

ARTICLE

Climate Ecology

Differential responses of coolwater fishes to a whole-lake reduction of a warmwater thermal guild

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Abstract

Climate change is transforming the ecology of lakes at a rapid pace, shifting some lakes toward warmwater-dominant habitats. As a result, warmwater fishes are increasingly becoming more prevalent in lakes where they already existed, altering the patterning and strength of species interactions. Understanding shifting species interactions (e.g., competition, predation), and the role of lake management in shaping these interactions, will be critical for lake stewardship in response to climate change. Here, we present results from an intensive 5-year experimental removal of ~285,000 warmwater fishes from a north-temperate lake. The goal of the experiment was to test whether warmwater fish reduction is effective for rewiring lake food webs to reverse undesirable conditions for coolwater species, leading to increased recruitment and abundance of coolwater fishes. Throughout the experiment, warmwater fishes were resilient to reductions, with biomass declines of 23% averaged across five species. Among coolwater fishes, the top predator walleye showed no biomass response, while yellow perch biomass increased by ~914%. Fish species biomass changes translated to food web shifts, including a yellow perch trophic position decline of 0.4, decreased zooplankton abundances, and increased zoobenthos abundances. Our results highlight differential species responses to a management action aimed at adapting to climate change. Despite similar

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thermal tolerances, two coolwater species responded differently to removal of warmwater fishes, highlighting the characteristics (e.g., life history strategies, adaptive capacity) that contribute to species resilience. Given the importance of biotic interactions, climate adaptation may need to go beyond a “one-size-fits-all” approach even when species have similar thermal tolerances.

KEYWORDS

adaptation, climate change, fisheries, food webs, freshwater, species interactions

INTRODUCTION

Climate change is transforming the ecology of lakes at a rapid rate, leading to rising and increasingly variable water temperatures (O'Reilly et al., 2015; Woolway & Maberly, 2020). North-temperate lakes often support multiple thermal guilds of fishes, including warm, cool, and coldwater species (Krabbenhoft et al., 2020). Climate warming is generally shifting thermal habitats toward increased suitability for warmwater fishes while decreasing suitability for cold and coolwater fishes in some areas. As a result, warmwater fish abundances are generally increasing, alongside potentially amplified interactions between previously segregated thermal guilds (Figure 1;

Hansen et al., 2015, 2017; Robillard & Fox, 2006). Further, some lakes with a combination of warm- and cool- or cold-water thermal habitat (e.g., “two-story” lakes) may lose coldwater and/or coolwater habitats and species altogether (Figure 1; Hansen et al., 2017). Thermal habitat mediates the interactions between warm- and coolwater fishes, and in lakes where thermal guilds coexist, biotic interactions may play an increasingly important role (Hellmann et al., 2012; Klanderud, 2005). Yet it is unknown how management actions aimed at shifting biotic interactions under climate change impact various thermal guilds and species, especially in freshwater ecosystems (Bartley et al., 2019; Hellmann et al., 2012; Klanderud, 2005; Suttle et al., 2007).

