



Characterizing Shifts in Fish Community Diversity of Isle Royale National Park's Inland Lakes



Lake Whittlesey.

UNIVERSITY OF MINNESOTA DULUTH / DAVID GALLAGHER

Characterizing Shifts in Fish Community Diversity of Isle Royale National Park's Inland Lakes

Science Report NPS/SR—2026/375

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Please cite this publication as:

Gallagher, D.J., T.R. Hrabik, J.D. Glase, S.A. Moore, and M.C. Romanski. 2026. Characterizing Shifts in Fish Community Diversity of Isle Royale National Park's Inland Lakes. Science Report NPS/SR—2026/375. National Park Service, Fort Collins, Colorado.
<https://doi.org/10.36967/2316629>

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Contents

	Page
Figures.....	v
Tables.....	vi
Appendices.....	vii
Abstract.....	viii
List of Terms or Acronyms.....	ix
Acknowledgments.....	x
Introduction.....	1
Background	1
Objectives	3
Methods.....	5
Previous Surveys	5
Current Survey Methods.....	5
Limnological Sampling	7
Data Analysis	7
Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity	7
Objective 2: Lakes and Species Most Likely to Change.....	9
Objective 3: Spatial Patterns in Community Composition.....	10
Objective 4: Temporal Patterns of Size and Abundance.....	10
Results.....	12
Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity	12
Alpha Diversity	12
Gamma Diversity.....	12
Spatial Beta Diversity.....	16
Objective 2: Lakes and Species Most Likely to Change.....	19
Lakes Changing Most.....	19
Species Changing Most.....	21
Objective 3: Spatial Patterns in Community Composition.....	22
Objective 4: Temporal Patterns of Size and Abundance.....	26

Contents (continued)

	Page
Size Structure.....	26
Abundance.....	31
Discussion.....	33
Overview	33
Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity	33
Objective 2: Lakes and Species Most Likely to Change	34
Objective 3: Spatial Patterns in Community Composition.....	36
Objective 4: Temporal Patterns of Size and Abundance.....	36
Conclusions	37
Literature Cited	39

Figures

	Page
Figure 1. Inland lakes of Isle Royale National Park, Michigan. Colors indicate the decade(s) in which fisheries surveys were performed in each lake.	3
Figure 2. Species-area curves for three fish surveys conducted on 23 lakes on Isle Royale, Michigan, in the 1920s, 1990s, and 2020s.....	12
Figure 3. NMDS ordination of species composition using Jaccard’s dissimilarity between 23 inland lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan.	16
Figure 4. NMDS ordination of species composition using Jaccard’s dissimilarity between the six largest lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan.	18
Figure 5. Contribution of species gains and losses to temporal beta diversity in 23 inland lakes on Isle Royale, Michigan, from A) 1920s to 2020s, B) 1920s to 1990s, and C) 1990s to 2020s.	21
Figure 6. NMDS ordination of species composition using Jaccard dissimilarity between 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey.....	25
Figure 7. Length frequency distributions color coded by survey year for A) northern pike, B) yellow perch, C) white sucker, and D) walleye populations across the inland lakes of Isle Royale, Michigan.....	27

Tables

	Page
Table 1. Gillnet and trap effort with mean deployment times in hours (standard deviation) for 23 lakes sampled in 2023–2024 on Isle Royale, Michigan.....	6
Table 2. Species composition of 23 inland lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan.	14
Table 3. Temporal beta diversity of fish communities in 23 inland lakes between the 1920s, 1990s, and 2020s on Isle Royale, Michigan.....	19
Table 4. Global correlations (r) and p-values for each species with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey.....	22
Table 5. Global correlations (r) and p-values for each lake characteristic with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey.	23
Table 6. Mean total length and range (minimum, maximum) in millimeters for northern pike during 1990s and 2020s surveys on Isle Royale, Michigan.....	27
Table 7. Mean total length and range (minimum, maximum) in millimeters for yellow perch during 1990s and 2020s surveys on Isle Royale, Michigan.....	29
Table 8. Mean total length and range (minimum, maximum) in millimeters for white sucker during 1990s and 2020s surveys on Isle Royale, Michigan.	30
Table 9. Mean total length and range (minimum, maximum) in millimeters for walleye during 1990s and 2020s surveys on Isle Royale, MI.	31
Table 10. Catch per unit effort (CPUE) for species caught in gillnets during the two most recent surveys on Isle Royale, Michigan.	32
Table 11. Lake names and abbreviations for 23 inland lakes on Isle Royale, Michigan.	45
Table 12. Species names and abbreviations for 30 species in the inland lakes of Isle Royale, Michigan.	46
Table 13. Water quality variables for the inland lakes of Isle Royale, Michigan, sampled between mid-July and mid-August of 2023 or 2024.....	47
Table 14. Morphometry and physical variables for inland lakes on Isle Royale, Michigan.	49
Table 15. Similarity percentages (SIMPER) showing contribution of each species to differences in community composition of the six largest lakes between each pair of surveys on Isle Royale, Michigan.	51
Table 16. Thermal classes of 30 species found on Isle Royale, Michigan, based on Gorman et al. (2014) with total number of gains and losses during the entire study.....	54

Appendices

	Page
Appendix 1: Lake Names and Codes.....	45
Appendix 2: Fish Species and Codes.....	46
Appendix 3: Water Quality Variables.....	47
Appendix 4: Lake Morphometry and Physical Variables.....	49
Appendix 5: SIMPER Results	51
Appendix 6: Species Thermal Classes and Net Changes.....	54

Abstract

The inland lakes of Isle Royale National Park have remained relatively isolated from human impact, providing an opportunity to explore how fish diversity responds to climate change with minimal confounding effects. We analyzed fish assemblages of 23 lakes sampled in the 1920s, 1990s, and 2020s to 1) assess shifts in multiple diversity metrics, 2) identify lakes and species experiencing the most change, 3) explore environmental factors driving community structure, and 4) determine changes in length and abundance of common species. We used species-area curves, Permutational Multivariate Analysis of Variance (PERMANOVA), and multivariate dispersion tests to quantify differences in diversity between surveys, temporal beta diversity indices to identify lakes and species changing most, and Non-metric Multidimensional Scaling (NMDS) to examine lake factors influencing composition. We assessed changes in length and abundance using linear mixed-effect models and Wilcoxon signed-rank tests. Mean richness and species-area curves did not significantly differ between survey dates, although both declined slightly. PERMANOVA and dispersion tests indicated overall community composition and spatial variability remained mostly stable, but larger lakes became more dominated by cool-water species. Species gains and losses were associated with isostatic rebound rate, where lakes with fast and slow rebound rates tended to gain and lose species, respectively, compared to prior studies. Sculpin and stickleback species were most commonly lost, while blackchin shiner and pumpkinseed were most commonly gained. Larger lakes hosted more diverse communities, and lakes with higher elevation lacked northern pike and yellow perch. Abundance increased for northern pike but declined for yellow perch and walleye, while average size increased for northern pike and walleye. Overall, these results suggest the inland lake fish communities of Isle Royale have not homogenized over time, but assemblages have gained cool-water and lost several cold-water species. More consistent surveys will be required to determine which species will persist in the future and whether undetected species have been extirpated.

List of Terms or Acronyms

TBI: Temporal beta diversity index, measure of dissimilarity between two time points of a single site

NMDS: Non-metric multidimensional scaling

PERMANOVA: Permutational multivariate analysis of variance

SIMPER: Similarity percentage

Acknowledgments

This project was made possible through support from the National Park Service Inventory and Monitoring Division, University of Minnesota Duluth, and Grand Portage Band of Lake Superior Chippewa. Thanks to Sami Awwad, Emily Mydlowski, Tessa Tormoen, Abby Hietala, and Ayse Kelemet, and all Isle Royale biotechnicians for help with fieldwork. Thanks to Lynette Potvin, Alex Egan, and Jared Myers for assistance with water quality sampling, logistics, and equipment. Thank you to Scott Esser, Rick Damstra, and Lisa Nelson for helpful comments on improving the report.

Introduction

Background

Identifying drivers of species diversity over various temporal and spatial scales remains a central focus of ecological research for many organisms (Jackson et al. 2001). Aquatic communities, particularly those in lakes, offer a unique set of conditions to isolate sources of variability in species diversity because of their discrete boundaries and isolated nature (Hrabik et al. 2005; Magnuson et al. 1998). Several frameworks have been proposed to explain patterns of fish diversity (Jackson and Harvey 1989; Tonn 1990), with isolation, extinction, and environmental drivers identified as significant factors. These frameworks analyze current fish communities as products of several filters with increasing specificity spanning continental, regional, and local scales (Tonn 1990). Continental filters including continental drift and glaciation act over broad scales to determine original species source pools with diverse characteristics and life history strategies (Tonn 1990). Regional filters such as climate, dispersal routes, and underlying geology act over smaller spatial and temporal scales to establish latitudinal gradients of species composition, richness, and productivity (Eadie et al. 1986; Tonn 1990). Finally, local abiotic and biotic filters including physiochemical conditions, morphometry, resource availability, and predation determine the specific community composition of individual lakes (Tonn 1990). Large-scale factors structuring original source pools of North American fish communities are generally well established and remain constant over relevant time scales, such as the Mississippian glacial refugia for the Great Lakes area (Crossman and McAllister 1986; Gorman et al. 2014). However, interactions between smaller-scale filters can be more dynamic.

As environmental conditions change over time, communities gain or lose species via immigration and extinction. Assemblage shifts can be challenging to predict over longer time scales due to species-specific responses to certain conditions, seasonal and annual variability in those conditions, and stochastic events affecting migration or extinction. Many studies have used physical lake gradients to represent potential temporal changes in diversity to address these difficulties (Jackson et al. 2001). Several studies have found lakes with multiple stream connections, few dispersal barriers, and close proximity to source pools have higher fish species richness and likelihood of immigration (Eadie et al. 1986; Hrabik et al. 2005; Schlosser and Kallemeyn 2000). Conversely, higher elevation lakes generally exhibit lower immigration rates and species richness due to dispersal barriers (Minns 1989). Whereas external lake features generally influence immigration, within-lake features determine species extinctions (Magnuson et al. 1998; Minns 1989). Species richness is positively correlated with surface area and depth in many regions due to greater habitat diversity and predation refuge in larger, more complex habitat matrices (Barbour and Brown 1974; Eadie et al. 1986; Minns 1989). Schlosser and Kallemeyn (2000) found richness of small ponds increases with habitat complexity along a successional gradient due to more diverse habitat availability, which reduced probability of extinction for small-bodied species. Lake hydrological position also impacts species composition via indirect effects on productivity and littoral complexity (Hrabik et al. 2005; Kratz et al. 1997; Minns 1989). Other factors affecting extinction are predators (Chapleau et al. 1997; Findlay et al. 2000), temperature (Magnuson et al. 1979), dissolved oxygen (Magnuson et al. 1998), and

acidity (Matuszek et al. 1990), which may alter species richness and composition depending on species' tolerance and degree of spatial and temporal variability in conditions.

Many studies of fish community diversity have emerged recently due to the availability of long-term datasets (Magurran et al. 2010), development of analysis methods (Buckley et al. 2021), and potential misrepresentations of space for time substitution (Damgaard 2019). Common measures of diversity include average species richness within individual lakes (alpha diversity), total species richness across a region (gamma diversity), and variation in species composition (beta diversity) over different spatial and temporal scales. Analyzing species composition often provides more insight into mechanisms guiding community structure than richness alone (Cardinale et al. 2018). Heino et al. (2024) provide a framework outlining multiple ways to holistically examine community variation, namely through spatial and temporal beta diversity, temporal variation in spatial beta diversity, and spatial variation in temporal beta diversity. Dissimilarity indices and multivariate methods have been commonly used for analysis of spatial beta diversity along environmental gradients (Anderson and Walsh 2013; Anderson et al. 2011). Repeating these analyses over time provides insight into temporal variation in spatial diversity and ultimately patterns of community homogenization and differentiation (Rolls et al. 2023). These methods have more recently been extended to temporal beta diversity analysis, which is the magnitude of change within a community over time (Legendre 2019; Lindholm et al. 2021). Identifying habitat types in which diversity shifts and species contributing most is essential for understanding mechanisms of community change. Others have subsequently studied this spatial variation in temporal beta diversity, demonstrating the importance of land use change (Lawson et al. 2024; Liang et al. 2024), species introductions (Cazelles et al. 2019; Kuczynski et al. 2018), and environmental gradients (Wu et al. 2024). However, many studies focus only on gradients of direct human impact and are unable to isolate the role of more natural variables governing community structure. It can be challenging to characterize how fish communities change naturally in response to climate change without other confounding variables, highlighting the need to explore this process in a natural setting.

Isle Royale National Park is a 72 km long and 14 km wide archipelago consisting of roughly 400 islands in northwestern Lake Superior (Figure 1). The main island is 99% wilderness, making Isle Royale an ideal site for studies on climate change or atmospheric deposition requiring isolation from direct human impact. While direct human impact may not be extensive currently, the island has a history of human habitation and disturbances including commercial fisheries and periods of small-scale logging and mining investigations. Current direct impacts are minimal but not absent as the park is visited by thousands of people each year. Isle Royale contains over 40 named inland lakes, and comprehensive fish community surveys in most inland lakes have been conducted only twice in the past century (Hubbs and Lagler 1949; Kallemeyn 2000; Koelz 1929). Several smaller-scale surveys have been performed in smaller subsets of inland lakes and surrounding Lake Superior waters (Gorman et al. 2008), but no comprehensive surveys have been conducted since the mid-1990s (Kallemeyn 2000). Previous inland lake surveys documented several rare or cold-water species such as cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), and finescale dace (*Chrosomus neogaeus*). Gorman et al. (2014) suggested suitable habitat in particular refuge lakes may be threatened by climate change but also noted the climate of

Lake Superior may effectively buffer and preserve habitat for these species. Since 1970, mean annual air temperature on Isle Royale has increased at a rate of 2.6°C per century, and precipitation has steadily increased but remained highly variable (NPS CCRP 2024). Projections indicate that by 2050, mean annual temperatures will increase between 1.6°C to 5.6°C with mean annual precipitation changing between −2.3 cm/year and +15.0 cm/year (NPS CCRP 2024). Despite these changes, it remains unclear how fish assemblages have responded in recent decades due to limited surveys. Furthermore, invasive species are common in Lake Superior waters and even some areas surrounding the island (Gorman et al. 2014). Given potential effects of climate change and invasive species on inland lake fish communities, it is crucial to understand if and how the fish community diversity of Isle Royale’s inland lakes has changed over time.

