleye	-0.429	-0.846			
Ryan	1.250	1.284	Slimy Sculpin	-1.727	-1.283			
Shoepack	2.288	0.799	Mudminnow	3.800	2.349			
Tooth	0.743	1.942	Bluntnose Minnow	0.177	-0.600			
Club	0.892	1.709	Common Shiner	-1.172	4.848			
Weir	1.773	1.289	Mottled Sculpin	-1.727	-1.283			
Wiyapka	3.859	0.495	Rock Bass	-0.478	1.975			
Sum of Scores	34.28	30.71	Johnny Darter	1.448	0.475			
			Muskellunge	2.860	1.185			
			Sauger	0.249	-1.167			
			Burbot	-1.727	-1.283			
			Pygmy Madtom	0.231	0.127			
			Sum of Scores	43.38	17.89			

Appendix XV. Canonical Correspondence Analysis (CCA) Community Scores, Species Scores, Environmental Variable Loadings, and Eigenvalues for 26 VOYA Inland Lake Communities with Two or More Species.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Environ. Variable	Axis 1	Axis 2	Eigenvalue	Variance Explained	
Agnes	-0.962	-0.458	Cisco	0.908	-0.299	L.area_log	0.659	0.376	Axis 1	0.319	32%
Beast	-0.855	0.076	Lake trout	1.265	0.818	Zmax_log	0.628	0.073	Axis 2	0.203	52%
Brown	-0.653	-0.311	N. pike	-0.251	-0.273	Alk	0.350	0.213	Axis 3	0.175	70%
Cruiser	-0.105	1.820	Pearl dace	-0.739	0.337	Hypo_temp	-0.440	0.259	Axis 4	0.092	79%
Ek	-0.340	-0.595	Gold shiner	-0.437	0.129	SpCond_log	0.457	-0.303	Axis 5	0.063	85%
Fishmouth	-0.004	-0.779	Emerald shiner	-0.258	1.333	Secchi	0.657	0.302	Axis 6	0.000	85%
Jorgens	-0.636	0.121	Blacknose shiner	-0.282	-0.111						
Little Shoepack	-1.456	1.712	Spottail shiner	0.105	-0.870						
Little Trout	1.422	0.645	Mimic shiner	0.468	-0.281						
Locator	0.273	-1.247	NR dace	-0.391	0.483						
Loiten	0.469	-1.422	FS dace	-0.098	0.429						
Lucille	-0.521	0.415	FH minnow	-0.480	-0.462						
McDevitt	-0.758	-1.005	White sucker	-0.068	0.267						
Mukooda	2.812	0.355	Brook stickleback	-0.587	-1.004						
Net	-0.377	-0.462	Burbot	2.248	0.083						
O'Leary	0.231	0.675	NLE sunfish	2.248	0.083						
Oslo	-0.653	-0.311	Pumpkinseed	0.119	-0.342						
Peary	-0.104	0.088	Iowa darter	-0.125	0.483						
Quarter Line	-0.942	-0.480	Yel perch	-0.234	-0.136						
Quill	0.682	-1.632	Logperch	-0.627	-1.320						
Ryan	-0.439	-0.092	Walleye	1.341	0.441						
Shoepack	-1.056	2.096	Slimy sculpin	2.248	0.083						
Tooth	-0.507	-1.059	Mudminnow	-0.202	-1.491						
War Club	0.182	-1.855	Bluntnose minnow	0.669	0.176						
Weir	-1.157	0.733	Common shiner	0.848	-1.021						
Wiyapka	-1.123	-2.024	Mottled sculpin	2.248	0.083						
			Rock bass	0.564	-0.390						
			Johnny darter	0.292	0.007						
			Muskellunge	-1.370	1.469						
			Sauger	1.174	0.463						
			Tadpole madtom	0.601	0.778						

Appendix XVI. Detrended Correspondence Analysis (DCA) Community Scores, Species Scores, and Eigenvalues for 19 SLBE Inland Lake Communities with Two or More Species.