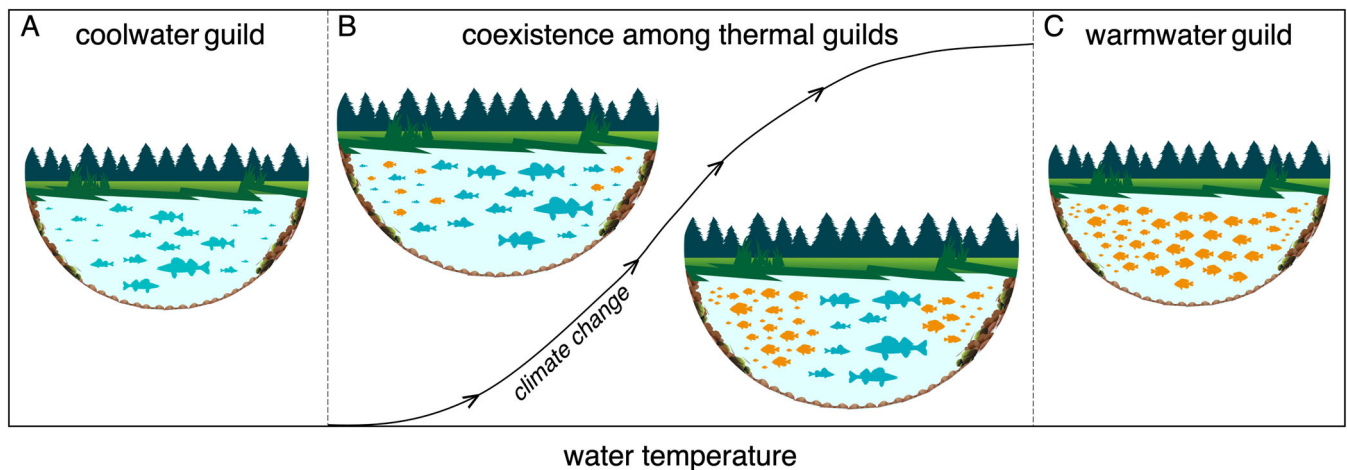


FIGURE 1 The anticipated shift from the dominance of cool- and cold-water fish guilds to warmwater guilds with warming water temperatures due to climate change. (A) In lakes with low water temperatures, thermal habitat necessitates a cold- or coolwater fish guild (blue fish). (C) For lakes with high water temperatures, thermal habitat necessitates a warmwater fish guild (orange fish). (B) Many lakes are intermediate and have both cool- and warm-water thermal habitats, especially deeper lakes which undergo thermal stratification. This allows sympatry of the two thermal guilds. In these lakes, cool- and warm-water fishes may loosely partition thermal habitat. But given that lake habitats are closely coupled, there is strong potential for ecological interactions (predation and competition) between cool- and warm-water guilds. Climate change is shifting thermal conditions toward warmwater conditions. This can manifest in several ways depending on the lake type. (1) historically cool lakes may become suitable for warmwater fish, resulting in expansion of warmwater fish, and coexistence of warmwater and coolwater guilds (A to B); (2) in coexistence lakes, abiotic conditions shift to give an advantage to warmwater fishes (relative dominance of species shifts within B); or (3) lakes with warm- and coolwater thermal habitat lose coolwater thermal habitat and become only suitable for the warmwater guild (B to C). The relative influence of abiotic and biotic drivers in these contexts may influence community compositions.

In many warming north-temperate lakes, abundances of coolwater fishes (e.g., Percidae species) have declined (Brandt et al., 2022; Holbrook et al., 2021; Rypel et al., 2018), while warmwater fishes (e.g., Centrarchidae species; hereafter centrarchids) have increased in abundance (Hansen et al., 2015, 2017). Coolwater fish declines accompanied by warmwater fish increases may alter the strength of species interactions (e.g., competition, predation) wherein coolwater fishes experience increased predation and/or competition, creating additional and unexpected constraints for sensitive species. We defined and measured species interactions according to long standing experimental community ecology approaches (e.g., Paine, 1980) where interaction strength is measured as the effect that a change in abundance of one species or aggregate (here thermal guild) has on the abundance of other species. This approach included quantifying the outcome or effect of all interactions, direct and indirect, including, for example, predation, competition, and other types of community interactions such as non-consumptive interactions.

The relative dominance of a species hinges on a combination of abiotic and biotic drivers (Hellmann et al., 2012; Suttle et al., 2007), thus understanding the importance of food web interactions relative to thermal habitat is key to developing effective climate adaptation approaches for coolwater fishes in a changing climate. One potential solution that is occasionally discussed in fisheries management is the direct removal of warmwater

species. Targeted fish removals have been used to control invasive species, reduce competition, and restore declining fish populations by selectively removing undesirable species while promoting the growth of ecologically or economically valuable fish populations (Carpenter et al., 1995; McQueen et al., 1989; Mrnak et al., 2025; Schindler, 1974); however, some whole-lake manipulations and theoretical approaches have revealed that continuous intervention is necessary, while others have successfully resulted in long-term regime shifts (Jarvis et al., 2024; Mehner et al., 2002; Tunney et al., 2017). Aside from the potential for a compensatory response (Weber et al., 2016; Zipkin et al., 2008), it remains an open question whether the reduction of warmwater species, while inherently expensive, might confer a fitness advantage or turnaround for declining coolwater species because of reduced biotic pressures.

Here, we present results from an intensive 5-year experimental removal of warmwater fishes from a north-temperate lake to test the hypothesis that warmwater-coolwater biotic interactions (e.g., competition, predation) regulate coolwater fish biomass and prey use. From 2018 to 2021, we removed ~285,000 warmwater centrarchids from a 33.1 ha lake in northern Wisconsin, USA, and contrasted biomass changes in that lake with a nearby unmanipulated 44.5 ha reference lake. Prior to removal, both lakes had warmed substantially since the mid-2000s, which increased warm and coolwater habitat (Figure 2). While performing