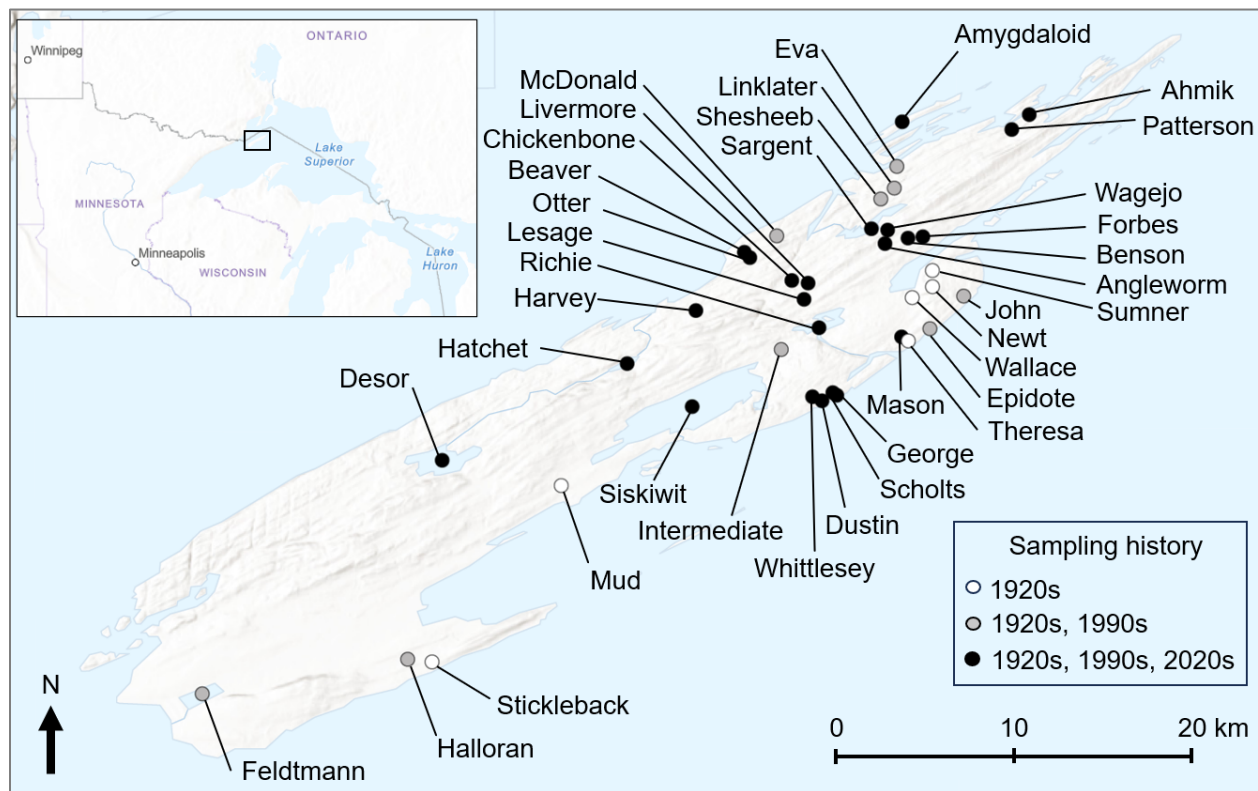


Figure 1. Inland lakes of Isle Royale National Park, Michigan. Colors indicate the decade(s) in which fisheries surveys were performed in each lake.

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Objectives

We compared fish communities of 23 inland lakes within Isle Royale National Park surveyed in 1929, 1995–1997, and 2023–2024. Main objectives were to 1) quantify change in alpha, gamma, and spatial beta diversity over time (temporal variation in spatial diversity), 2) identify which lakes and species were most subject to change (spatial variation in temporal beta diversity), and 3) explore the influence of environmental conditions in shaping current fish communities (spatial beta diversity). We also aimed to 4) quantify changes in abundance and size structure of common species. To address

objective one, we hypothesized alpha, beta, and gamma diversity would decline due to losses of cold-water species and homogenization of historical communities. For objective two, we hypothesized cold-water species and shallower lakes with historically rich communities would experience the most change due to loss of suitable oxythermal habitat. For objective three, we hypothesized environmental factors such as lake area and elevation would be most important in structuring current community composition. For objective four, we hypothesized that abundance and average size would remain stable. We used survey data on the composition of fish species collected using similar gear and effort conducted in 1929 (Koelz 1929), 1995–1997 (Kallemeyn 2000), and the present survey in 2023–2024 to address each hypothesis. Surveys are hereafter addressed as the decade in which they occurred (1920s, 1990s, 2020s).

Methods

Previous Surveys

The first comprehensive fisheries survey of Isle Royale's inland lakes was conducted by Koelz (1929), who sampled 38 lakes with a seine and gillnets. Several small-scale surveys were conducted in the following decades (Hubbs and Lagler 1949), but the next comprehensive survey occurred in the 1990s (Kallemeyn 2000). Survey methods included gillnets, minnow traps, and beach seines to sample 32 inland lakes, and effort scaled with lake surface area. No comprehensive survey has been conducted since then.

Current Survey Methods

In the present survey, conventional fisheries survey methods were used to sample fish communities of 23 inland lakes within Isle Royale National Park. Lake and species abbreviations are shown in Appendices 1–2, respectively. Ten lakes were sampled in 2023, and 13 lakes were sampled in 2024. All sampling occurred between May and August of both years. Lakes were selected to represent the wide gradient in fish community diversity documented in previous surveys (Kallemeyn 2000; Koelz 1929). Sampling methods were designed to closely mirror Kallemeyn (2000), with exceptions made only when necessary due to weather, logistics, or high catch rates. Conventional methods included nylon experimental gillnets, minnow traps, and a seine net. Gillnet dimensions were 76.2 m × 1.8 m with five equal length panels of 19.1, 25.4, 31.8, 38.1, and 50.8 mm mesh sizes. In four lakes sampled in 2023 (Ahmik, Benson, Forbes, Wagejo), three 24.4 m × 1.8 m monofilament gillnets with equivalent mesh sizes were used as substitutes for single nylon gillnets. Gee minnow traps were 419 mm long and 229 mm in diameter with a 3.2 mm wire mesh size. The seine net was 1.2 m × 6.1 m with 6 mm bar mesh. The number of gillnets set in each lake was stratified based on lake surface area (Table 1; Kallemeyn 2000). Exceptions were made if catch rates were excessively high, which occurred in Benson and Harvey. Gillnets were spread haphazardly around each lake to sample a variety of depth ranges in all basins. Gillnets were oriented both across and with depth contours when possible. The number of minnow traps set per lake varied roughly with lake area and depended on the number of days spent sampling each lake (Table 1). Minnow traps were baited with a handful of dry cat food and always set in less than one meter of depth around the perimeter of the lake. Trap locations were chosen haphazardly to sample all present habitats, including muck, rock, sand, macrophytes, and woody debris. All sampling with gillnets and minnow traps was done via canoe. Seining was also performed at a number of haphazardly selected sites, but success was often limited due to steep shorelines and woody debris. Seining effort also increased with lake area, and at least three hauls were performed at multiple sites spread around each lake.

Table 1. Gillnet and trap effort with mean deployment times in hours (standard deviation) for 23 lakes sampled in 2023–2024 on Isle Royale, Michigan. One set indicates one night spent sampling. Effort was stratified based on lake area and nights spent at each lake.

Lake	Gillnet Sets	Mean Deployment Time	Trap Sets	Mean Deployment Time
Ahmik	2	24.2 (1.0)	24	25.5 (0.0)
Amygdaloid	2	19.4 (0.1)	12	20.0 (0.5)
Angleworm	6	21.8 (1.3)	24	19.0 (8.5)
Beaver	4	21.0 (0.5)	12	19.6 (0.7)
Benson	3 ^A	22.3 (1.6)	36	23.4 (0.4)
Chickenbone	6	23.2 (1.5)	24	20.5 (0.6)
Desor	6	21.0 (1.7)	12	22.1 (0.8)
Dustin	1	20.6 (N/A)	12	20.4 (0.0)
Forbes	2	23.3 (0.5)	24	23.0 (0.9)
George	1	N/A	6	N/A
Harvey	4 ^A	20.1 (2.2)	24	20.4 (0.9)
Hatchet	5	19.7 (1.8)	24	20.3 (0.7)
Lesage	6	20.0 (0.8)	24	21.7 (1.6)
Livermore	4	20.9 (0.5)	12	19.3 (0.4)
Mason	4	20.9 (0.1)	12	20.5 (0.7)
Otter	4	20.0 (0.4)	12	19.8 (0.0)
Patterson	2	19.3 (0.3)	12	22.1 (0.1)
Richie	9	21.6 (1.3)	36	20.5 (0.8)
Sargent	9	22.4 (3.7)	36	22.3 (5.3)
Scholts	0	N/A	6	N/A
Siskiwit	16	27.7 (13.2)	36	28.1 (11.2)
Wagejo	2	22.1 (0.8)	24	23.5 (1.3)
Whittlesey	6	22.3 (5.3)	24	22.8 (3.7)

^A Reduced effort compared to Kallemeyn 2000.

All fish collected in gillnets and minnow traps were identified, enumerated, and measured. Fish collected in the seine were identified and measured if not captured in other equipment. Several individuals of each species in each lake were preserved in 70% ethanol to later confirm identification. When piscivores including northern pike (*Esox lucius*), walleye (*Sander vitreus*), or lake trout were captured, stomach contents of at least five individuals of each species in each lake were analyzed in search of previously-documented species not effectively sampled with standard equipment, such as sculpins. Stomach contents of larger yellow perch (*Perca flavescens*) and lake whitefish were also analyzed when no piscivores were present. Remaining individuals from gillnets, minnow traps, and seines were released if alive. It is possible that our current sampling or that of previous surveys did not effectively capture all species present in a lake at the time of sampling. In this study, we use the terms “gain” and “loss” of species when referring new detections or non-

detections, although we recognize species may have been present but remained undetected due to low abundance or sampling deficiency.

Limnological Sampling

Limnological sampling was performed in a canoe over the deepest point in each lake during late July or early August. Temperature, oxygen, pH, and conductivity profiles were measured using a Eureka MM774 sonde calibrated before each use. Water clarity was measured using a Secchi disk. Water for chlorophyll-*a* and chemistry analyses was collected via hand-grab samples just below the surface. All samples were transported back to a lab and prepared for later analysis within 24 hours.

In the lab, water was filtered through a 47 mm glass microfiber GF/C filter for chlorophyll-*a* analysis. The filter was frozen and processed via acetone extraction and spectrophotometry. Raw water was refrigerated for alkalinity, chloride, and sulfate analysis and frozen for total phosphorus and total nitrogen analyses. Water was filtered through a 47 mm pall filter and either preserved in sulfuric acid and refrigerated for dissolved organic carbon (DOC) analysis, preserved in nitric acid and refrigerated for silicate and cation analysis, or frozen for nitrate, nitrite, and ammonia analysis. Analyses for alkalinity, chloride, sulfate, DOC, silicate, and cation analyses were performed by CT Laboratories in Baraboo, Wisconsin. All chlorophyll-*a*, nitrogen, and phosphorus samples were analyzed by the St. Croix Watershed Research Station in Marine on St. Croix, Minnesota.

Lake morphometry data including surface area, maximum depth, watershed area, and shoreline development were taken from Kallemeyn (2000). Elevation data and isostatic rebound rates were taken from Gorman et al. (2014). We also estimated mean hypolimnion dissolved oxygen (DO) and temperature using profile data. We characterized the hypolimnion as all depths below the point at which temperature declines by more than 1°C over one meter change in depth. For unstratified lakes, we used dissolved oxygen and temperature values at the bottom of the water column as a proxy for hypolimnetic values. Water quality data for five lakes in 2023 lacked conductivity profiles, so we substituted conductivity data sampled during mid-July from 2022. Lake characteristics are displayed in Appendices 3–4.

Data Analysis

Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity

To test hypothesis one, we assessed patterns of alpha, beta, and gamma diversity in each survey. To assess changes in alpha diversity, we tested for differences in mean species richness between surveys across all lakes. Species richness data were right skewed, so we used Friedman's test (non-parametric version of repeated measures ANOVA) with survey year as a predictor and lake as a block to account for variability in richness between lakes. We also used linear regression to assess how species-area curves differed between surveys. We used species richness as a response variable and tested for an interaction between lake surface area and survey year to detect any differences in slope. A declining slope over time would indicate that smaller lakes may have gained species, larger lakes may have lost species, or both. We also assessed differences in gamma diversity using counts of total species found across all lakes during each survey period. To analyze changes in spatial beta diversity, we tested for differences in multivariate dispersion and ordination between surveys. We pooled presence-absence

data from all three surveys into a single table with a column for each species and row for each lake-survey year observation, such that each lake was represented as an observation three times. We calculated pairwise dissimilarities for all lake-survey pairs using Jaccard's dissimilarity (Jaccard 1908).

$$D = (b + c)/(a + b + c)$$

where

D = Jaccard dissimilarity between two sites

a = number of shared species between sites 1 and 2

b = number of species unique to site 1

c = number of species unique to site 2

Values of zero and one indicate complete similarity and dissimilarity, respectively. We used presence-absence data due to wide variability in catch rates among gear types, which may bias abundance estimates. We chose Jaccard's dissimilarity because it excludes the impact of joint absences and emphasizes the differences among sites more than other dissimilarity measures like Sorenson's index (Anderson et al. 2011). Nonmetric multidimensional scaling (NMDS) was used to ordinate each lake from each survey into two dimensions based on the matrix of Jaccard's dissimilarity, and Kruskal's stress was used to assess fit. The metaMDS function in the R package *vegan* was used for NMDS ordination with 100 random starts (Oksanen et al. 2024). Convex hulls were plotted around lakes grouped by survey year to visually assess whether ordinations differed in placement and variability between surveys. We also plotted convex hulls around the three survey ordinations for each lake to assess the relative amount and direction of change for each lake. To evaluate general patterns of community change, species vectors were plotted over the ordination using the envfit function in *vegan* with 1,000 permutations. We used the adonis2 function in *vegan* to run PERMANOVA analysis with survey year and lake as factors to characterize how fish community composition across all lakes shifted over time, as PERMANOVA tests whether multivariate centroids of groups (three surveys) are significantly different from one another (Anderson and Walsh 2013). We included lake as a factor to account for differences in community composition between lakes, which may obscure more subtle community shifts across lakes over time. If significant differences were detected, we used the pairwise.adonis2 function from the *pairwiseAdonis* package to run multiple comparisons tests with a Bonferroni correction. We also tested whether multivariate dispersion (mean distance to group centroid) varied between surveys, another potential measure of temporal variation in spatial beta diversity (Buckley et al. 2021). For this analysis, we used the betadisper function in *vegan*, where significantly lower variability (shorter mean distance to survey centroid) would indicate homogenization of fish communities, and higher variability (longer mean distance to survey centroid) would indicate differentiation.