Results are shown for a 12-segment model which has the fewest segments for the level of variance explained.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Species	Axis 1	Axis 2	Eigenvalues	Variance Explained
Bass.S	1.215	1.411	N.Pike	0.844	2.175	Bluegill	3.032	0.992	Axis 1 0.441	44%
Bass.N	1.530	1.208	Gold.Shiner	3.033	-0.068	Gr.Sunfish	-2.364	-0.870	Axis 2 0.209	65%
Day.Mill	1.179	2.888	Blacknose.Shiner	2.188	-0.601	LM.Bass	1.323	0.978	Axis 3 0.181	83%
Deer	1.510	0.961	Spottail.Shiner	-0.343	0.060	NLE.Sunfish	0.482	2.610	Axis 4 0.146	98%
Fisher	0.586	0.566	Mimic.Shiner	1.246	1.773	Rock.Bass	1.424	1.310	Axis 5 0.023	100%
Florence	0.544	0.973	NR.Dace	5.237	0.732	SM.Bass	0.268	-0.402		
Hidden	4.109	0.814	FH.Minnow	4.614	-0.617	Johnny.Darter	0.769	-0.146		
Long	1.323	0.426	Creek.Chub	0.431	-1.081	Sum of Scores	39.166	15.892		
Loon	0.853	0.296	White.Sucker	1.291	0.208					
Manitou	0.000	0.000	Br.Stickleback	4.631	1.971					
Mud	1.311	0.870	Pumpkinseed	3.032	0.992					
Narada	1.964	1.251	Iowa.Darter	0.159	1.214					
N.Bar	1.104	0.718	Yel.Perch	0.904	0.904					
Otter	1.154	0.326	Logperch	0.365	-1.707					
Round	1.803	0.234	LN.Gar	-0.287	-1.073					
School	1.552	1.299	Bowfin	-0.273	-1.658					
Shell	1.283	0.520	Mudminnow	1.515	3.600					
Traverse	0.868	0.077	Bluntnose.Minnow	1.052	0.504					
Tucker	1.517	1.680	Common.Shiner	-0.047	-1.466					
Sum of Scores	24.406	16.516	Hornyhead.Chub	-0.539	-0.940					
			Sand.Shiner	1.038	-0.790					
			N.Redhorse	-0.287	-1.073					
			Bl.Bullhead	0.619	3.813					
			Br.Bullhead	1.490	1.443					
			Yl.Bullhead	1.446	3.197					
			Banded.Killifish	1.278	0.017					
			Brook.Silverside	0.348	0.849					
			Mottled.Sculpin	-1.311	-1.557					
			Bl.Crappie	0.558	0.600					

Appendix XVII. Canonical Correspondence Analysis (CCA) Community Scores, Species Scores, and Environmental Variable Loadings for 19 SLBE Inland Lake Communities with Two or More Species.

Lake	Axis 1	Axis 2	Species	Axis 1	Axis 2	Environ. Variable	Axis 1	Axis 2	Eigenvalue	Variance Explained	
Bass.S	-0.297	-1.048	N.Pike	-0.237	0.153	L.area_log	0.781	-0.080	Axis 1	0.2067	21%
Bass.N	-0.154	0.028	Gold.Shiner	0.298	-0.465	Wshd.Area_log	0.452	0.487	Axis 2	0.1700	38%
Day.Mill	-2.083	1.349	Blacknose.Shiner	-0.517	-0.910	Zmax_log	0.676	0.015	Axis 3	0.0929	47%
Deer	-0.488	-1.002	Spottail.Shiner	-0.387	1.176	Hypo_temp	-0.337	-0.309	Axis 4	0.0600	53%
Fisher	0.007	1.011	Mimic.Shiner	0.122	-0.143	Secchi	0.280	-0.417	Axis 5	0.0000	53%
Florence	-0.019	-0.419	NR.Dace	-2.788	0.895						
Hidden	-5.840	1.441	FH.Minnow	-1.726	-0.174						
Long	0.658	-0.895	Creek.Chub	-0.226	-0.730						
Loon	0.461	2.548	White.Sucker	0.383	-0.075						
Manitou	2.997	0.404	Br.Stickleback	-1.156	0.704						
Mud	-0.250	-0.565	Pumpkinseed	-0.183	-0.100						
Narada	-0.649	0.349	Iowa.Darter	-0.099	-0.406						
N.Bar	-0.242	0.061	Yel.Perch	0.107	0.036						
Otter	0.202	-1.021	Logperch	1.495	-0.242						
Round	-0.385	-1.174	LN.Gar	0.189	2.164						
School	-0.336	0.071	Bowfin	1.048	1.172						
Shell	0.386	-0.916	Mudminnow	-0.624	0.306						
Traverse	1.573	0.505	Bluntnose.Minnow	0.148	-0.047						
Tucker	-0.937	0.342	Common.Shiner	0.623	0.538						
			Hornyhead.Chub	0.353	1.121						
			Sand.Shiner	0.250	-0.283						
			N.Redhorse	0.189	2.164						
			Bl.Bullhead	-0.108	-1.060						
			Br.Bullhead	0.004	0.317						
			Yl.Bullhead	-0.553	0.391						
			Banded.Killifish	0.178	-0.358						
			Brook.Silverside	-0.312	0.343						
			Mottled.Sculpin	1.831	0.407						
			Bl.Crappie	0.228	-0.592						
			Bluegill	-0.183	-0.100						
			Gr.Sunfish	1.754	0.633						
			LM.Bass	-0.066	-0.092						
			NLE.Sunfish	-0.210	-0.359						
			Rock.Bass	-0.103	0.076						
			SM.Bass	0.213	-0.069						
			Johnny.Darter	0.085	-0.231						