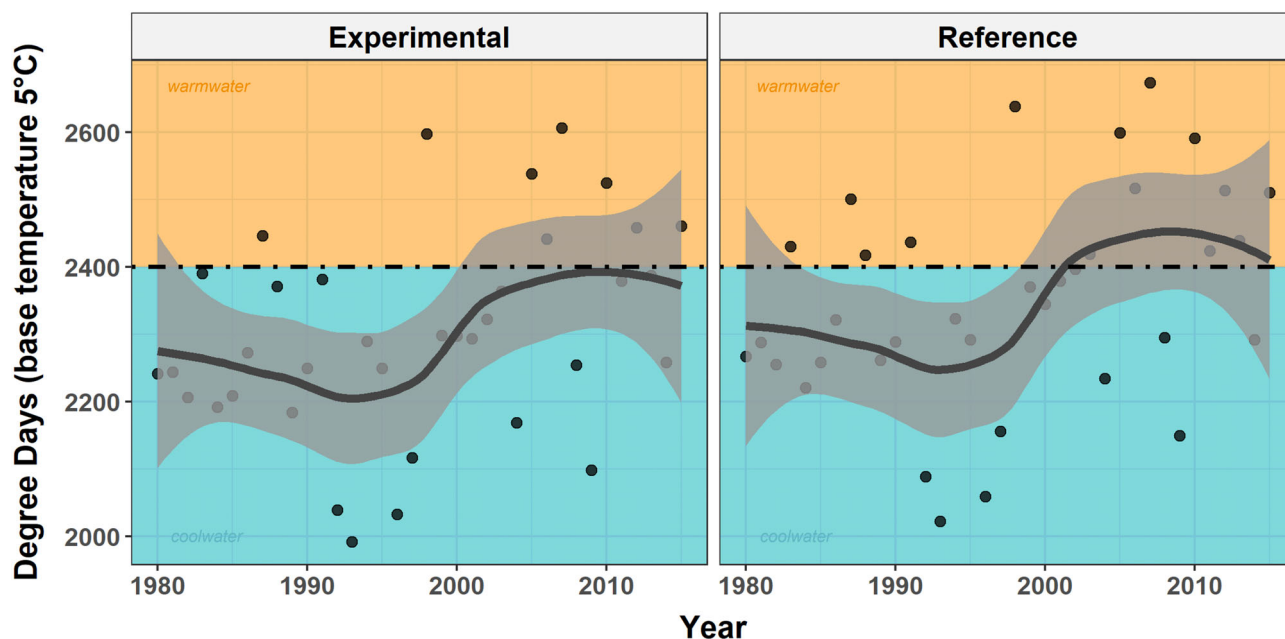


FIGURE 2 Estimated growing degree days (GDD, base water temperature 5°C, Winslow et al., 2017) for the experimental and reference lakes from 1980 to 2015. Black dots correspond to annual GDD estimates. Gray shaded area and line correspond to loess smoother. Horizontal dot-dash lines correspond to the approximate Hansen et al. (2017) degree day (base temperature 5°C) threshold between warmwater (orange) and coolwater (blue) species dominance.

extensively targeted removals, we quantified relative biomasses of cool and warmwater fishes, fish habitat reliance (i.e., carbon stable isotopes), fish prey reliance (i.e., stomach contents, nitrogen stable isotopes), as well as abundances of lower trophic level organisms (i.e., zooplankton, zoobenthos). If warmwater species interactions (e.g., competition, predation) were regulating coolwater species abundances, we predicted that the reduction of warmwater fishes would lead to reduced competition and predation on coolwater species, leading to increased coolwater fish abundances. We hypothesized these changes would be mediated through altered competition and predation dynamics; specifically, that reduced warmwater species would reduce predation on coolwater fishes and invertebrates, leading to higher coolwater species abundances, reduced invertebrate abundances, as well as increased fish reliance on benthic resources (e.g., enriched carbon stable isotopes) and lower trophic levels (e.g., decreased fish trophic positions). Understanding the importance of abiotic and biotic drivers in regulating warming food webs can inform trophic ecology as well as enable ecosystem-based fisheries management.

METHODS

Study area

We used a 2×2 study design wherein we evaluated an experimental and reference lake before and after manipulation. The experimental unit was “lake,” the manipulation involved warmwater fish removals, and response variables included percid biomasses and trophic positions as well as invertebrate relative abundances. By employing a whole-lake experiment, we manipulated one component (warmwater fish abundance) and then compared results to a nearby reference lake in which all other factors (environmental drivers, fish species assemblage, management regime) were kept constant. This is a method grounded by decades of studies using whole-ecosystem manipulations aimed at understanding the role of biotic interactions in regulating ecosystems (Carpenter et al., 2001; He & Kitchell, 1990; Radinger et al., 2023).

Selecting the experimental and reference lakes involved a lengthy community outreach and lake evaluation process that began with >50 candidate lakes and included extensive consultation with the Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) biologists, and public meetings with lakeshore property owners. Additionally, the experimental and reference lakes were selected based on a series of abiotic and biotic

characteristics. Selection criteria for study lakes included: existing coolwater fish (e.g., walleye *Sander vitreus*, yellow perch *Perca flavescens*) populations supported by natural recruitment, available coolwater fish spawning habitat, and an increase in warmwater centrarchid abundances. The two lakes were also chosen to be relatively close together in space and similar in area and depth characteristics. The experimental (McDermott Lake; 46.00299280 N, 90.16081610 W) and reference (Sandy Beach Lake; 46.10614350 N, 89.97131020 W) lakes are in Iron County in northern Wisconsin. The experimental lake has a surface area of 33.1 ha, a mean depth of 3.0 m, and a maximum depth of 5.7 m. The reference lake has a surface area of 44.5 ha, a mean depth of 2.1 m, and a maximum depth of 4.0 m. Both lakes are headwater drainage lakes and contain a variety of substrates (e.g., rock, gravel, and sand) and areas of submerged and emergent vegetation. Throughout the study, we aimed to maintain consistency in the factors potentially affecting the study lakes, except for the removal of warmwater species in the experimental lake. To achieve this, existing management measures, such as harvest regulations, were kept unchanged.