Objective 2: Lakes and Species Most Likely to Change

We evaluated hypothesis two by examining which lakes experienced the greatest change in species composition and testing whether lake characteristics were related to the magnitude of change. For these analyses, we used the TBI function in the R package *adespatial* to calculate temporal beta diversity indices (TBI) based on Legendre (2019). This approach calculates the Jaccard dissimilarity, or TBI in this context, between two time points for each lake and subsequently decomposes each dissimilarity into gains and losses, allowing exploration of which process contributes most to community change (Legendre 2019). The relative contributions of losses and gains to overall dissimilarity in each lake were calculated as:

$$D_L = b/(a + b + c)$$

$$D_G = c/(a + b + c)$$

where

D_L = contribution of losses to Jaccard dissimilarity between two surveys

D_G = contribution of gains to Jaccard dissimilarity between two surveys

a = number of species found during both surveys of a single lake

b = number of species found only in the earlier survey (losses)

c = number of species found only in the later survey (gains)

The sum of gains and losses equals the total Jaccard dissimilarity for a given lake. We plotted gains and losses as coordinates on TBI plots to visually assess the relative importance of each process for each lake. Furthermore, we used permutational t-tests to determine whether any lakes showed exceptionally different communities between surveys relative to other lakes (Legendre 2019). We also used a paired permutational t-test to assess whether a single process (gains or losses) dominated across all lakes by comparing the mean contribution of gains and mean contribution of losses (Legendre 2019), and these results were also displayed on each TBI plot as a red one to one line through the centroid of all coordinates. We used Holm corrections for multiple testing in both analyses. We also explored whether lake characteristics were associated with overall dissimilarity, gains, losses, or the difference between gains and losses (hereafter gain-loss difference, calculated as gain contribution minus loss contribution). Gain-loss difference represents a gradient from lakes in which losses caused the greatest dissimilarity to lakes in which gains caused the greatest dissimilarity. We used the *rpart* function in the R package *rpart* (Therneau et al. 2025) to run regression trees with each of these four variables as a response in separate models and lake characteristics as predictors. Because only 23 lakes were sampled, initial model parameters required 3 observations in each leaf with at least 6 observations and 1% additional explained variability to allow a split. We used leave-one-out-cross-validation (LOOCV) to assess model fit. This process trains each model on 22 observations and tests the remaining observation a total of 23 times. We

pruned each tree by selecting the simplest tree within one standard error of the split with the lowest cross-validation error, although some more complicated trees were explored if errors were similar (De'ath and Fabricius 2000). Lake characteristics included in regression trees were lake surface area (hereafter area), maximum depth, geometry ratio (hereafter GR, calculated as fourth root of area/maximum depth), watershed area, ratio of surface to watershed area, elevation above Lake Superior (elevation ALS), isostatic rebound rate (hereafter rebound rate), shoreline development, total phosphorus (TP), total nitrogen (TN), magnesium (Mg), sodium (Na), sulfate (SO₄), silicate (Si), alkalinity, dissolved organic carbon (DOC), Secchi depth, mean hypolimnetic DO, mean hypolimnetic temperature, mean pH of the water column, and mean specific conductivity of the water column. Several predictor variables were highly skewed and log-transformed when necessary.

We also explored which species experienced the most change using three approaches. Following PERMANOVA analyses, we ran similarity percentages (SIMPER) analysis in the R package *vegan* using Jaccard's dissimilarity to assess which species contributed most to differences between surveys. We also ran permutational paired t-tests with Holm corrections to assess for which species presence changed significantly between surveys. The *tpaired.krandtest* function in the *adespatial* package (Dray et al. 2024) was used for this second analysis. We also assessed differences in the frequency of gains and losses by species thermal tolerance using thermal guilds outlined in Gorman et al. (2014). All TBI analyses were performed for each survey pair (1920s–1990s, 1990s–2020s, and 1920s–2020s).

Objective 3: Spatial Patterns in Community Composition

For hypothesis 3, we assessed spatial variation in current community composition and the potential role of environmental factors in causing these differences between lakes. We again used Jaccard's dissimilarity on presence-absence data to ordinate current lake communities into two dimensions with NMDS. We then plotted either species or environmental vectors over the ordination and assessed correlations with the ordination using the *envfit* function in *vegan* with 1,000 permutations. This function projects each lake from the two-dimensional space onto an environmental vector and then calculates the correlation between original values of the environmental variable and the values when projected onto the environmental vector in the NMDS ordination. We chose NMDS for ordination given its few assumptions relative to other parametric approaches. Our main objective was also to explore many potential predictors of community composition, and therefore we had no major a priori hypotheses with which to constrain the ordination for an approach like distance-based redundancy analysis. For this NMDS, only data from the most recent survey was used, and we eliminated highly correlated environmental variables ($r > 0.70$) and standardized all remaining variables prior to plotting environmental vectors.

Objective 4: Temporal Patterns of Size and Abundance

We assessed changes in size structure and abundance for northern pike, yellow perch, white sucker, and walleye captured in gillnets. For each species, we visualized length frequency distributions from the 1990s and 2020s surveys using histograms. Differences in mean length between the two surveys were evaluated using linear mixed-effect models with lake as a random effect. Sample sizes of each population varied between surveys, so we also calculated mean length of each species in each lake.

We then used paired Wilcoxon signed-rank tests to evaluate whether mean length changed between surveys using the mean length value from each lake during each survey. If a species was captured in gillnets during only one survey, we dropped the corresponding lake from the length analysis. This may limit detections of declining population sizes not effectively sampled with gillnets, but this is necessary for a paired test, and we address this possibility with our abundance analysis.

We evaluated changes in abundance using catch per unit effort (CPUE), where each overnight set was one unit of effort. We assessed differences between surveys for each species using paired Wilcoxon signed-rank tests. There were several cases where gillnets only captured species during one survey. Therefore, we assigned a $CPUE = 0$ to current populations that were previously detected and historical populations that were currently detected. We also assigned zeroes to populations that were detected by other methods but not captured in gillnets. All analyses were performed in R version 4.4.2. Figures were created using the *ggplot2* package.

Results

Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity

Alpha Diversity

Measures of alpha diversity, gamma diversity, and spatial beta diversity generally remained stable over time but showed some slight shifts between surveys. Mean alpha diversity declined from 5.48 (SD = 3.76) species per lake in the 1920s and 1990s to 5.17 (SD = 3.05) species per lake in the 2020s, although no significant differences were detected between surveys (Friedman's $\chi^2_{(df=2)} = 1.033, p = 0.597$). Analysis of species-area curves showed the interaction between lake surface area and survey year was nonsignificant ($F_{2,63} = 0.533, p = 0.590$), although the slope did decline slightly from 0.235 in the first two surveys to 0.219 during the most recent survey (Figure 2).

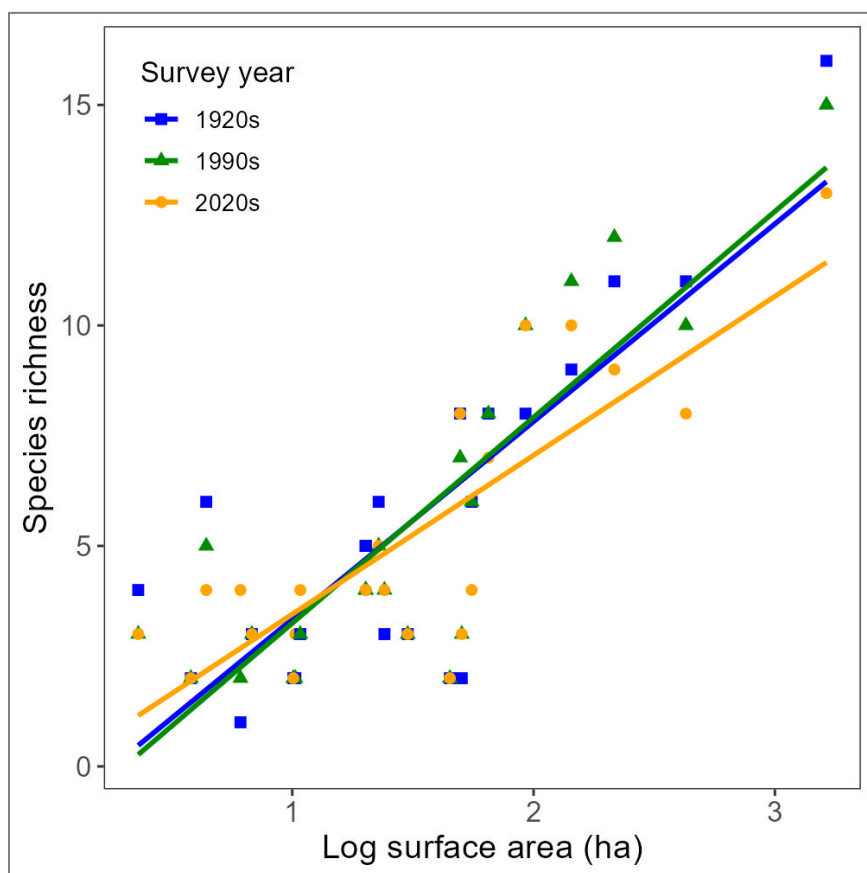


Figure 2. Species-area curves for three fish surveys conducted on 23 lakes on Isle Royale, Michigan, in the 1920s, 1990s, and 2020s.

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Gamma Diversity

Gamma diversity remained relatively stable over time, as the total number of species found across all lakes changed from 28 species in the 1920s and 1990s to 27 species in the 2020s. Spoonhead sculpin (*Cottus ricei*) was the only species detected in the first two surveys that went undetected in any lake

in the current survey (Table 2). The 1990s survey failed to detect two species (brook trout (*Salvelinus fontinalis*), mottled sculpin (*Cottus bairdii*)) found in the 1920s survey but found two additional species (blackchin shiner (*Notropis heterodon*), northern redbelly dace (*Chrosomus eos*)) (Table 2).

Table 2. Species composition of 23 inland lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Numbers indicate the survey(s) in which each species was detected (1920s = 1, 1990s = 2, 2020s = 3), and no change (NC) indicates the species was present in all surveys. Dashes (-) indicate a species has never been detected. Lake codes are presented in Appendix 1.

Species	AHM	AMY	ANG	BEA	BEN	CHI	DES	DUS	FOR	GEO	HAR	HAT	LES	LIV	MAS	OTT	PAT	RIC	SAR	SCH	SIS	WAG	WHI
Cisco	–	–	–	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	NC	NC	–	NC	–	–
Lake whitefish	–	–	–	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–
Brook trout	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Lake trout	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–
Northern pike	NC	NC	NC	NC	–	NC	–	NC	–	NC	–	–	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
Lake chub	–	–	–	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pearl dace	–	–	–	–	–	–	NC	–	NC	–	1/2	NC	–	–	–	–	–	–	–	–	–	–	–
Golden shiner	–	–	–	NC	–	3	–	–	–	–	–	–	–	–	NC	1	–	NC	NC	–	–	–	–
Emerald shiner	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–
Blackchin shiner	–	–	–	–	–	2/3	–	–	–	–	–	–	–	–	–	–	–	–	2/3	–	–	3	–
Blacknose shiner	–	–	–	NC	NC	2/3	–	NC	NC	–	NC	–	–	NC	NC	NC	–	NC	NC	NC	NC	–	2/3
Spottail shiner	–	NC	–	1	–	NC	–	3	–	–	–	–	–	–	–	NC	–	NC	1/2	–	NC	–	NC
Mimic shiner	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–	–	–	–
Northern redbelly dace	–	–	–	–	–	2/3	2	–	–	–	–	2/3	–	–	–	–	–	–	–	–	–	–	–
Finescale dace	–	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fathead minnow	–	–	–	–	–	–	–	–	–	–	NC	NC	–	–	–	–	–	–	–	–	–	–	–
Creek chub	–	–	–	–	–	–	–	–	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	–
White sucker	3	–	2/3	–	–	1/2	NC	1/2	–	–	NC	NC	–	–	–	–	–	NC	NC	1	NC	–	NC
Trout-perch	–	–	–	–	–	–	NC	–	–	–	–	NC	–	–	–	–	–	1/2	–	–	NC	–	1/2
Burbot	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–
Brook stickleback	–	–	–	–	2/3	–	NC	–	–	–	1/2	NC	–	–	–	–	–	2	–	–	1	–	–
Ninespine stickleback	–	–	–	–	–	–	NC	–	–	–	–	1/3	–	–	–	–	–	–	–	–	1/2	–	–
Pumpkinseed	–	–	–	–	–	2/3	–	–	–	–	–	–	–	–	NC	–	–	NC	2/3	–	–	3	–
Iowa darter	–	3	–	–	–	NC	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	–	–	–

Table 2 (continued). Species composition of 23 inland lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Numbers indicate the survey(s) in which each species was detected (1920s = 1, 1990s = 2, 2020s = 3), and no change (NC) indicates the species was present in all surveys. Dashes (-) indicate a species has never been detected. Lake codes are presented in Appendix 1.

Species	AHM	AMY	ANG	BEA	BEN	CHI	DES	DUS	FOR	GEO	HAR	HAT	LES	LIV	MAS	OTT	PAT	RIC	SAR	SCH	SIS	WAG	WHI
Yellow perch	NC	NC	NC	NC	NC	NC	–	NC	NC	NC	NC	–	NC	NC	NC	NC	NC	NC	NC	NC	NC	2/3	NC
Logperch	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	NC	–	NC
Walleye	–	–	–	–	–	NC	–	1/2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	NC
Mottled sculpin	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Slimy sculpin	–	–	–	–	–	1	1	–	–	–	–	–	–	–	1	–	–	1/2	NC	–	NC	–	–
Spoonhead sculpin	–	–	–	–	–	–	1/2	–	–	–	–	–	–	–	–	–	–	–	–	–	1/2	–	1

Spatial Beta Diversity

NMDS ordinations of all lakes during the three surveys (Kruskal's stress = 0.111) showed wide variability between lakes and large overlap of convex hulls (Figure 3). No significant shifts in overall community composition were detected between surveys of all lakes when controlling for between-lake variability (PERMANOVA, $F_{2,44} = 1.488$, $p = 0.125$). No differences in beta diversity represented as mean distance to centroid were detected between surveys (betadisper, $F_{2,66} = 0.201$, $p = 0.819$).

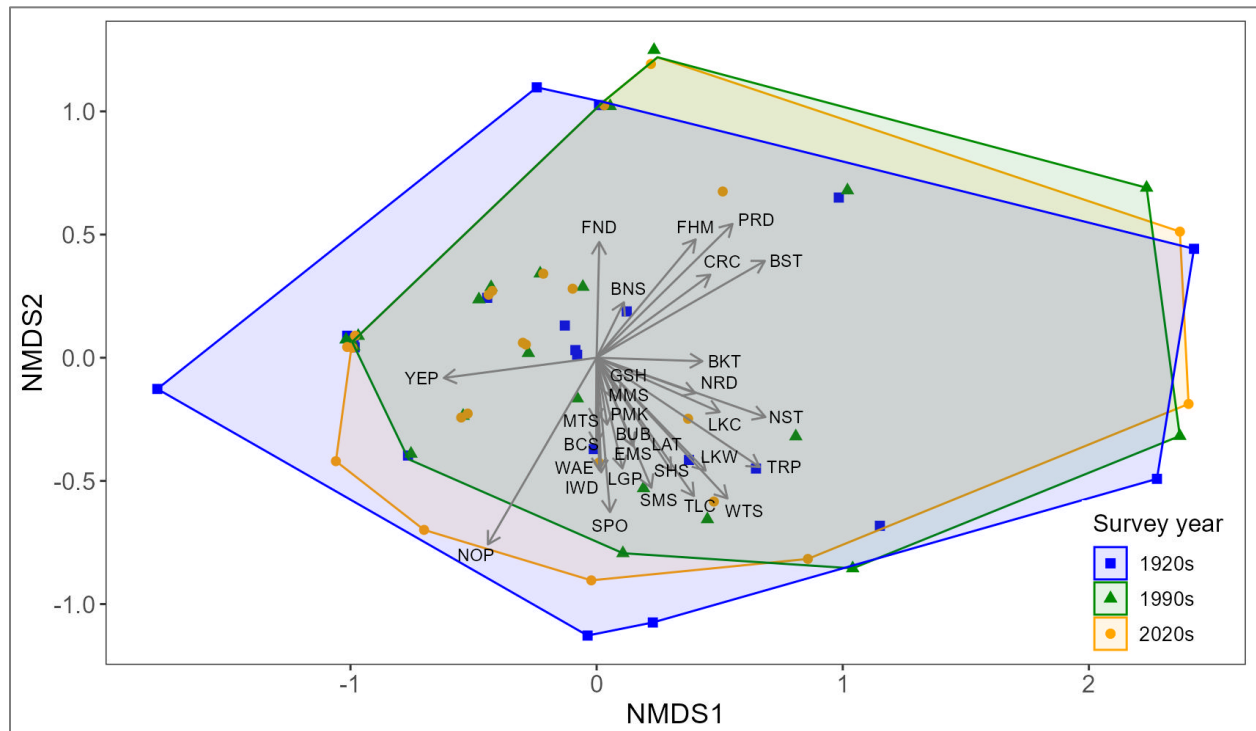


Figure 3. NMDS ordination of species composition using Jaccard's dissimilarity between 23 inland lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Convex hulls are plotted around all lakes for each survey. Species vectors are plotted over the convex hulls, and species codes are presented in Appendix 2.