Appendix XVIII. Global Detrended Correspondence Analysis (DCA) Lake Community Scores and Eigenvalues for 77 Inland Lake Communities at ISRO, VOYA, and SLBE with Two or More Species.

Results are shown for a 10-segment model which has the fewest segments for the level of variance explained.

ISRO Lake	Axis 1	Axis 2	VOYA Lake	Axis 1	Axis 2	SLBE Lake	Axis 1	Axis 2	Eigenvalues	Variance Explained	
Ahmik	1.432	2.485	Agnes	1.756	2.232	Bass.S	0.354	1.444	Axis 1	0.5365	43%
Amygdaloid	1.647	2.839	Beast	2.609	0.584	Bass.N	0.223	1.465	Axis 2	0.3082	76%
Angleworm	1.805	2.045	Brown	2.019	1.882	DayMill	0.678	1.450	Axis 3	0.2605	100%
Beaver	1.982	2.022	Cruiser	2.462	1.548	Deer	0.264	1.242			
Benson	2.879	0.802	Ek	1.470	1.769	Fisher	0.412	2.040			
Chickenbone	2.089	1.938	Fishmouth	1.280	2.117	Florence	0.835	1.936			
Desor	4.309	2.417	Jorgens	1.291	1.914	Hidden	2.142	0.000			
Dustin	2.141	2.196	Lit. Shoepack	2.545	1.054	Long	0.462	1.581			
Epidote	1.432	2.485	Little Trout	1.670	2.233	Loon	0.024	1.774			
Eva	2.001	2.327	Locator	1.575	2.202	Manitou	0.635	2.129			
Feldtmann	1.805	2.045	Loiten	0.672	1.773	Mud	0.000	1.268			
Forbes	2.790	1.200	Lucille	1.952	1.105	Narada	0.846	1.206			
George	1.432	2.485	McDevitt	1.432	2.485	NorthBar	0.117	1.908			
Halloran	1.982	2.022	Mukooda	1.540	2.672	Otter	0.451	1.179			
Harvey	2.969	0.621	Net	1.733	1.396	Round	0.713	1.251			
Hatchet	3.504	0.341	O'Leary	1.882	1.919	School	0.012	1.493			
Intermediate	2.093	2.134	Oslo	2.019	1.882	Shell	0.278	1.380			
John	2.869	0.933	Pearry	1.611	1.620	Traverse	0.093	1.741			
LeSage	1.432	2.485	Quarter Line	1.982	2.022	Tucker	0.174	1.201			
Linklater	1.982	2.022	Quill	0.751	1.573						
Livermore	1.841	2.120	Ryan	1.592	1.540						
Mason	1.679	1.806	Shoepack	2.635	1.053						
McDonald	1.432	2.485	Tooth	1.497	1.825						
Otter	1.900	2.477	War Club	1.431	2.007						
Patterson	1.432	2.485	Weir	2.666	1.275						
Richie	2.350	2.292	Wiyapka	2.545	0.387						
Sargent	2.134	2.361									
Scholts	1.841	2.120									
Shesheeb	1.982	2.022									
Siskiwit	3.286	3.377									
Wagejo	1.432	2.485									
Whittlesey	2.463	2.620									

Appendix XIX. Global Detrended Correspondence Analysis (DCA) Species Scores for 53 Species from 77 Lakes at ISRO, VOYA, and SLBE with Two or More Species.

Results are shown for a 10-segment model which has the fewest segments for the level of variance explained.

Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
Cisco	3.330	3.774	Spnhd_sculpin	5.136	4.418
L.Whitefish	5.136	4.418	LN_Gar	-1.127	2.688
Lake_Trout	3.190	3.902	Bowfin	-1.072	2.781
N._Pike	1.222	2.649	Mudminnow	0.134	0.252
L._Chub	5.774	3.474	Bluntnose_Minnow	-0.176	1.604
Pearl_dace	4.069	-0.112	Common_Shiner	-0.632	1.321
Gold.Shiner	2.404	1.727	Hornyhead_Chub	-0.855	3.010
Emer.Shiner	3.482	3.190	Sand_Shiner	-0.706	1.109
BlackChin_Shiner	2.828	3.430	N.Redhorse	-1.127	2.688
Blacknose_Shiner	2.660	1.391	Bl.Bullhead	-0.494	1.341
Spottail_Shiner	2.078	3.549	Br.Bullhead	-0.702	0.734
Mimic_Shiner	0.411	2.818	Yl.Bullhead	-0.854	0.869
NR_Dace	3.802	-0.291	Banded_Killifish	-0.704	1.007
FS_Dace	3.422	-0.101	Brook_Silverside	-0.911	3.214
FH_Minnow	3.096	-0.633	Mottled_Sculpin	0.068	3.579
Creek_Chub	2.857	-0.652	Bl.Crappie	-0.658	0.854
White_Sucker	2.551	1.166	Bluegill	-0.448	0.389
Trout-Perch	4.358	3.311	Gr.Sunfish	-0.115	3.456
Burbot	3.526	4.769	LM_Bass	-0.639	1.030
Br.Stickleback	3.795	-0.404	NLE_Sunfish	-0.023	3.437
NS.Stickleback	5.136	4.418	Rock_Bass	-0.091	2.059
Pumpkinseed	0.466	0.940	SM_Bass	-0.531	2.002
Iowa_Darter	1.009	0.773	Johnny_Darter	0.464	1.405
Yel_Perch	1.642	2.321	Muskellunge	3.480	0.115
Logperch	2.559	3.117	Sauger	2.103	3.210
Walleye	2.632	3.453	Tadpole_Madtom	2.355	2.847
S_Sculpin	3.283	4.256			

Appendix XX. Global Canonical Correspondence Analysis (CCA) Species Scores, Environmental Variable Loadings, and Eigenvalues for 77 Inland Lake Communities at ISRO, VOYA, and SLBE with Two or More Species.

Species	Axis 1	Axis 2	Species	Axis 1	Axis 2	Environ. Variable	Axis 1	Axis 2	Eigenvalue	Variance Explained	
Cisco	0.815	0.998	Mudminnow	-1.137	-0.362	L.area_log	0.125	0.666	Axis 1	0.369	37%
L.Whitefish	1.135	2.535	Bluntnose_Minnow	-0.812	0.188	Wshd.Area_log	-0.074	0.535	Axis 2	0.633	63%
Lake_Trout	0.824	1.520	Common_Shiner	-0.808	0.569	Shore_D	0.591	-0.049	Axis 3	0.764	76%
N._Pike	0.260	-0.335	Hornyhead_Chub	-1.179	0.872	Zmax_log	0.031	0.596	Axis 4	0.855	85%
L._Chub	0.679	1.744	Sand_Shiner	-1.146	0.280	Alk	-0.727	0.210	Axis 5	0.937	93%
Pearl_dace	0.688	-0.481	N.Redhorse	-1.651	0.476	Temp	-0.563	0.121			
Gold.Shiner	0.380	-0.307	Bl.Bullhead	-0.122	-0.169	Hypo_temp	-0.201	-0.270			
Emer.Shiner	0.889	0.712	Br.Bullhead	-1.177	0.208	SpCond_log	-0.592	0.218			
BlackChin_Shiner	1.497	0.452	Yl.Bullhead	-0.930	-0.287	pH	-0.463	0.293			
Blacknose_Shiner	0.579	-0.446	Banded_Killifish	-1.004	0.206	Secchi	0.162	0.487			
Spottail_Shiner	0.563	0.164	Brook_Silverside	-1.144	-0.276						
Mimic_Shiner	-0.081	0.354	Mottled_Sculpin	-0.764	1.390						
NR_Dace	0.504	-0.274	Bl.Crappie	-0.685	0.312						
FS_Dace	0.702	-0.278	Bluegill	-1.036	0.022						
FH_Minnow	-0.068	-0.798	Gr.Sunfish	-0.586	1.147						
Creek_Chub	-0.262	-0.124	LM_Bass	-0.649	-0.034						
White_Sucker	0.273	0.061	NLE_Sunfish	-0.734	0.267						
Trout-Perch	0.956	1.086	Rock_Bass	-0.628	0.063						
Burbot	1.591	3.326	SM_Bass	-0.595	0.314						
Br.Stickleback	0.210	-0.211	Johnny_Darter	-0.296	0.072						
NS.Stickleback	1.135	2.535	Muskellunge	0.647	-0.726						
Pumpkinseed	-0.274	-0.171	Sauger	0.859	0.828						
Iowa_Darter	-0.039	-0.073									
Yel_Perch	0.355	-0.328									
Logperch	0.356	0.974									
Walleye	0.666	0.260									
S_Sculpin	1.010	1.555									
Spnhd_sculpin	1.135	2.535									
LN_Gar	-1.651	0.476									
Bowfin	-1.385	1.176									

Appendix XXI. Global Canonical Correspondence Analysis (CCA) lake community scores for 77 inland lake communities of ISRO, VOYA, and SLBE with 2 or more species.