At the start of the study, the experimental and reference lake fish communities were similar with high overall centrarchid abundances (e.g., black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, and pumpkinseed *Lepomis gibbosus*); however, there were some lake-specific differences in which species were highest and lowest in abundance (Table 1). Both lakes had few adult walleye and a history of natural walleye recruitment, albeit at low rates. Yellow perch and walleye are highly sought-after coolwater fishes, supporting economically important recreational and culturally important Tribal fisheries, but have declined by ~30% in some parts of their range (Cichosz, 2017; Embke et al., 2019; Hansen et al., 2022). For Wisconsin lakes, the natural recruitment of walleye is defined as the relative abundance of non-stocked age-0 individuals collected in fall electrofishing surveys (Cichosz, 2017). Natural recruitment was last detected in both lakes in 2003–2004, with higher age-0 catch per unit effort (CPUE) in the reference lake (annual mean = ~6.51 individuals/km) compared to the experimental lake (annual mean = ~1.67 individuals/km; see below for further information on recruitment survey methodology). Like other walleye populations across the upper Midwest United States, both lakes have experienced declines in adult walleye abundance and have been stocked with extended growth fingerlings (~150–225 mm TL) during the fall of every other year since at least 2011. Other coolwater species present included yellow perch, northern pike *Esox lucius*, and muskellunge *Esox masquinongy*, as well as warmwater species such as black bullhead *Ameiurus melas* and golden

TABLE 1 Species-specific thermal guild, mean optimal maximum water temperature (in degrees Celsius; Mandeville et al., 2019), age-1+ relative biomass (BPUE; in kilograms per gear), log response ratio, and percent (in percentage) change for the experimental (McDermott) and reference (Sandy Beach) lakes before (2017) and after (2021) warmwater fishes were removed from the experimental lake.

Lake	Thermal guild	Fish species	MOM water temperature (°C)	Biomass per unit effort (kg/gear)		Log response ratio	Percent change	Statistically significant
				Pre-removal	Post-removal			
Experimental	Warm	Black Crappie	26.56	2.087	0.242	−0.936	−88.42	Yes
		Bluegill	31.59	1.645	0.777	−0.326	−52.79	Yes
		Largemouth Bass	31.38	0.046	0.068	0.170	47.78	No
		Pumpkinseed	29.78	0.055	0.092	0.223	67.27	No
		Rock Bass	30.24	0.134	0.013	−1.024	−90.54	Yes
	Cool	Walleye*	25.99	1.455	0.698	−0.319	−52.07	No
		Yellow Perch	25.01	0.456	4.627	1.006	914.06	Yes
Reference	Warm	Black Crappie	26.56	1.239	4.776	0.586	285.55	No
		Bluegill	31.59	0.076	0.133	0.243	75.00	No
		Largemouth Bass	31.38	0.006	0.014	0.379	139.06	No
		Pumpkinseed	29.78	0.024	0.022	−0.041	−8.91	No
	Cool	Walleye*	25.99	5.339	1.637	−0.513	−69.33	No
		Yellow Perch	25.01	0.521	2.068	0.599	296.81	No

Note: If no individuals were collected in 2017, 2018 values are shown. Modeled predictions are presented for statistically significant trends, and empirical estimates are presented for statistically insignificant trends. For walleye, the total population biomass (in kilograms per hectare) is presented.

Abbreviation: MOM, mean optimal maximum.

* $\alpha = 0.05$ (adjusted for multiple comparisons) was used for to assess statistical significance.

shiner *Notemigonus crysoleucas*. We recognize fish thermal guilds are a continuum and species categorizations may vary depending on context; for example, here we consider all centrarchids to be warmwater species given the relative thermal requirement differences to other focal fishes (e.g., walleye, yellow perch), but some studies categorize black crappie as coolwater (Wszola et al., 2024).

Limnological sampling

Each year, we deployed continuously recording HOBO temperature loggers at three sites in the littoral zone and four loggers spaced evenly along a rope fixed at 1 m increments at the deepest point of the lake from early May until mid-September. Water temperature was recorded every 30 min. From these data, we calculated mean daily littoral and pelagic water temperatures.

Fish sampling

Standardized surveys

During 2017–2021, standardized monitoring surveys were conducted using numerous sampling techniques to test