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We also reran these analyses for the six largest lakes in an attempt to detect more subtle community shifts, which may be obscured by the high number of lakes with more tolerant, species-poor communities. For the six largest lakes, NMDS ordinations (Kruskal's stress = 0.071) showed a shift in the position of convex hulls between surveys (Figure 4A). Centroids shifted towards cool-water and thermally tolerant species such as blacknose shiner (*Notropis heterolepis*), blackchin shiner, golden shiner (*Notemigonus crysoleucas*) and pumpkinseed (*Lepomis gibbosus*), all of which were gained in at least one lake since the 1920s survey. Centroids shifted away from cold-water species including spoonhead sculpin and trout-perch (*Percopsis omiscomaycus*), both of which were lost from at least one lake (Table 2). For these six lakes, PERMANOVA indicated a significant shift in community composition between surveys (PERMANOVA, $F_{2,10} = 3.090$, $p = 0.010$). Subsequent

post-hoc tests indicated significant differences between all three pairs of surveys after controlling for between lake variability (all $p < 0.003$). Mean distance to centroid was not significantly different between surveys for these six lakes (betadisper, $F_{2,15} = 0.0963$, $p = 0.909$). Plotting convex hulls around each lake also showed relatively consistent directional shifts between surveys (Figure 4B). Ordinations of each lake generally shifted away from cold-water species towards cool-water species over time.

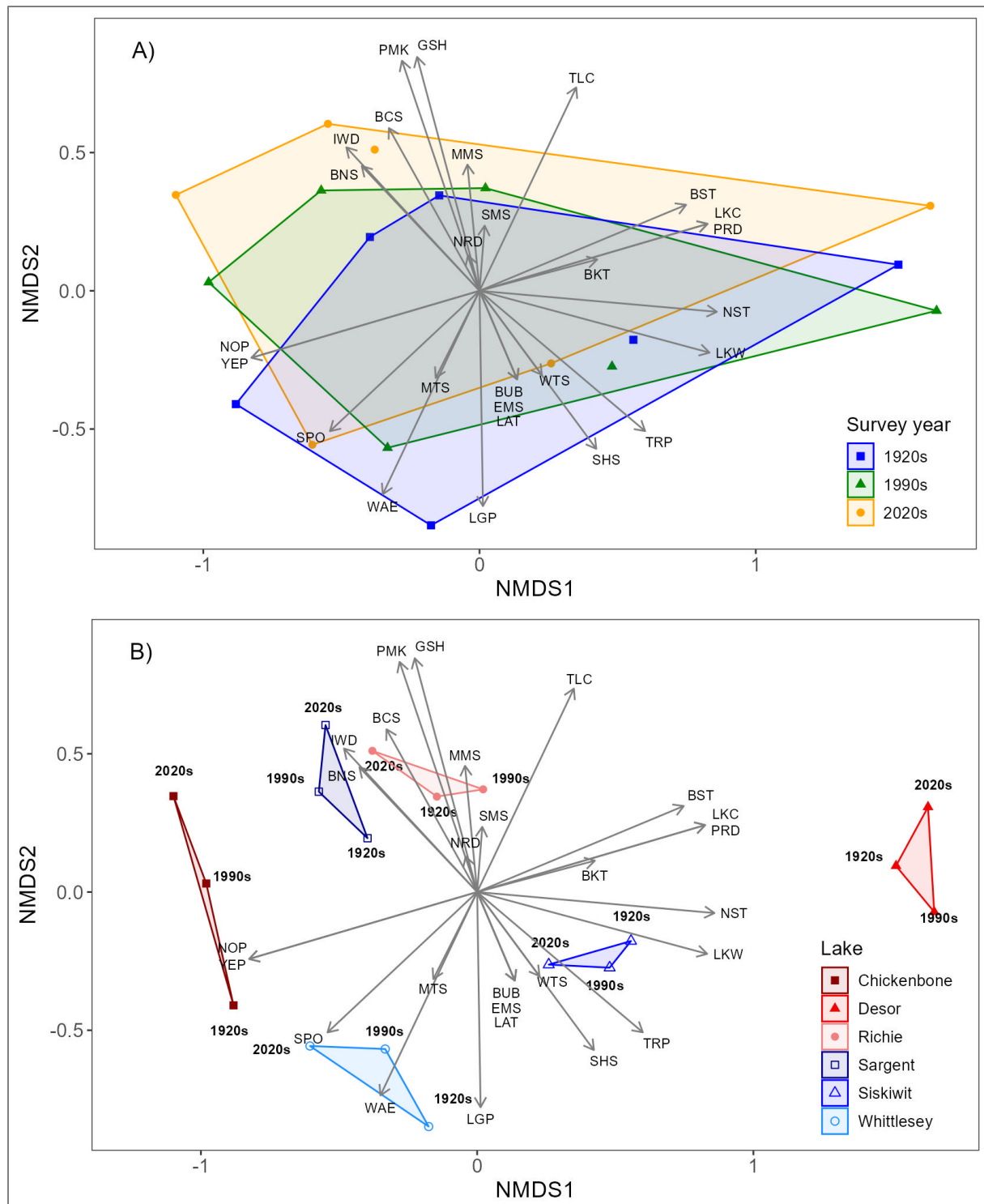


Figure 4. NMDS ordination of species composition using Jaccard's dissimilarity between the six largest lakes sampled in the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Convex hulls group communities by A) survey, showing shifts in average composition across all six lakes, and B) lakes, showing directional change of each fish community over time, with survey decades noted in bold. Species vectors are plotted over the convex hulls, and species codes are presented in Appendix 2.

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Objective 2: Lakes and Species Most Likely to Change

Lakes Changing Most

TBI analyses between all survey pairs indicated three lakes experienced relatively more community change than others. Wagejo, Chickenbone, and Dustin lakes showed mean TBI values of 0.583, 0.432, and 0.413, respectively, while all remaining dissimilarities ranged from no change in five lakes to 0.241 in Lake Desor across all time periods (Table 3). However, permutational t-tests indicated no lakes experienced extreme change compared to others after correcting for multiple comparisons (all $p > 0.138$). Mean temporal dissimilarity was 0.161 between the 1920s and 1990s, 0.249 between the 1990s and 2020s, and 0.131 across the entire study. Neither gains nor losses were dominant during any period (all $p > 0.743$), although the largest difference occurred between the 1920s and 1990s where gains contributed 53.7% and losses contributed 46.3% dissimilarity on average.

Table 3. Temporal beta diversity of fish communities in 23 inland lakes between the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Jaccard's dissimilarity was calculated between each pair of surveys for each lake. Means for each lake and survey are also shown. Zeros indicate no change in species composition between surveys, while values closer to one indicate greater dissimilarity.

Lake	1920s/1990s	1920s/2020s	1990s/2020s	Mean
Ahmik	0.000	0.333	0.333	0.222
Amygdaloid	0.000	0.250	0.250	0.167
Angleworm	0.333	0.333	0.000	0.222
Beaver	0.200	0.200	0.000	0.133
Benson	0.250	0.250	0.000	0.167
Chickenbone	0.500	0.615	0.182	0.432
Desor	0.250	0.273	0.200	0.241
Dustin	0.167	0.571	0.500	0.413
Forbes	0.000	0.000	0.000	0.000
George	0.000	0.000	0.000	0.000
Harvey	0.000	0.333	0.333	0.222
Hatchet	0.333	0.222	0.125	0.227
Lesage	0.000	0.000	0.000	0.000
Livermore	0.000	0.000	0.000	0.000
Mason	0.167	0.167	0.000	0.111
Otter	0.200	0.200	0.000	0.133
Patterson	0.000	0.000	0.000	0.000
Richie	0.083	0.182	0.250	0.172
Sargent	0.182	0.273	0.091	0.182
Scholts	0.250	0.250	0.000	0.167
Siskiwit	0.062	0.188	0.133	0.128

Table 3 (continued). Temporal beta diversity of fish communities in 23 inland lakes between the 1920s, 1990s, and 2020s on Isle Royale, Michigan. Jaccard's dissimilarity was calculated between each pair of surveys for each lake. Means for each lake and survey are also shown. Zeros indicate no change in species composition between surveys, while values closer to one indicate greater dissimilarity.

Lake	1920s/1990s	1920s/2020s	1990s/2020s	Mean
Wagejo	0.500	0.750	0.500	0.583
Whittlesey	0.222	0.333	0.125	0.227
Mean	0.161	0.249	0.131	0.180

Regression tree analyses detected few relationships among dissimilarity, gains, losses, gain-loss difference, and lake characteristics. The strongest model for the 1920s to 2020s predicted gain-loss difference at a single split in rebound rate at 0.845 m/100 years. Linear regression showed a moderately strong positive relationship between gain-loss difference and rebound rate ($R^2 = 0.320$, $p = 0.005$). Grouping lakes by rebound rate showed a clear distinction between lakes tending to gain and lose species, where lakes with slower isostatic rebound experienced more species losses than gains (Figure 5A). Regression trees for the 1920s and 1990s indicated null models were strongest, but predicting gain-loss difference with three splits resulted in a similar cross-validation error to the corresponding null model (1.093 vs 1.123) and explained a large portion of variability ($R^2 = 0.803$). An initial split occurred at rebound rate >0.845 m/100 years, plus one subsequent split for watershed area in lakes with faster rebound and one subsequent split for Secchi depth in lakes with slower rebound (Figure 5B). Regression trees for the 1990s to 2020s revealed two main relationships between gain-loss difference, dissimilarity, and lake factors. Predicting gain-loss difference with one split for DOC (<7.4 mg/L) was within 1 SE of the null model. Linear regression showed a positive relationship between DOC and gain-loss difference ($p = 0.012$), and this relationship is also evident in a TBI plot (Figure 5C). These results indicate the contribution of gains to dissimilarity were more prevalent in lakes with higher DOC. For dissimilarity, the strongest model was a single split with shoreline development at 1.75, indicating lakes with less shoreline development had greater dissimilarity during this time.

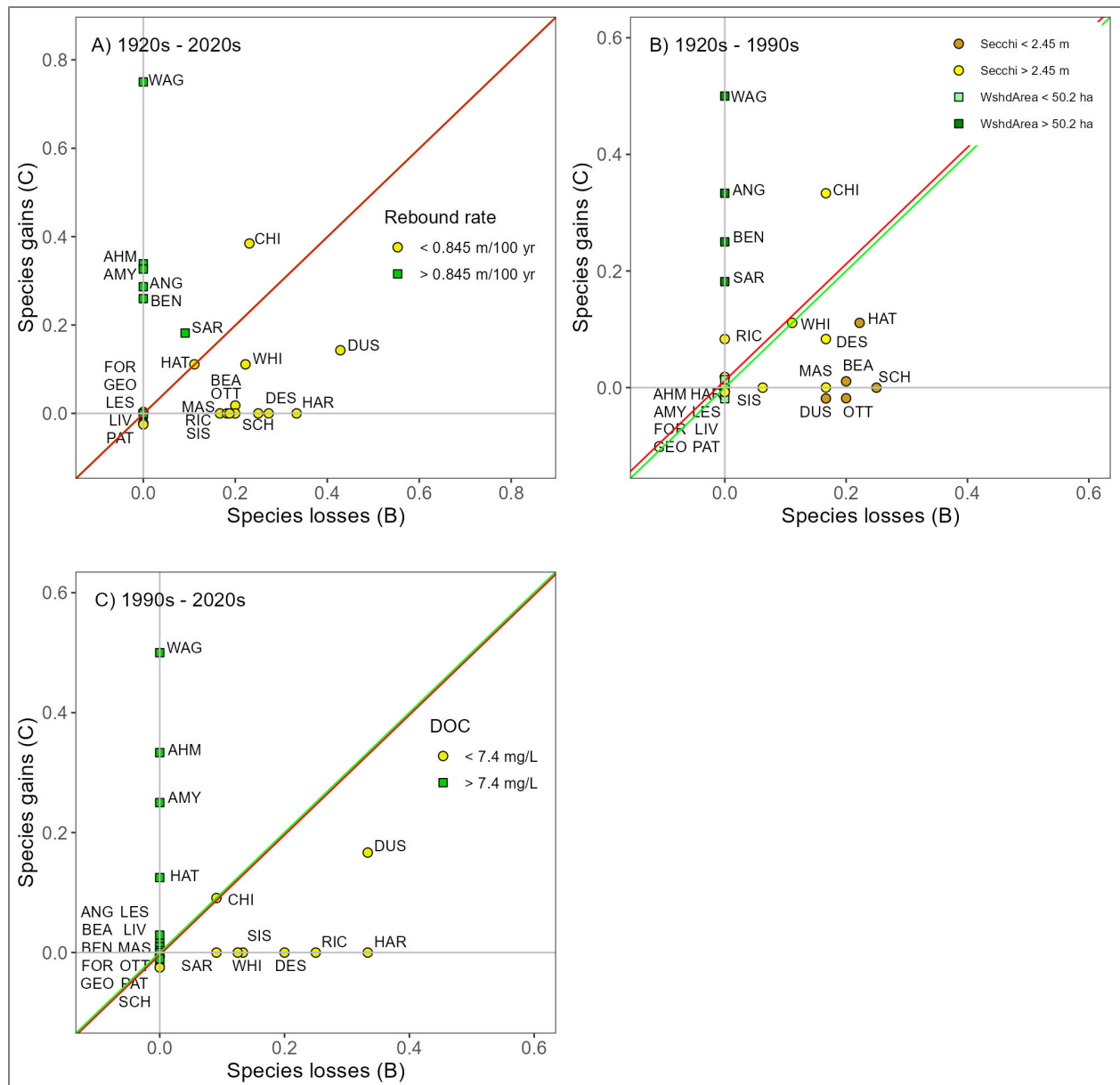


Figure 5. Contribution of species gains and losses to temporal beta diversity in 23 inland lakes on Isle Royale, Michigan, from A) 1920s to 2020s, B) 1920s to 1990s, and C) 1990s to 2020s. Symbols represent lake groups based on top variables from regression tree results, including isostatic rebound rate, Secchi depth, watershed area, and dissolved organic carbon (DOC). For the 1920s–1990s, squares and circles represent rebound rates faster and slower than 0.845 m/100 years, respectively. One to one lines are shown in green, and the parallel red lines run through the centroid of all points in each plot. Lake codes are presented in Appendix 1.