Park	Lakes	Axis 1	Axis 2	Park	Lakes	Axis 1	Axis 2	Park	Lakes	Axis 1	Axis 2
ISRO	Ahmik	0.833	-1.256	VOYA	Agnes	0.591	-1.078	SLBE	Bass.S	-1.069	-0.132
ISRO	Amygdaloid	1.063	-0.630	VOYA	Beast	0.546	-0.843	SLBE	Bass.N	-1.287	-0.017
ISRO	Angleworm	0.802	-0.760	VOYA	Brown	0.993	-0.993	SLBE	DayMill	-1.188	-1.320
ISRO	Beaver	1.065	-1.341	VOYA	Cruiser	1.130	0.249	SLBE	Deer	-1.208	-0.101
ISRO	Benson	1.250	-1.196	VOYA	Ek	-0.038	-0.349	SLBE	Fisher	-0.818	0.341
ISRO	Chickenbone	1.187	-0.262	VOYA	Fishmouth	0.608	-0.983	SLBE	Florence	-0.013	-0.400
ISRO	Desor	2.039	3.986	VOYA	Jorgens	-0.050	-0.730	SLBE	Hidden	-0.360	-1.084
ISRO	Dustin	1.155	-0.597	VOYA	LitS	1.115	-1.244	SLBE	Long	-0.992	0.235
ISRO	Epidote	0.833	-1.256	VOYA	LitT	0.445	0.985	SLBE	Loon	-1.849	0.739
ISRO	Eva	1.157	-0.948	VOYA	Locator	0.299	-0.123	SLBE	Manitou	-0.838	1.459
ISRO	Feldtmann	0.802	-0.760	VOYA	Loiten	-0.810	-0.445	SLBE	Mud	-1.660	0.053
ISRO	Forbes	1.464	-1.584	VOYA	Lucille	0.274	-0.500	SLBE	Narada	-0.956	-0.381
ISRO	George	0.833	-1.256	VOYA	McDevitt	0.833	-1.256	SLBE	NorthBar	-1.381	0.117
ISRO	Halloran	1.065	-1.341	VOYA	Mukooda	-0.409	1.336	SLBE	Otter	-1.165	0.160
ISRO	Harvey	0.920	-1.390	VOYA	Net	0.172	-0.970	SLBE	Round	-0.952	-0.238
ISRO	Hatchet	0.890	-0.401	VOYA	O'Leary	0.399	-0.273	SLBE	School	-1.471	-0.039
ISRO	Intermediate	1.088	-0.752	VOYA	Oslo	0.993	-0.993	SLBE	Shell	-1.197	0.281
ISRO	John	1.407	-1.115	VOYA	Peary	0.162	-0.444	SLBE	Traverse	-1.595	1.163
ISRO	LeSage	0.833	-1.256	VOYA	Quarter Line	0.501	-1.099	SLBE	Tucker	-1.423	-0.491
ISRO	Linklater	1.065	-1.341	VOYA	Quill	-0.666	-0.149				
ISRO	Livermore	1.077	-1.400	VOYA	Ryan	0.521	-0.816				
ISRO	Mason	0.704	-1.202	VOYA	Shoepack	1.153	-0.712				
ISRO	McDonald	0.833	-1.256	VOYA	Tooth	0.623	-1.212				
ISRO	Oter	1.189	-0.895	VOYA	WarClub	-0.008	-0.236				
ISRO	Patterson	0.833	-1.256	VOYA	Weir	1.149	-0.998				
ISRO	Richie	1.138	0.763	VOYA	Wiyapka	0.204	-0.552				
ISRO	Sargent	1.334	0.540								
ISRO	Scholts	1.077	-1.400								
ISRO	Shesheeb	1.065	-1.341								
ISRO	Siskiwit	2.144	4.263								
ISRO	Wagejo	0.833	-1.256								
ISRO	Whittlesey	1.357	0.679								

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