for changes in fish communities of both lakes. Sampling began immediately after ice-out (~mid-April) with the deployment of five fyke nets (1.2 × 1.8 m frames, 1.9 cm bar mesh) for 1 week at nonrandom locations in habitats that were probable walleye spawning sites (Hansen et al., 1991). The fyke-net surveys served two purposes: (1) to capture walleye for marking as part of the mark–recapture survey to attain an adult population estimate (PE); and (2) to estimate relative abundances (fish per net night) of black crappie and yellow perch. All collected walleye were measured (total length [TL]; in millimeters), sexed, checked for a uniquely coded passive integrated transponder (PIT) and implanted with a PIT if one was not present. Adult walleye were defined as: fish ≥ 381 mm or fish for which sex could be determined by extrusion of gametes (regardless of length; Cichosz, 2017). Walleye of unknown sex < 381 mm were classified as juvenile (immature). WDNR protocols were followed to estimate walleye populations, where the goal was to mark 10% of the anticipated spawning population (based on previous PEs; Cichosz, 2017). Marking continued until the target number was reached or spent females began appearing in fyke nets. Tagged walleye were recaptured using nighttime AC boat electrofishing of the entire shoreline within 1 week (typically 1–4 days) after netting and marking were completed (Beard et al., 1997). PEs

were calculated using Chapman's modification of the Petersen estimator (Chapman, 1951; Cichosz, 2017). To determine black crappie and yellow perch relative abundances and size distributions, all individuals were counted, and TL (in millimeters) was measured from a subsample of 30 fish per species per day for each lake.

We used a combination of standardized surveys to quantify centrarchid relative abundances of species other than black crappie (i.e., bluegill, largemouth bass *Micropterus salmoides*, pumpkinseed, and rock bass *Ambloplites rupestris*). In early summer (May, water temperatures = 13.0–21.0°C), we began surveys with an AC boat electrofishing. During June–August, we sampled fish once monthly when lake surface water temperatures were $\geq 13.0^\circ\text{C}$ in both lakes (water temperatures = 18.3–26.7°C; Simonson et al., 2008). Both lakes were sampled for 1 week each month using three gears (AC boat electrofishing, mini-fyke nets, cloverleaf traps; Sullivan et al., 2019). Lakes were sampled on consecutive nights in each 1-week period, but only one gear type was used per night. All gears sampled shallow littoral zones (0–5 m from bank, depth ≤ 2 m) and were deployed in fixed locations following standard approaches (Bonar et al., 2009). Sampling locations were evenly distributed along the lake shoreline, and all gears were deployed in similar habitat types. Five 10-min nighttime boat electrofishing (Wisconsin-style; AC; 2.0–3.0 A, 200–350 V, 25% duty cycle) transects were conducted using two dipnetters covering the majority (>80%) of the shoreline and spanning a variety of habitat types (e.g., vegetation, sediment, and gravel). Five mini-fyke nets (0.9 × 0.61-m frames, 3.2-mm mesh [bar measure], 7.6-m-long lead, and a double throat) were deployed in areas where the net frames would be in 1.0–1.5 m of water, with leads fixed onshore. Five cloverleaf traps (three lobed, height = 41 cm, 50 cm diameter, 6.0-mm bar wire mesh with 12.7-mm-wide openings between lobes, and an attractant [beef liver]) were deployed in littoral habitats. Mini-fyke nets and cloverleaf traps were set in the early afternoon, fished overnight, and retrieved the following afternoon (~24-h soak time). All catches were standardized according to gear-specific effort. For boat electrofishing, CPUE was calculated as the number of individuals captured per hour. For mini-fyke nets and cloverleaf traps, CPUE was calculated as the number of individuals captured per net-night or trap-night.

To estimate walleye recruitment, we used multiple gears including ichthyoplankton surface trawls, micro-mesh gillnets, beach seines, and boat electrofishing. A 1000- μm mesh ichthyoplankton net was towed within 1 m of the water surface at five locations in each lake at night roughly every 7 days, beginning 2 weeks after the presumed walleye spawn until June (Isermann & Willis, 2008). During late July/early August, four standard

horizontal gillnets (46 × 1.2-m with 0.64-cm bar mesh) were deployed. Sampling locations were evenly distributed along the shoreline, and locations were fixed each year. Gillnets were set at night at depths ranging from 0 to 5 m. Set duration ranged from 1 to 2 h to minimize bycatch (Boehm et al., 2020). When water temperatures were $< 21^\circ\text{C}$ (early September), age-0 walleye were targeted using nighttime boat electrofishing of the entire shoreline of each lake (Wisconsin-style; AC; 2.0–3.0 A, 200–350 V, two netters). Surveys were conducted prior to walleye fingerling stocking, meaning any collected age-0 walleye were produced via natural recruitment.

Warmwater fish removals

In addition to standardized surveys, centrarchid removal efforts began in 2018 in the experimental lake using a variety of techniques including fyke nets, boat electrofishing, mini-fyke nets, and cloverleaf traps. Following spring fyke net surveys, fyke nets remained in the experimental lake to remove centrarchids. In 2018, 10 fyke nets were used to remove fish daily from May 14 to June 7 and in 2019, from May 9 to June 27. In 2020 and 2021, only five fyke nets were used from late spring (April 30 and May 10) until late June (June 25 and June 11) due to personnel limitations. Additionally, five mini-fyke nets and 21 cloverleaf traps were sampled from late May to mid-August each year. All gears were emptied every 1–2 days where centrarchids were retained while other species were returned to the lake. Sites were rotated throughout the sampling season to maximize centrarchid catches. Collected fish were identified to species and up to 30 individuals per species per gear type were measured daily (TL, in millimeters). Centrarchid species were retained while other species were returned to the lake. Species removed included black crappie, bluegill, green sunfish *Lepomis cyanellus*, pumpkinseed, rock bass, largemouth bass, and smallmouth bass *Micropterus dolomieu*. Removed centrarchids were used for age estimation (see below) or donated to local wildlife health centers.