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Species Changing Most

SIMPER results indicated that species contributing most to differences between surveys in the six largest lakes were slimy sculpin (*Cottus cognatus*), trout-perch, blacknose shiner, and pumpkinseed, although no species was dominant in its contribution (all <7%, Appendix 5). Results of permutational

paired t-tests indicated that no species shifted significantly between any of the surveys, although slimy sculpin was the closest to significance ($p = 0.068$) between the 1920s and 2020s. Gains and losses varied by species thermal guild between the 1920s and 2020s (Appendix 6). On average, each cold-water species experienced 1.3 losses and 0.1 gains, each cool-water species experienced 0.6 losses and 1.5 gains, and each thermally-tolerant species experienced 0.8 losses and 0.3 gains.

Objective 3: Spatial Patterns in Community Composition

The NMDS ordination of current communities showed several evident assemblage types and gradients with environmental variables (Tables 4–5; Figure 6). The simplest assemblages contained only northern pike and yellow perch (George, Lesage, Patterson) or lakes with one additional species such as white sucker (*Catostomus commersonii*) (Ahmik, Angleworm) or blacknose shiner (Livermore, Scholts). Some lakes included at least two species in addition to northern pike and yellow perch, including a combination of blacknose shiner, blackchin shiner, spottail shiner (*Notropis hudsonius*), golden shiner, pumpkinseed, and Iowa darter (*Etheostoma exile*) (Amygdaloid, Beaver, Dustin, Mason, Otter, Wagejo). The most diverse lakes grouped together and contained northern pike and yellow perch plus several minnows (Chickenbone, Whittlesey) and cold-water species such as cisco or slimy sculpin (Siskiwit, Richie, Sargent). Lakes lacking northern pike but containing yellow perch and least one other species grouped together (Benson, Forbes, Harvey), and lakes lacking both but hosting rare species like ninespine stickleback (*Pungitius pungitius*), lake chub (*Couesius plumbeus*), creek chub (*Semotilus atromaculatus*), and trout-perch were most extreme (Desor, Hatchet). Plotting environmental vectors over the NMDS ordination of current fish communities showed significant patterns with several variables, although two gradients were most evident (Table 5; Figure 6). Lakes with northern pike and yellow perch transitioned to lakes lacking both along an elevation ALS gradient, indicating higher elevation lakes tended to lack northern pike and occasionally yellow perch. Simple communities hosting only two to four species transitioned to the most diverse communities hosting between eight and 13 species with increasing area and decreasing hypolimnetic temperature and rebound rate.

Table 4. Global correlations (r) and p -values for each species with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the envfit function in the R package *vegan*.

Species	r	p
Northern pike	0.761	0.001
Brook stickleback	0.650	0.002
Pearl dace	0.636	0.002
Trout-perch	0.737	0.002
Cisco	0.504	0.004
Pumpkinseed	0.485	0.005
Ninespine stickleback	0.783	0.006
Yellow perch	0.783	0.006

Table 4 (continued). Global correlations (r) and p-values for each species with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the envfit function in the R package *vegan*.

Species	r	p
Blackchin shiner	0.384	0.014
Golden shiner	0.368	0.016
Lake whitefish	0.415	0.017
White sucker	0.344	0.017
Fathead minnow	0.376	0.023
Creek chub	0.416	0.036
Iowa darter	0.270	0.038
Slimy sculpin	0.210	0.086
Lake chub	0.405	0.107
Northern redbelly dace	0.187	0.113
Finescale dace	0.239	0.116
Spottail shiner	0.174	0.122
Walleye	0.096	0.309
Burbot	0.085	0.352
Emerald shiner	0.085	0.352
Lake trout	0.085	0.352
Mimic shiner	0.055	0.438
Logperch	0.061	0.479
Blacknose shiner	0.008	0.922

Table 5. Global correlations (r) and p-values for each lake characteristic with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the envfit function in the R package *vegan*.

Lake characteristic	r	p
Area	0.495	0.001
Rebound rate	0.559	0.002
Elevation above Lake Superior (ALS)	0.413	0.006
Mean hypolimnion temperature	0.407	0.007
Dissolved organic carbon (DOC)	0.190	0.120
Sulfate (SO ₄)	0.182	0.130
Total phosphorus (TP)	0.096	0.360
Shoreline development (SD)	0.087	0.401

Table 5 (continued). Global correlations (r) and p-values for each lake characteristic with the NMDS ordination of 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey. Jaccard dissimilarities were calculated between all lake pairs using species presence data for the ordination. Values were calculated by the envfit function in the R package *vegan*.

Lake characteristic	r	p
pH	0.070	0.487
Conductivity	0.058	0.556
Area:watershed	0.052	0.590
Silicate (Si)	0.036	0.714
Mean hypolimnion DO	0.009	0.912
Secchi depth	0.002	0.981

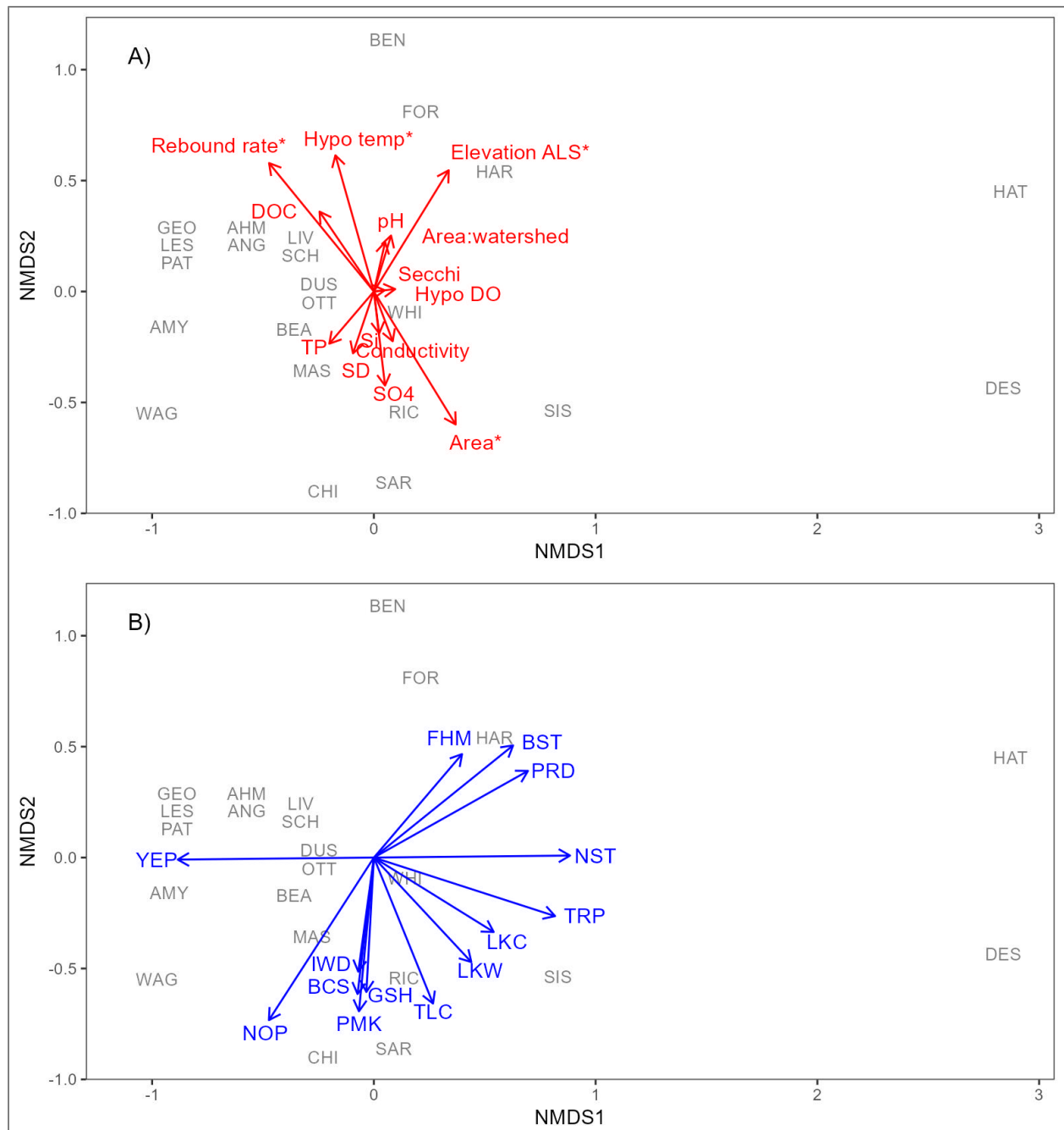


Figure 6. NMDS ordination of species composition using Jaccard dissimilarity between 23 inland lakes on Isle Royale, Michigan, based on the 2020s survey. A) Environmental vectors include surface area, area to watershed ratio, shoreline development (SD), rebound rate, elevation above Lake Superior (ALS), dissolved organic carbon (DOC), total phosphorus (TP), sulfate (SO₄), silicate (Si), pH, Secchi depth, mean hypolimnetic dissolved oxygen (DO), mean hypolimnetic temperature, and mean specific conductivity. Asterisks for environmental variables indicate a significant correlation with the overall ordination. B) Species vectors show only those with a significant correlation with the ordination. Lake and species abbreviations are shown in Appendices 1–2.

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Objective 4: Temporal Patterns of Size and Abundance

Size Structure

Some species exhibited shifts in size structure between the 1990s and 2020s while others did not. The mixed-effect model showed northern pike mean length significantly increased from 521 mm to 557 mm ($p < 0.001$) (Figure 7A). A paired Wilcoxon signed-rank test using mean lengths from each lake also showed a similar increase in size ($p = 0.031$). Lakes with the largest increases were Mason, Chickenbone, and Richie, while northern pike mean length decreased most in Angleworm (Table 6). For yellow perch, mean length significantly decreased from 199 mm to 179 mm based on the mixed-effect model ($p < 0.001$) (Figure 7B). However, the Wilcoxon signed-rank test showed no significant size shifts when using mean length from each lake ($p = 0.747$). Ahmik, Otter, and Wagejo showed the largest decline in yellow perch length, while Siskiwit and Harvey showed large increases in yellow perch mean length (Table 7). No yellow perch were sampled in gillnets during the recent survey in Amygdaloid, Beaver, and Dustin, so it remains unclear whether mean length has declined or if overall population sizes are low in these lakes. We found mean length of white sucker significantly increased from 308 mm to 322 mm based on the mixed-effect model ($p = 0.001$) (Figure 7C). Similar to yellow perch, however, the Wilcoxon test using means for each lake showed no significant changes ($p = 0.641$). These patterns may be driven by variable sample sizes of measured fish between surveys (Table 8). For walleye, the mixed-effect model showed mean length significantly increased from 339 mm to 439 mm across two lakes ($p < 0.001$) (Figure 7D), and this shift was more prevalent in Chickenbone (Table 9).

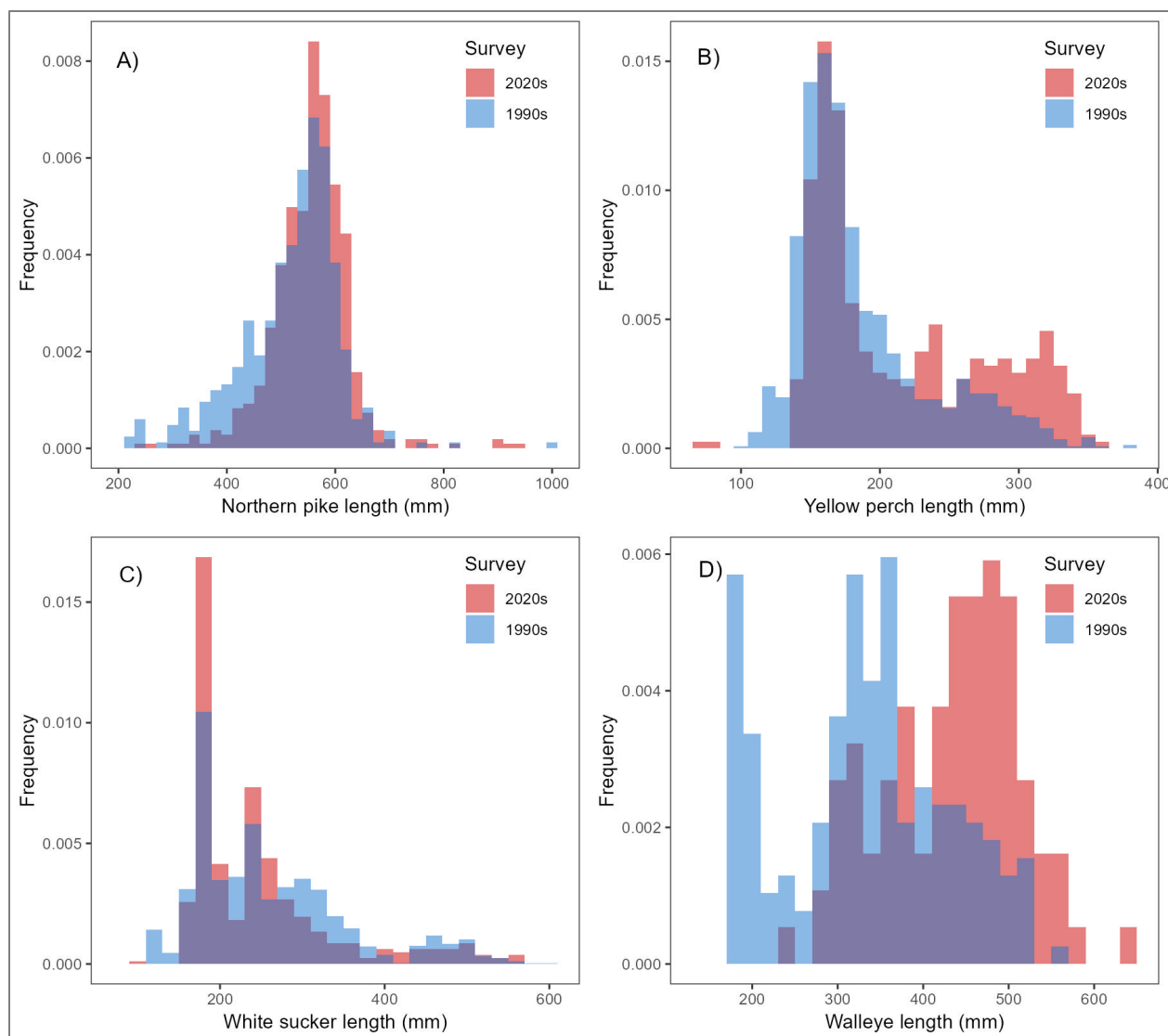


Figure 7. Length frequency distributions color coded by survey year for A) northern pike, B) yellow perch, C) white sucker, and D) walleye populations across the inland lakes of Isle Royale, Michigan. Histograms include data pooled from all lakes. Blue and red represent the 1990s and 2020s surveys, respectively, and purple indicates overlapping length distributions. Bars are divided in 10 mm increments for yellow perch and 20 mm increments for other species.