Fish processing

To understand demographic changes of centrarchid and yellow perch populations in the experimental and reference lakes, up to 20 individuals per ~25 mm size interval were retained for analyses from each lake. In the lab, individuals were dissected and species, TL (in millimeters), mass (in grams), and stomach contents (in percentage of wet mass) were recorded. Stomach contents were weighed,

then components were identified to the lowest taxonomic resolution possible and recorded as percentage of wet mass. Dorsal tissue samples were taken and frozen until processing for stable isotope analyses. All tissue samples were dried for ~24–48 h at 60°C, ground, and ~1.25 g was sealed in a capsule. Samples were sent to the UC Davis Stable Isotope Facility for carbon and nitrogen stable isotope analysis. Sagittal otoliths were removed from fish to determine if an individual was age-0 or age-1+. Ages were estimated using a combination of whole and thin-sectioned otoliths. To generalize across species, whole otoliths were typically used for fish <150 mm TL and sectioned otoliths were always used for fish >150 mm TL (Hoyer et al., 1985; Schramm, 1989). Whole otoliths were submerged in water in a black dish and viewed using a Nikon 1500 SMZ stereomicroscope under reflected light; images were projected to a 76 × 45 cm flat-screen LCD monitor via a Nikon DS-Fi2 or DS-Fi3 color camera connected to Nikon NIS-Elements software (Schramm & Doerzbacher, 1982). To section otoliths, one otolith was embedded in epoxy and a transverse section (1.2 mm) through the focus was obtained using a low-speed saw (Wegleitner & Isermann, 2017). Otolith sections were glued to microscope slides with cyanoacrylic cement and were projected using the same microscope, camera, and software configuration but under transmitted light. Ages were estimated independently by two readers; when disagreements occurred, consensus ages were obtained by the two readers viewing the otoliths together. If a consensus age could not be reached, the fish was not used for age assignment.

Zooplankton and zoobenthos sampling

In both lakes each year, we sampled the invertebrate community, including both zooplankton and zoobenthos. From May to mid-August, we sampled zooplankton during the day and night at bi-weekly intervals. Zooplankton samples were taken at the deepest point in each lake by pulling a conical net (15 cm diameter, 80 µm mesh) vertically through the water column (i.e., vertical tow sample). After the net was raised and the sides rinsed, the sample was transferred to a bottle and preserved in 90% ethanol. Each sample was standardized to a sample volume of 100 mL; organisms were identified to family and enumerated in three separate 1-mL subsamples obtained by a Hensen-Stemple pipette. Abundances for each sample were standardized to the volume of water sampled based on the sampling depth and net opening area (in number of individuals per liter).

Twice each summer (late June and early August) we sampled zoobenthos using an Ekman sampler

(3 L, 0.02 m²) along three transects per lake. At each transect, we took three samples at depths of 0.5–1, 2, and 3–4 m. Ekman samples were transferred into a sieving bucket (500 µm). All material remaining on the sieve was transferred into sampling bottles and preserved in 90% ethanol. In the laboratory, macroinvertebrates were identified from the samples using a dissecting microscope and taxonomic keys by Merritt and Cummins (1996). We identified most taxa to order (i.e., Amphipoda, Bivalvia, Coleoptera, Diptera, Ephemeroptera, Gastropoda, Odonata, Oligochaeta, and Trichoptera). A few groups were classified to class (i.e., Hirudinae and Ostracoda). Nematoda was identified to phylum. Densities were expressed as the number of individuals per square meter.

For stable isotope analyses, we collected zooplankton and zoobenthos samples in June and August. Zooplankton and zoobenthos samples were collected using the same methods employed to measure relative abundance; however, samples were not stored in ethanol following collection. Samples were instead frozen until processing for stable isotope analyses. Samples were dried for ~24–48 h at 60°C, ground, and ~1.25 g was sealed in a capsule. Samples were sent to the UC Davis Stable Isotope Facility for carbon and nitrogen stable isotope analysis.

Data analyses

Water temperature

Winslow et al. (2017) estimated annual growing degree days (base temperature 5°C; GDD_{5°C}) for both study lakes from 1980 to 2015. From these estimates, it was found that for lakes with ~2400 GDD_{5°C}, the probability of largemouth bass (i.e., warmwater guild) versus walleye (i.e., coolwater guild) dominance is relatively equal (Hansen et al., 2017). Therefore, we used estimated GDD_{5°C} as a metric to assess the thermal characteristics of the study lakes across the study period (Figure 2).

Fish biomass

Walleye biomass density (in kilograms per hectare) was estimated by multiplying lake-year-specific PEs (*n*) by mean individual mass (in kilograms), which was then divided by lake area (in hectares) to derive biomass density (in kilograms per hectare). For centrarchids and yellow perch, we estimated trends in biomass per unit effort (BPUE) over the study period by extrapolating lengths and masses to unmeasured fish for each species and gear type. On each sampling day, a subset of fishes was measured (daily maximum = 30 per species per gear), while

all individuals were counted. Daily lengths were then used to assign TL (in millimeters) to unmeasured individuals according to the total number of individuals collected. Measured fish lengths were sampled with replacement and used to assign lengths to unmeasured fish. To estimate species-specific biomass (in kilograms), species-specific mass-length regressions were developed for each year within each lake to predict masses (in grams) of fishes that were not weighed by regressing $\ln$ -transformed mass on $\ln$ -transformed length, then back-transforming these to predict individual mass from individual length. Once all sampled fish had an assigned mass, we calculated species-specific daily BPUE for each lake-gear combination.

We assessed temporal trends of fishes that collectively comprised the majority (>95%) of overall species abundances: black crappie, bluegill, pumpkinseed, rock bass, largemouth bass, walleye, and yellow perch. To remain consistent across years, removal sampling dates were separated from survey sampling dates. Removal data were used to estimate abundance (n) and biomass (in kilograms) of centrarchids removed from the experimental lake. Standardized survey BPUE was compared across years to test for changes due to the removal experiment. Species susceptibility to gears varies across seasons. Therefore, depending on the species of interest, different (or a combination of) surveys were used to test for changes in abundance over time. To test for changes in black crappie and yellow perch relative abundances, spring fyke net survey catches were used, whereas boat electrofishing survey catches were used for largemouth bass, as these surveys tend to best reflect adult relative abundance shifts (Rypel et al., 2019). Further, once lengths had been assigned for all sampled fish during spring electrofishing surveys, largemouth bass <203 mm were removed from analyses, as they were not fully recruited to the sampling gear.

Bluegill, pumpkinseed, and rock bass were susceptible to multiple gears during the sampling season. Therefore, gear-specific BPUE from each standardized survey gear (cloverleaf trap, mini-fyke net, fyke net, boat electrofishing) was used. We were primarily interested in understanding the adult population dynamics of these species while avoiding the influence of highly variable age-0 recruitment dynamics. Therefore, we used otolith age data from 2017 to 2020 to develop lake-species-specific minimum length-at-age-1 thresholds to designate fishes into two categories: age-1+ and age-0 (i.e., young-of-year). Based on assigned lengths, if a fish was below the age-1+ length threshold, it was considered age-0. If the fish was equal to or exceeded the age-1+ threshold, it was considered age-1+ and included in the analyses. Once age-1+ fish were identified, BPUE was

calculated for each lake-gear-species combination. For all data, Shapiro-Wilk tests were run to test whether BPUE were normally distributed. Based on findings, BPUE data were $\log_e$ -transformed prior to analysis. To test for differences in mean annual BPUE during the study period for each lake, we fit linear regressions where $\log_e(\text{BPUE})$ was the dependent variable and year was the independent variable. We then calculated the log response ratio and temporal percent changes for all fish species (Table 1). We were also interested in understanding how changes in biomass between warm- and coolwater fishes varied over the study period; therefore, we summed the mean annual biomass (in kilograms per gear) for each thermal guild annually and calculated the ratio between cool- and warm-water fish biomass.

Stable isotope analyses

Resource support of experimental and reference lake consumers was assessed using stable isotope values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Isotope samples were collected in both lakes from May 2017 to August 2021 from fishes as well as primary consumers (i.e., zooplankton, zoobenthos). Isotope samples from fishes were analyzed from individuals age-1+, with a minimum of three individuals per species lake year analyzed. Benthic primary consumer $\delta^{13}\text{C}$ samples were taken from two depths: <1 and 2–3 m. Thus, we assessed whether site depth significantly affected $\delta^{13}\text{C}$ values in each lake. As both the experimental and reference lakes were small waterbodies (<35 ha, mean depth = 3 m), it was unsurprising that there was no statistically significant difference between zooplankton and zoobenthos $\delta^{13}\text{C}$ sampled at different depths; therefore, no correction was necessary (Vander Zanden et al., 1999).

Given data limitations of primary consumer stable isotope estimates (annual $n = 3\text{--}7$), we assessed lake-specific annual primary consumer $\delta^{15}\text{N}$ to determine if annual means were statistically significantly different. Specifically, we performed a lake-specific ANOVA for $\delta^{15}\text{N}$ values for primary consumers and assessed annual differences using a post hoc Tukey honestly significant difference (HSD) test. Data from years that were not statistically different were combined to generate a lake-specific primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines. For years that were significantly different, primary consumer values were maintained as year specific.