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Table 6. Mean total length and range (minimum, maximum) in millimeters for northern pike during 1990s and 2020s surveys on Isle Royale, Michigan. Number of measured fish (n) is also shown.

Lake	Survey	n	Mean length (range)
Ahmik	1990s	11	469 (390, 702)
	2020s	10	531 (431, 612)
Amygdaloid	1990s	7	574 (531, 615)
	2020s	17	577 (510, 627)

Table 6 (continued). Mean total length and range (minimum, maximum) in millimeters for northern pike during 1990s and 2020s surveys on Isle Royale, Michigan. Number of measured fish (n) is also shown.

Lake	Survey	n	Mean length (range)
Angleworm	1990s	25	575 (513, 656)
	2020s	75	536 (415, 604)
Beaver	1990s	34	535 (319, 626)
	2020s	46	558 (510, 620)
Chickenbone	1990s	36	510 (347, 695)
	2020s	24	608 (338, 815)
Dustin	1990s	2	562 (535, 589)
	2020s	3	458 (344, 669)
George	1990s	3	529 (449, 626)
	2020s	8	523 (418, 645)
Lesage	1990s	42	510 (296, 643)
	2020s	49	495 (236, 582)
Livermore	1990s	25	567 (399, 664)
	2020s	58	587 (502, 654)
Mason	1990s	15	384 (212, 530)
	2020s	14	531 (316, 921)
Otter	1990s	30	483 (304, 598)
	2020s	36	509 (381, 627)
Patterson	1990s	6	513 (294, 663)
	2020s	17	540 (471, 611)
Richie	1990s	62	474 (289, 678)
	2020s	81	572 (268, 690)
Sargent	1990s	78	561 (433, 633)
	2020s	66	586 (511, 666)
Siskiwit	1990s	5	720 (325, 1000)
	2020s	5	841 (700, 949)
Wagejo	1990s	17	471 (224, 562)
	2020s	11	489 (386, 610)
Whittlesey	1990s	19	526 (348, 642)
	2020s	21	564 (475, 790)

Table 7. Mean total length and range (minimum, maximum) in millimeters for yellow perch during 1990s and 2020s surveys on Isle Royale, Michigan. Number of measured fish (n) is also shown. Cells with N/A indicate yellow perch were sampled only with equipment other than gillnets.

Lake	Survey	n	Mean length (range)
Ahmik	1990s	3	265 (239, 287)
	2020s	9	176 (138, 243)
Amygdaloid	1990s	7	115 (106, 125)
	2020s	0	N/A
Angleworm	1990s	36	161 (144, 202)
	2020s	9	164 (154, 175)
Beaver	1990s	20	202 (144, 383)
	2020s	0	N/A
Benson	1990s	482	196 (142, 325)
	2020s	55	174 (71, 268)
Chickenbone	1990s	128	193 (134, 320)
	2020s	7	213 (149, 256)
Dustin	1990s	2	161 (155, 166)
	2020s	0	N/A
Forbes	1990s	124	181 (153, 260)
	2020s	3	173 (168, 180)
George	1990s	3	150 (147, 153)
	2020s	8	178 (148, 222)
Harvey	1990s	184	209 (137, 335)
	2020s	135	277 (156, 354)
Lesage	1990s	49	160 (102, 222)
	2020s	4	177 (155, 230)
Livermore	1990s	137	179 (138, 281)
	2020s	31	168 (140, 235)
Mason	1990s	11	149 (138, 159)
	2020s	1	162 (162, 162)
Otter	1990s	1	348 (348, 348)
	2020s	19	228 (139, 359)
Patterson	1990s	4	166 (140, 198)
	2020s	6	218 (140, 345)
Richie	1990s	43	190 (135, 322)
	2020s	43	188 (148, 345)
Sargent	1990s	1	164 (164, 164)
	2020s	29	168 (141, 236)

Table 7 (continued). Mean total length and range (minimum, maximum) in millimeters for yellow perch during 1990s and 2020s surveys on Isle Royale, Michigan. Number of measured fish (n) is also shown. Cells with N/A indicate yellow perch were sampled only with equipment other than gillnets.

Lake	Survey	n	Mean length (range)
Siskiwit	1990s	57	127 (109, 185)
	2020s	6	207 (181, 260)
Wagejo	1990s	11	336 (298, 356)
	2020s	2	206 (200, 211)
Whittlesey	1990s	107	157 (131, 241)
	2020s	7	167 (152, 211)

Table 8. Mean total length and range (minimum, maximum) in millimeters for white sucker during 1990s and 2020s surveys on Isle Royale, Michigan. Number of measured fish (n) is also shown. Cells with N/A indicate white sucker were not sampled with any equipment.

Lake	Survey	n	Mean length (range)
Ahmik	1990s	0	N/A
	2020s	16	434 (385, 484)
Angleworm	1990s	9	498 (450, 554)
	2020s	12	409 (230, 562)
Chickenbone	1990s	8	341 (160, 480)
	2020s	0	N/A
Desor	1990s	445	220 (115, 469)
	2020s	99	210 (167, 455)
Dustin	1990s	4	390 (223, 480)
	2020s	0	N/A
Harvey	1990s	248	267 (158, 377)
	2020s	120	251 (164, 366)
Hatchet	1990s	265	241 (159, 432)
	2020s	124	209 (162, 410)
Richie	1990s	80	397 (170, 580)
	2020s	16	436 (108, 510)
Sargent	1990s	9	290 (163, 543)
	2020s	1	449 (449, 449)
Siskiwit	1990s	76	234 (112, 502)
	2020s	26	257 (164, 522)
Whittlesey	1990s	58	435 (210, 594)
	2020s	12	473 (210, 567)

Table 9. Mean total length and range (minimum, maximum) in millimeters for walleye during 1990s and 2020s surveys on Isle Royale, MI. Number of measured fish (n) is also shown. Cells with N/A indicate walleye were not sampled with any equipment.

Lake	Survey	n	Mean length (range)
Chickenbone	1920s	109	299 (178, 566)
	2020s	58	442 (232, 555)
Dustin	1920s	1	513 (513, 513)
	2020s	0	N/A
Whittlesey	1920s	84	383 (212, 512)
	2020s	35	419 (271, 639)

Abundance

Changes in abundance also varied by species based on Wilcoxon signed-rank tests. Mean CPUE of northern pike increased from 5.15 to 7.75 between surveys ($p = 0.045$), with Angleworm increasing CPUE over five-fold and four additional lakes increasing over two-fold (Table 10). Yellow perch exhibited a slight decline in average CPUE from 16.7 to 12.8, although this difference was non-significant ($p = 0.143$). Lakes varied widely with regards to abundance shifts of yellow perch. Otter and Sargent showed 19-fold and 29-fold increases in yellow perch CPUE, respectively, while 12 lakes showed declines ranging from 56% to 100% (Table 10). The most extreme declines occurred in Forbes, Chickenbone, and Whittlesey. For white sucker, mean CPUE shifted from 19.0 to 14.1 but did not vary significantly between surveys ($p = 0.308$). We did not run analyses for the remaining species captured in gillnets due to limited distributions, although walleye abundance appeared to decline (Table 10).

Table 10. Catch per unit effort (CPUE) for species caught in gillnets during the two most recent surveys on Isle Royale, Michigan. Values of 0 indicate a species was present in the lake but not sampled with gillnets. Dashes indicate the species was not captured in any gear.

Lake	Northern pike		Yellow perch		Walleye		White sucker		Lake trout		Lake whitefish		Cisco		Burbot	
	1990s	2020s	1990s	2020s	1990s	2020s	1990s	2020s	1990s	2020s	1990s	2020s	1990s	2020s	1990s	2020s
Ahmik	5.50	5.00	1.50	4.50	–	–	–	8.00	–	–	–	–	–	–	–	–
Amygdaloid	3.50	8.50	3.50	0.00	–	–	–	–	–	–	–	–	–	–	–	–
Angleworm	4.17	22.00	6.00	2.50	–	–	1.50	2.67	–	–	–	–	–	–	–	–
Beaver	8.50	11.50	5.00	0.00	–	–	–	–	–	–	–	–	–	–	–	–
Benson	–	–	120.75	173.67	–	–	–	–	–	–	–	–	–	–	–	–
Chickenbone	6.00	4.00	21.33	1.17	18.17	9.67	1.33	–	–	–	–	–	–	–	–	–
Desor	–	–	–	–	–	–	83.50	65.33	–	–	13.00	17.33	1.33	4.17	–	–
Dustin	2.00	3.00	2.00	0.00	1.00	–	4.00	–	–	–	–	–	–	–	–	–
Forbes	–	–	62.00	1.50	–	–	–	–	–	–	–	–	–	–	–	–
George	3.00	8.00	3.00	8.00	–	–	–	–	–	–	–	–	–	–	–	–
Harvey	–	–	30.67	37.25	–	–	41.33	37.25	–	–	–	–	–	–	–	–
Hatchet	–	–	–	–	–	–	53.00	35.40	–	–	–	–	–	–	–	–
Lesage	7.00	8.17	8.17	0.67	–	–	–	–	–	–	–	–	–	–	–	–
Livermore	6.25	14.75	34.25	7.75	–	–	–	–	–	–	–	–	–	–	–	–
Mason	3.75	3.50	2.75	0.25	–	–	–	–	–	–	–	–	–	–	–	–
Otter	7.50	9.00	0.25	4.75	–	–	–	–	–	–	–	–	–	–	–	–
Patterson	3.00	8.50	2.00	3.00	–	–	–	–	–	–	–	–	–	–	–	–
Richie	6.78	9.11	4.78	4.89	–	–	8.89	1.89	–	–	–	–	0.00	0.11	–	–
Sargent	8.67	7.33	0.11	3.22	–	–	1.00	0.11	–	–	–	–	0.67	1.33	–	–
Siskiwit	0.31	0.31	3.56	0.38	–	–	4.69	2.19	5.31	4.19	2.94	4.56	0.44	0.00	1.19	0.69
Wagejo	8.50	5.50	5.50	1.00	–	–	–	–	–	–	–	–	–	–	–	–
Whittlesey	3.17	3.50	17.83	1.17	14.00	5.83	9.67	2.00	–	–	–	–	–	–	–	–

Discussion

Overview

We found measures of alpha, gamma, and beta diversity remained relatively stable across the study lakes, with only slight declines in species richness, shifts from cold-water species towards cool-water species, and no homogenization between surveys. TBI analyses indicated no lakes or species changed in exceptional ways between surveys, although patterns of gains and losses could be explained by several lake characteristics and species thermal guild. Lake area and elevation explained gradients in species richness and predator presence, respectively. Mean length and abundance also appeared to shift only slightly for certain species. Overall, this study highlights how a group of fish communities relatively isolated from direct human impact has responded to climate change, lake characteristics, and geological processes without other confounding anthropogenic effects, an important step in our understanding of diversity trends.

Objective 1: Temporal Patterns of Alpha, Beta, and Gamma Diversity

Alpha diversity remained relatively constant, and gamma diversity declined by one species across Isle Royale's inland lakes in the past century. This consistency indicates that either individual lakes experienced no net change or lakes differed in gains and losses but change balanced out across the region. Slopes of species-area curves did not significantly change over time but declined slightly in the most recent survey, suggesting gains and losses may be more common in small and large lakes, respectively. The full range of species richness contracted from 1–16 species in the 1920s to 2–13 species in the 2020s, and these findings could indicate consistent alpha diversity was caused by opposite shifts in richness along a lake size gradient. Previous studies have found high and low diversity lakes in Ontario tend to lose and gain species, respectively (Cazelles et al. 2019). Given the positive relationship between lake area and species richness, these results might suggest a similar pattern is occurring on a smaller scale in Isle Royale's inland lakes.

Spatial beta diversity across all lakes remained relatively constant between the three surveys. Neither differentiation nor homogenization of fish communities was evident based on dispersion tests, and community composition remained consistent based on multivariate centroid location. Wide variability in composition and richness among lakes may have obscured patterns at this broader scale, but analyzing only the larger, more diverse lakes highlighted shifts toward cool-water species and away from cold-water species. These findings indicate species shifts altered general composition but not variability among larger lakes, and there are a few plausible explanations for these patterns. First, suitable oxythermal habitat is decreasing in several lakes that have historically hosted cold-water species (Damstra et al. 2014; Xu et al. 2024), likely causing extirpation for species including sculpins, trout-perch, ninespine stickleback, and brook trout. It is unclear whether these losses were driven by lack of suitable habitat or sampling deficiency as other cold-water species including cisco, lake whitefish, and lake trout were detected in some lakes where these losses occurred. However, extirpation is certainly plausible given mid-summer temperature and oxygen profiles indicate at least some level of stress in non-refuge lakes (Gorman et al. 2014). Second, cool-water habitat is expanding within the inland lakes of Isle Royale given increased water temperatures (Xu et al. 2024).

Increased precipitation may create more persistent stream connections and facilitate immigration to new lakes (Magnuson et al. 1998; NPS CCRP 2024), and losses of cold-water species could promote colonization via reduced competition (Cornell and Lawton 1992). Species gains between the first two surveys could generally be attributed to stream dispersal (Kallemeyn 2000), and the same is true for the most recent survey as species gained in Wagejo were present in Sargent, species gained in Dustin were present in Whittlesey, and species gained in Ahmik, Amygdaloid, and Chickenbone likely migrated from Lake Superior. Wide variability in gains among lakes likely prevented homogenization despite common losses of sculpin species. No species colonized more than two of the six largest lakes, and the total number of gains varied from zero in Siskiwit to five in Chickenbone during the past century. Although both lakes have low elevation and direct stream outlets to Lake Superior, the Siskiwit outlet contains a barrier falls likely limiting immigration (Jay Glase, personal communication), while the Chickenbone outlet shows a more gradual, unobstructed gradient.

Objective 2: Lakes and Species Most Likely to Change

Our analysis of species contributions to community change further supports the pattern of changing composition but not homogenization. No species was dominant in its effect on community change based on SIMPER analysis, highlighting how the shift towards greater cool-water dominance was driven by multiple species. Both cool-water (pumpkinseed, blacknose shiner) and cold-water species (trout-perch, slimy sculpin) were among those with the largest contributions, and similar patterns emerged when assessing gains and losses by thermal guild. Cold-water species were most commonly lost, and cool-water species most commonly gained across all lakes, and opposite but relatively balanced trends among thermal guilds highlight how general community composition was able to shift but not homogenize. These results align with several previous studies highlighting the general northward range expansions and contractions of cool-water and cold-water species, respectively (Comte et al. 2013).

The lack of homogenization or differentiation also aligns with our temporal beta diversity analyses, which indicated a balance between gains and losses during all periods. Despite several gains and losses in multiple lakes, temporal beta diversity analyses showed no lake experienced significantly greater change than others. However, combinations of high stream connectivity, disturbance events, and reduced intensity of biotic interactions may explain why Chickenbone, Dustin, and Wagejo showed noticeably higher temporal dissimilarity (Magnuson et al. 1998; Rolls et al. 2023). At least one stream connection to a more diverse waterbody is present in all three lakes, likely facilitating immigration of new species. Winterkill could be an important disturbance allowing colonization via reduced competition and predation given relatively shallow depths (Henriksson et al. 2015). Low or declining northern pike, walleye, and yellow perch abundances were documented across these lakes coinciding with colonization by small-bodied species (Table 10). Two of these lakes lost at least three species in the last century, suggesting biotic interactions and opening of niche space may increase likelihood of species gains and overall temporal beta diversity (Cornell and Lawton 1992).

Several environmental variables explained spatial patterns in temporal beta diversity and gain-loss difference across our study lakes. Between the 1920s and 2020s, gains contributed more to temporal dissimilarity in lakes with faster isostatic rebound rates, while losses contributed more in lakes with

slower rebound. Differences in species saturation are one possible explanation, as mean richness shifted from 3.1 to 4.1 and from 6.7 to 5.7 in lakes with fast and slow rebound rates, respectively. Lakes with slower rebound may have initially experienced more colonization given longer exposure to the regional source pool during water level decline and lake formation (Hinch et al. 1991; Stephenson and Momot 2011; Illyes et al. 2023). The resulting higher richness may have subsequently limited future immigration success (Stachowicz and Byrnes 2006). Biotic interactions including competition and predation are generally more intense in diverse communities (Cornell and Lawton 1992), which reduces available niche space and likelihood of establishment even if stream connections are present. Recent introductions to Lake Superior's regional source pool combined with stable or declining alpha diversity in our study lakes also provides evidence of saturation (Tonn et al. 1990), and this pattern may explain why extirpation is dominant in lakes with slower rebound rates. In contrast, limited dispersal opportunity from faster isostatic rebound may have created historically species-poor communities. Low richness can indicate available niche space and facilitate establishment once dispersal becomes possible (Henriksson et al. 2015), explaining why gains were more common in lakes with faster isostatic rebound. However, there are several caveats to this explanation as we cannot explicitly quantify the degree of species saturation, available niche space, or specific factors limiting richness (Mateo et al. 2017; Olivares et al. 2018). Isle Royale's lakes are generally unproductive and consequently host depauperate communities relative to other regions, but low connectivity has likely prevented more recent introductions from the regional source pool to undersaturated lakes (Gorman et al. 2014). The strength of biotic interactions is also unclear, although northern pike are common and reduce colonization success in other contexts (Henriksson et al. 2015; Tonn et al. 1990). Niche opportunity also affects colonization (Shea and Chesson 2002), which also varies widely with habitat complexity among our study lakes. Consequently, although there is some evidence that saturation differences are driving variation in gains and losses, additional work is needed to explore these mechanisms of community change.

We also detected some relationships with lake factors over shorter time scales. Between the 1920s and 1990s, lakes with both fast rebound rates and larger watersheds experienced increased contribution of gains to dissimilarity compared to lakes with smaller watersheds. One possible explanation is larger watersheds have larger, more persistent stream outlets to facilitate fish movement, but we are unable to test this theory directly. For lakes with slower rebound rates, those with lower water clarity experienced more losses contributing to dissimilarity compared to clearer lakes. Low water clarity is mainly driven by high DOC in Isle Royale's lakes, which can correspond to increased acidity, low primary production, and less macrophyte cover (Erlandsson et al. 2010; Stasko et al. 2012). These conditions may be intolerable for species that experienced extirpation, although Matuszek et al. (1990) found pH thresholds of some lost species were well below levels measured in our study lakes. Interestingly, the opposite pattern was detected between the 1990s and 2020s during which gains contributed more to dissimilarity at higher DOC concentrations. One potential explanation is that tolerant species were responsible for gains in high DOC lakes, while more sensitive species were responsible for losses, although this remains unclear. DOC indirectly affects thermal, oxygen, and optical habitat in many ways that may be both beneficial and harmful to certain species (Stasko et al. 2012), which likely contributes to the conflicting patterns we observed.

We also observed a negative relationship between overall temporal dissimilarity and shoreline development during the most recent surveys. More convoluted shorelines can indicate more predation refuge and habitat variability that buffers environmental changes and biotic interactions, explaining why less change was detected in lakes with high shoreline development.

Objective 3: Spatial Patterns in Community Composition

Multivariate analyses highlighted two main environmental gradients, lake surface area and elevation, driving current community structure. Lake surface area was positively associated with species richness, as most species showed limited distributions in only the largest, deepest lakes with cold, oxygenated hypolimnions. These species included not only cold-water species such as cisco, lake whitefish, lake trout, and lake chub but also cool-water and thermally-tolerant species such as pumpkinseed, blackchin shiner, and golden shiner. It is well established that greater habitat complexity in larger lakes reduces extinction rates (Eadie et al. 1986; Minns 1989), particularly through more variable substrate types, macrophyte cover, and oxythermal habitat that can reduce the intensity of biotic interactions. Predator presence also shifted along an elevation gradient. Lakes in this study range from 1 m to 77 m above Lake Superior (Appendix 4), corresponding to lake formation times spanning roughly 140 to 10,000 years ago, respectively (Gorman et al. 2014). Five of the six highest lakes lacked northern pike, and two of the six were also missing yellow perch. Because high elevation is a common dispersal barrier and indicates earlier lake formation (Gorman et al. 2014; Illyes et al. 2023; Minns 1989), northern pike and potentially yellow perch were likely absent from the initial pool of colonizers. Both species have cool-water preferences, and cold conditions may have prevented early dispersal from glacial refuge through Lake Superior (Gorman et al. 2014). Some higher elevation lakes also hold cold-water species that were early migrants such as ninespine stickleback, lake chub, and trout perch, which further suggests thermal tolerance may have precluded initial colonization by northern pike. Freedom from predation is also evident in higher elevation lakes, which tend to host more unique small-bodied fish communities. For example, species such as lake chub, northern pearl dace (*Margariscus nachtriebi*), brook stickleback (*Culaea inconstans*), and fathead minnow (*Pimephales promelas*) were only found in lakes lacking northern pike. Previous research highlights the dominant influence of predation on community structure (Jackson et al. 2001), and this pattern highlights how dispersal barriers limited the effect of predation in high elevation lakes on Isle Royale.

Objective 4: Temporal Patterns of Size and Abundance

Despite some detected shifts in abundance and mean length, there are several caveats with this analysis. Catch data are based on two surveys over the past three decades, and the majority of lakes were sampled over only a few days with six gillnets or fewer. Lakes may also have been sampled at different times of the open-water season, which can impact these measures due to seasonal variation in habitat use. Variability in strong year classes may also drive the patterns we observed. However, it is possible that size structure and abundance have shifted due to biotic and or environmental factors. Bethke and Staples (2015) found declining CPUE of yellow perch and increasing CPUE of northern pike in recent decades across Minnesota lakes, and our results may indicate a similar pattern caused by greater predation pressure. Increases in northern pike abundance corresponded with declines of yellow perch in multiple lakes such as Angleworm and Livermore, although the direction and

magnitude of these patterns were highly variable across lakes. Yellow perch showed major declines in several lakes such as Forbes, Chickenbone, and Whittlesey, but it remains unclear whether these patterns were caused by lower abundance, shifts to smaller sizes, or both. Reduced catch rates of yellow perch due to smaller sizes have been documented in Minnesota (Holbrook et al. 2022), and this is certainly plausible given the concurrent increases in northern pike mean length and abundance in several lakes. Intraspecific competition may also be an important factor, especially in lakes that lack northern pike.

Conclusions

The fish communities of Isle Royale's inland lakes have been largely unimpacted by direct human effects, invasive species, and climate change in recent decades. No invasive or new native species were documented in the inland lakes, and cisco were found in all lakes where historically present. Despite this consistency, gains of cool-water species and losses of certain cold-water species like sculpins were common in larger lakes, suggesting some assemblages are becoming more cool-water dominated and may be at risk for additional change moving forward. More consistent monitoring will help determine how long certain populations will persist, whether undetected species have truly been extirpated, where immigration of new species may occur, and how fishing opportunities will persist in the future.

Projected increases in temperature and precipitation will likely have various impacts on different inland lakes. Although small, shallow lakes are generally the most susceptible to environmental change (Gorman et al. 2014), many of these communities on Isle Royale have already been filtered down to host limited fish diversity, containing only cool-water or thermally tolerant species such as northern pike, yellow perch, and blacknose shiner. Larger, deeper lakes are more buffered from climate effects, but these waterbodies on Isle Royale hold more sensitive species that require cold oxythermal habitat, which is currently threatened or absent in late summer, particularly in Richie Lake. Only one cisco was sampled from Richie Lake in the most recent survey, suggesting the population is on the brink of extirpation. Previous work predicted cisco had been extirpated from Lake Richie in the last decade, and it remains unclear how they have persisted to the present day. It is possible undocumented groundwater springs have facilitated survival, although there was no evidence of springs based on several sonde profiles taken in the western arm where the individual was sampled (Alex Egan, personal communication). Sargent and Desor also host cisco populations, and Desor contains lake whitefish as well. These two lakes appear to host suitable oxythermal habitat throughout the open water season in most years, but this volume of habitat can be limited in the late summer months, leaving potential for a complete oxythermal squeeze if warming continues. Siskiwit Lake contains the most abundant cold-water habitat of all Isle Royale's lakes, and this will likely remain stable in the foreseeable future given its size and depth. One interesting note is that cisco were not sampled in gillnets in Siskiwit Lake, although several small individuals were found in lake trout stomach contents.

It is possible that our current sampling and that of previous surveys failed to detect species present in a lake due to low sampling efficiency or low abundance, and different methods varied widely in their efficacy. Sculpin species accounted for most of our non-detections, and detections of slimy sculpin

only occurred via stomach content analysis in Siskiwit and Sargent Lakes. Other examples highlighting the importance of stomach content analysis were cisco in Siskiwit Lake, pearl dace in Lake Desor, and spottail shiner in Lake Whittlesey. Generally, minnow traps were ineffective even when baited, and all species caught in minnow traps were also caught in the seine. Future efforts should focus on seining to sample littoral habitat where the majority of fish diversity was located. It may also be worthwhile to seine during low-light hours, as seining was mostly performed mid-day in the most recent survey. Selectively using smaller mesh gillnets and vertical gillnets in lakes historically containing cisco and sculpin species may also be beneficial in future surveys.

Connectivity among inland lakes and with Lake Superior is another important consideration for predicting future change. Isolated, high elevation lakes such as Desor and Hatchet will more likely experience only losses, while connected, low elevation lakes such as Chickenbone may experience a combination of losses and gains. Changes in precipitation patterns may affect dispersal routes and immigration patterns, which may lead to new species including non-natives. It will be crucial to monitor a variety of these lake types moving forward, ideally every five years, to understand how fast changes will occur. We recommend the largest, most diverse lakes be regularly sampled (Siskiwit, Desor, Sargent, Richie, Chickenbone, Whittlesey), as well as those containing heritage species (Benson, Forbes, Harvey, Hatchet) based on Gorman et al. (2014). We also recommend sampling the other lakes at least every ten years, particularly those in which assemblage shifts occurred (Ahmik, Amygdaloid, Dustin, Wagejo) or where the most recent survey did not sample (Feldtmann, Intermediate, John, and others).

Recreational fishing for northern pike is important to many visitors of Isle Royale, particularly in Chickenbone and Richie Lakes (Kallemeyn 2000). Maximum size restrictions recently increased from 610 mm to 762 mm to expand the range of harvestable fish. It is unclear whether this regulation change is driving higher average size and abundance of northern pike, as fishing pressure across the island is relatively low. This highlights the importance of implementing future creel surveys, which will inform the park about angler harvest and success rates.

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Appendix 1: Lake Names and Codes

See Table 11 for lake names and codes.

Table 11. Lake names and abbreviations for 23 inland lakes on Isle Royale, Michigan.

Lake name	Lake code
Ahmik	AHM
Amygdaloid	AMY
Angleworm	ANG
Beaver	BEA
Benson	BEN
Chickenbone	CHI
Desor	DES
Dustin	DUS
Forbes	FOR
George	GEO
Harvey	HAR
Hatchet	HAT
Lesage	LES
Livermore	LIV
Mason	MAS
Otter	OTT
Patterson	PAT
Richie	RIC
Sargent	SAR
Scholts	SCH
Siskiwit	SIS
Wagejo	WAG
Whittlesey	WHI

Appendix 2: Fish Species and Codes

See Table 12 for fish species and codes.

Table 12. Species names and abbreviations for 30 species in the inland lakes of Isle Royale, Michigan.

Common name	Scientific name	Species code
Blackchin shiner	<i>Notropis heterodon</i>	BCS
Blacknose shiner	<i>Notropis heterolepis</i>	BNS
Brook stickleback	<i>Culaea inconstans</i>	BST
Brook trout	<i>Salvelinus fontinalis</i>	BKT
Burbot	<i>Lota lota</i>	BUB
Cisco	<i>Coregonus artedii</i>	TLC
Creek chub	<i>Semotilus atromaculatus</i>	CRC
Emerald shiner	<i>Notropis atherinoides</i>	EMS
Fathead minnow	<i>Pimephales promelas</i>	FHM
Finescale dace	<i>Chrosomus neogaeus</i>	FND
Golden shiner	<i>Notemigonus crysoleucas</i>	GSH
Iowa darter	<i>Etheostoma exile</i>	IWD
Lake chub	<i>Couesius plumbeus</i>	LKC
Lake trout	<i>Salvelinus namaycush</i>	LAT
Lake whitefish	<i>Coregonus clupeaformis</i>	LKW
Logperch	<i>Percina caprodes</i>	LGP
Mimic shiner	<i>Notropis volucellus</i>	MMS
Mottled sculpin	<i>Cottus bairdii</i>	MTS
Northern redbelly dace	<i>Chrosomus eos</i>	NRD
Ninespine stickleback	<i>Pungitius pungitius</i>	NST
Northern pike	<i>Esox lucius</i>	NOP
Northern pearl dace	<i>Margariscus nachtriebi</i>	PRD
Pumpkinseed	<i>Lepomis gibbosus</i>	PMK
Slimy sculpin	<i>Cottus cognatus</i>	SMS
Spoonhead sculpin	<i>Cottus ricei</i>	SHS
Spottail shiner	<i>Notropis hudsonius</i>	SPO
Trout-perch	<i>Percopsis omiscomaycus</i>	TRP
Walleye	<i>Sander vitreus</i>	WAE
White sucker	<i>Catostomus commersonii</i>	WTS
Yellow perch	<i>Perca flavescens</i>	YEP

Appendix 3: Water Quality Variables

See Table 13 for water quality variables (2023–2024).

Table 13. Water quality variables for the inland lakes of Isle Royale, Michigan, sampled between mid-July and mid-August of 2023 or 2024. ND = non-detection.

Lake	Chl-a (µg/L)	TP (µg/L)	TN (µg/L)	NOX (µg/L)	NHX (µg/L)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	K (mg/L)	SO4 (mg/L)	Si (mg/L)	Cl (mg/L)	Alkalinity (mg/L)	DOC (mg/L)	Secchi (m)
Ahmik	ND	29.11	702.0	ND	ND	11.1	4.4	2.16	ND	0.77	6.22	0.27 ^A	50 ^A	13	1.77
Amygdaloid	<1.00	15.80	466.0	49.0	12.5	8.7	3.1	1.70	0.325 ^A	0.59	3.83	0.42 ^A	44 ^A	8.7	4.16
Angleworm	2.22	15.20	403.0	8.4	13	5.3	1.8	1.12 ^A	0.200 ^A	1.60	4.79	0.21 ^A	29 ^A	4.7	6.02
Beaver	ND	17.06	505.0	ND	ND	9.9	4.2	2.35	0.285 ^A	1.40	7.53	0.30 ^A	40 ^A	8.7	2.43
Benson	ND	13.70	614.0	11.8	17.6	7.5	2.6	1.10 ^A	0.229 ^A	0.61	5.11	0.24 ^A	33 ^A	10	1.95
Chickenbone	ND	18.20	367.0	ND	ND	10.2	3.2	2.00	0.244 ^A	1.30	8.34	ND	37 ^A	6.6	2.55
Desor	3.01	9.48 ^A	505.1	ND	ND	12.5	3.7	1.75	0.404 ^A	1.30	2.06	0.50 ^A	43 ^A	5.3	2.50
Dustin	ND	11.30	463.0	<8.0	11.7	8.8	2.0	1.01 ^A	0.244 ^A	0.61	2.04	0.19 ^A	35 ^A	7.2	2.79
Forbes	ND	12.10	445.0	10.2	16.5	8.4	2.5	1.26	0.215 ^A	1.40	3.68	0.27 ^A	37 ^A	7.6	5.25
George	ND	10.95 ^A	456.1	ND	ND	19.4	1.5	1.11 ^A	ND	0.63	3.42	0.36 ^A	49 ^A	8.9	2.47
Harvey	1.00	11.94 ^A	468.5	ND	ND	9.0	3.4	1.84	ND	1.20	2.91	0.20 ^A	35 ^A	6.5	3.53
Hatchet	2.91	15.00	612.0	8.6	25.5	9.5	3.5	2.03	0.217 ^A	0.57	8.58	0.35 ^A	48 ^A	10	2.32
Lesage	<1.00	14.00	529.0	17.9	14.2	8.8	2.6	1.44	<0.190 ^A	1.30	4.15	0.24 ^A	42 ^A	10	2.55
Livermore	ND	17.80	442.0	8.6	12.1	10.4	3.6	1.97	0.234 ^A	1.50	6.63	0.30 ^A	43 ^A	7.2	5.20
Mason	1.84	13.70	650.0	<8.0	18.2	9.7	2.4	1.21	0.515 ^A	0.97	5.6	1.10	36 ^A	12	2.20
Otter	6.84	26.40	516.0	19.5	21.0	9.6	3.3	1.88	<0.190 ^A	0.43	5.13	0.27 ^A	49 ^A	9.1	1.64
Patterson	2.39	18.20	704.0	10.4	15.5	12.1	5.3	2.15	<0.190 ^A	0.18 ^A	6.01	0.20 ^A	57 ^A	16	1.44
Richie	1.69	24.82	445.5	8.3 ^A	10.0 ^A	9.2	2.5	1.53	0.265 ^A	1.40	5.58	0.74	32 ^A	7.2	3.16
Sargent	ND	21.83	408.8	ND	ND	10.0	3.4	2.06	0.290 ^A	1.40	8.53	0.53	46 ^A	6.7	3.43

^A Value was below the level of quantification.

Table 13 (continued). Water quality variables for the inland lakes of Isle Royale, Michigan, sampled between mid-July and mid-August of 2023 or 2024. ND = non-detection.

Lake	Chl-a (µg/L)	TP (µg/L)	TN (µg/L)	NOX (µg/L)	NHX (µg/L)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	K (mg/L)	SO4 (mg/L)	Si (mg/L)	Cl (mg/L)	Alkalinity (mg/L)	DOC (mg/L)	Secchi (m)
Scholts	ND	9.90	558.0	8.0	16.6	9.8	2.1	0.10 ^A	0.362 ^A	0.93	0.18 ^A	0.20 ^A	36 ^A	8.9	1.50
Siskiwit	ND	7.43 ^A	287.8	20.8	10.0 ^A	9.2	2.3	1.37	0.297 ^A	2.70	2.93	0.33 ^A	31 ^A	3.6	5.81
Wagejo	1.96	15.80	584.0	<8.0	13.7	9.0	3.2	2.03	<0.190 ^A	1.90	3.29	0.40 ^A	38 ^A	11	2.07
Whittlesey	ND	10.88 ^A	347.8	ND	15.2 ^A	8.2	1.8	1.22	ND	0.89	3.57	0.26 ^A	30 ^A	5.7	3.14

^A Value was below the level of quantification.

Appendix 4: Lake Morphometry and Physical Variables

See Table 14 for lake morphometry and physical variables.

Table 14. Morphometry and physical variables for inland lakes on Isle Royale, Michigan. Area, elevation (above Lake Superior), rebound rate, watershed area, shoreline development (SD), depth, and geometry ratio (GR) are from Gorman et al. (2014). Epilimnion and hypolimnion temperature and dissolved oxygen (DO), mean water column pH, and specific conductivity (EC) were measured between mid-July and mid-August of 2022, 2023, or 2024.

Lake	Area (ha)	Elevation (m)	Rebound (m/100 yr)	Watershed Area (ha)	SD	Depth (m)	GR	Epi Temp (°C)	Hypo Temp (°C)	Epi DO (mg/L)	Hypo DO (mg/L)	pH	EC (μS/cm)
Ahmik	10.3	9.5	0.90	35.4	2.1	3.4	5.3	20.62	18.64	8.59	1.51	7.25	97.2
Amygdaloid	10.8	3.8	0.87	26.1	2.7	8.8	2.1	23.79	16.20	8.00	0.89	7.19	80.9
Angleworm	50.4	57.3	0.85	495.6	3.0	8.4	3.2	22.74	17.16	8.72	2.63	7.36	47.0
Beaver	20.1	23.8	0.82	258.3	1.9	5.2	4.1	20.77	14.17	8.38	3.17	7.52	94.6
Benson	24.1	56.7	0.94	83.0	1.8	3.8	5.8	23.89	22.63	8.28	6.03	7.55	62.6
Chickenbone	92.6	1.2	0.83	1556.4	2.6	6.4	4.8	23.70	20.84	8.57	3.82	7.40	84.2
Desor	427.8	77.1	0.73	1436.7	1.8	14.0	3.2	20.10	10.62	9.08	4.30	7.66	104.1
Dustin	4.4	14.8	0.82	497.8	1.7	6.1	2.4	23.43	15.47	8.60	6.20	7.54	63.9
Forbes	6.8	52.8	0.86	40.8	3.0	5.8	2.8	23.77	16.74	8.60	6.98	7.59	70.0
George	3.8	20.7	0.82	18.1	2.0	2.7	5.2	22.68	22.24	8.50	8.64	7.65	109.2
Harvey	55.4	49.1	0.81	292.8	1.7	4.0	6.8	23.57	20.31	10.40	3.18	8.27	82.0
Hatchet	49.6	46.7	0.78	502.2	1.7	5.2	5.1	24.37	19.31	8.04	1.49	7.21	86.7
Lesage	45.0	40.2	0.83	933.0	2.4	6.4	4.0	24.48	17.76	7.77	1.37	7.14	73.4
Livermore	30.1	29.9	0.83	168.8	2.0	5.5	4.3	23.87	18.75	8.76	2.65	7.90	89.8
Mason	22.8	2.8	0.84	492.8	2.3	8.5	2.6	23.35	11.60	8.30	1.62	6.90	71.3
Otter	20.2	29.8	0.82	96.3	1.8	4.3	5.0	21.32	20.55	8.07	3.95	7.57	87.4
Patterson	10.1	6.8	0.89	43.3	1.8	3.6	5.0	22.90	18.10	7.52	0.24	7.38	99.1
Richie	216.2	8.2	0.83	2080.2	2.4	10.7	3.6	20.21	11.12	8.77	1.73	7.09	79.0
Sargent	143.4	28.8	0.85	1089.3	3.6	13.7	2.5	22.79	11.74	8.97	4.88	7.43	88.5

Table 14 (continued). Morphometry and physical variables for inland lakes on Isle Royale, Michigan. Area, elevation (above Lake Superior), rebound rate, watershed area, shoreline development (SD), depth, and geometry ratio (GR) are from Gorman et al. (2014). Epilimnion and hypolimnion temperature and dissolved oxygen (DO), mean water column pH, and specific conductivity (EC) were measured between mid-July and mid-August of 2022, 2023, or 2024.

Lake	Area (ha)	Elevation (m)	Rebound (m/100 yr)	Watershed Area (ha)	SD	Depth (m)	GR	Epi Temp (°C)	Hypo Temp (°C)	Epi DO (mg/L)	Hypo DO (mg/L)	pH	EC (µS/cm)
Scholts	2.3	20.8	0.82	469.3	2.1	1.5	8.1	21.54	21.55	8.04	8.00	7.62	69.0
Siskiwit	1635.2	17.8	0.78	7287.1	2.2	46.0	1.4	19.43	7.06	9.38	11.64	7.82	69.1
Wagejo	6.1	45.7	0.85	58.2	1.4	2.2	7.2	22.59	19.90	7.81	4.10	7.51	76.5
Whittlesey	65.0	24.8	0.82	450.5	2.4	7.6	3.7	22.25	14.38	8.82	3.26	6.96	66.5

Appendix 5: SIMPER Results

See Table 15 for SIMPER results: species contributions to community.

Table 15. Similarity percentages (SIMPER) showing contribution of each species to differences in community composition of the six largest lakes between each pair of surveys on Isle Royale, Michigan. Jaccard's dissimilarity was used for this analysis.

Survey Pair	Species	Contribution (%)
1920s/1990s	Slimy sculpin	0.056
	Blacknose shiner	0.055
	Pumpkinseed	0.053
	Spoonhead sculpin	0.052
	Cisco	0.049
	Walleye	0.049
	Iowa darter	0.048
	Trout-perch	0.048
	Golden shiner	0.047
	Logperch	0.047
	Brook stickleback	0.046
	Lake whitefish	0.045
	Ninespine stickleback	0.045
	Northern redbelly dace	0.037
	Blackchin shiner	0.036
	Lake chub	0.030
	Northern pike	0.030
	Pearl dace	0.030
	Spottail shiner	0.030
	Yellow perch	0.030
	Mimic shiner	0.028
	Burbot	0.025
	Emerald shiner	0.025
	Lake trout	0.025
	Mottled sculpin	0.020
	Brook trout	0.017
	Creek chub	0.000
	Fathead minnow	0.000
	Finescale dace	0.000
	White sucker	0.000

Table 15 (continued). Similarity percentages (SIMPER) showing contribution of each species to differences in community composition of the six largest lakes between each pair of surveys on Isle Royale, Michigan. Jaccard's dissimilarity was used for this analysis.

Survey Pair	Species	Contribution (%)
1920s/2020s	Slimy sculpin	0.065
	Trout-perch	0.057
	Blacknose shiner	0.054
	Golden shiner	0.052
	Pumpkinseed	0.051
	Spoonhead sculpin	0.050
	Cisco	0.048
	Walleye	0.048
	Iowa darter	0.047
	Logperch	0.046
	Lake whitefish	0.044
	Spottail shiner	0.041
	Brook stickleback	0.038
	Ninespine stickleback	0.038
	Blackchin shiner	0.034
	Lake chub	0.029
	Northern pike	0.029
	Pearl dace	0.029
	Yellow perch	0.029
	Mimic shiner	0.029
	Burbot	0.024
	Emerald shiner	0.024
	Lake trout	0.024
	Mottled sculpin	0.020
	Northern redbelly dace	0.017
	White sucker	0.017
	Brook trout	0.017
	Creek chub	0.000
	Fathead minnow	0.000
	Finescale dace	0.000
1990s/2020s	Trout-perch	0.061
	Pumpkinseed	0.054
	Golden shiner	0.054
	Slimy sculpin	0.052

Table 15 (continued). Similarity percentages (SIMPER) showing contribution of each species to differences in community composition of the six largest lakes between each pair of surveys on Isle Royale, Michigan. Jaccard's dissimilarity was used for this analysis.

Survey Pair	Species	Contribution (%)
1990s/2020s (continued)	Cisco	0.050
	Walleye	0.050
	Blackchin shiner	0.048
	Iowa darter	0.048
	Logperch	0.048
	Lake whitefish	0.047
	Northern redbelly dace	0.043
	Spottail shiner	0.043
	Brook stickleback	0.043
	Ninespine stickleback	0.041
	Spoonhead sculpin	0.034
	Blacknose shiner	0.032
	Lake chub	0.032
	Northern pike	0.032
	Pearl dace	0.032
	Yellow perch	0.032
	Mimic shiner	0.030
	Burbot	0.026
	Emerald shiner	0.026
	Lake trout	0.026
	White sucker	0.018
	Mottled sculpin	0.000
	Brook trout	0.000
	Creek chub	0.000
	Fathead minnow	0.000
	Finescale dace	0.000

Appendix 6: Species Thermal Classes and Net Changes

See Table 16 for species thermal classes and net change.

Table 16. Thermal classes of 30 species found on Isle Royale, Michigan, based on Gorman et al. (2014) with total number of gains and losses during the entire study. Note mottled sculpin were classified as a cool-warm species but included in the thermally tolerant group for analyses.

Species	Thermal Class	Gains	Losses	Net Change
Brook trout	Cold	0	2	-2
Burbot	Cold	0	0	0
Lake trout	Cold	0	0	0
Lake chub	Cold	0	0	0
Lake whitefish	Cold	0	0	0
Ninespine stickleback	Cold	1	2	-1
Spoonhead sculpin	Cold	0	3	-3
Slimy sculpin	Cold	0	4	-4
Cisco	Cold	0	0	0
Trout-perch	Cold	0	2	-2
Blackchin shiner	Cool	3	0	3
Blacknose shiner	Cool	2	0	2
Brook stickleback	Cool	2	3	-1
Finescale dace	Cool	0	0	0
Iowa darter	Cool	1	0	1
Northern pike	Cool	0	0	0
Northern redbelly dace	Cool	3	1	2
Pumpkinseed	Cool	3	0	3
Pearl dace	Cool	0	1	-1
Spottail shiner	Cool	1	2	-1
Yellow perch	Cool	1	0	1
Creek chub	Tolerant	0	0	0
Emerald shiner	Tolerant	0	0	0
Fathead minnow	Tolerant	0	0	0
Golden shiner	Tolerant	1	1	0
Logperch	Tolerant	0	1	-1
Mimic shiner	Tolerant	0	0	0
Mottled sculpin	Tolerant	0	1	-1
Walleye	Tolerant	0	1	-1
White sucker	Tolerant	2	3	-1

National Park Service
U.S. Department of the Interior



Science Report NPS/SR—2026/375
<https://doi.org/10.36967/2316629>

Natural Resource Stewardship and Science

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