We then used corresponding mean primary consumer nitrogen values to estimate trophic positions for fishes according to Cabana and Rasmussen (1996). In the experimental lake, primary consumer $\delta^{15}\text{N}$ increased from $\sim 2.0\text{‰}$ to $\sim 3.6\text{‰}$ between 2019 and 2020 (Appendix S1:

Figure S1), mean primary consumer $\delta^{15}\text{N}$ from 2017 to 2019 was used to calculate trophic position for fishes collected during that time, while values from 2020 to 2021 were used for fishes collected during that period (Vander Zanden et al., 1999). We assessed species-specific annual temporal changes in $\delta^{13}\text{C}$ and trophic position for each lake using an ANOVA and post hoc Tukey HSD test. Once we identified whether temporal changes were statistically significant, we calculated percent changes.

Lower trophic levels—Zooplankton and zoobenthos abundances

We quantified taxa-specific mean abundance of zooplankton (in number of individuals per liter) and zoobenthos (in number of individuals per square meter) for each lake over the study period. For all data, we ran Shapiro–Wilk tests to test whether densities were normally distributed. Based on the results of these tests, data were $\log_e$ -transformed prior to analysis. To test for differences in abundances before and after the experiment, we fit linear regressions where $\log_e(\text{relative abundance})$ was the dependent variable and year was the independent variable. An $\alpha = 0.05$ (adjusted for multiple comparisons) was used for all statistical analyses. Only statistically significant taxa responses are displayed.

Availability of data

All calculations and statistical analyses were performed in R version 4.2.1 (R Core Team, 2024). Raw data and accompanying metadata for species-specific BPUE, carbon and nitrogen stable isotopes of primary and secondary consumers, as well as zooplankton and zoobenthos relative abundances are freely available to the public, supported by the U.S. Geological Survey (USGS) Climate Adaptation Science Centers (<https://doi.org/10.5066/P14MU9WM>, Embke, 2024).

RESULTS

Both the experimental and reference lakes had suitable thermal habitats for coolwater fishes (Figure 2) but were projected to become centrarchid dominant by 2050 (Hansen et al., 2017). Mean annual growing degree days (base water temperature 5°C ; $\text{GDD}_{5^\circ\text{C}}$) increased from 1980 to 2015 for both the experimental and reference lakes (Figure 2; Winslow et al., 2017). In 2007, both the experimental and reference lakes reached maximum $\text{GDD}_{5^\circ\text{C}}$ of 2606 and 2673, respectively, exceeding the

GDD where a rapid shift from dominance by walleye to largemouth bass is expected (Figure 2; Hansen et al., 2017). Annual littoral and pelagic temperature profiles (~ 1 m depth) were variable, with peak water temperatures increasing over the study years (Figure 3). Littoral temperatures were more variable and were significantly warmer than pelagic temperatures, reaching a maximum temperature of $\sim 28.8^\circ\text{C}$ in 2020 and $\sim 27.8^\circ\text{C}$ in 2021 in the experimental and reference lakes, respectively, and occasionally exceeding optimal thermal conditions for coolwater fishes (Figure 3; Mandeville et al., 2019). Therefore, although there was suitable coolwater habitat available in the pelagic, littoral habitat is increasingly warming, highlighting that these lakes appear to be at the point of shifting from cool- to warm-water suitability (Figure 3).

We removed $\sim 285,100$ warmwater fishes (~ 3190 kg) comprising seven centrarchid species from the experimental lake from 2018 to 2021, with a mean annual removal of 23.74 kg/ha (Figure 4; Embke et al., 2022). The majority of biomass removed was bluegill ($\sim 64\%$ of total), in addition to black crappie and pumpkinseed (Figure 4). In response to removals, some warmwater species relative biomass (BPUE) declined significantly, including bluegill, black crappie, and rock bass by $\sim 28\%$, $\sim 61\%$, and $\sim 64\%$, respectively ($p < 0.001$; Table 1, Figure 5; Appendix S1: Figure S2). However, other warmwater species including largemouth bass and pumpkinseed relative biomass remained relatively constant or increased (Table 1, Figure 5; Appendix S1: Figure S2).

No natural walleye recruitment occurred during the study in either study lake as no age-0 walleye were collected, indicating the experimental removal of centrarchids did not result in a detectable boost for early walleye life stages. Adult walleye biomass did not significantly change in either lake (experimental lake mean biomass = 0.84 kg/ha). Further, walleye diets and trophic positions did not significantly change during the experiment. The other coolwater species, yellow perch (*P. flavescens*), showed a marked response to warmwater species removals, increasing by 914% since the start of removal (BPUE change from ~ 0.46 to ~ 4.63 kg/net night, $p < 0.001$; Figure 5, Table 1), compared to a 296% increase in yellow perch abundance in the reference lake over the same time period. For the experimental lake, we found that coolwater fish biomass increased relative to warmwater fish biomass once warmwater fish removals began in 2018 (Figure 6). The dominance of coolwater fishes (cool-to-warm ratio > 1) began in 2019 (cool:warm = 2), increased in 2020 (cool:warm = 5.6), but declined in 2021 (cool:warm = 1.6). In the reference lake, warmwater fishes were always dominant relative to coolwater fishes for the entire study period (cool:warm = 0.34; Figure 6). In the experimental lake,

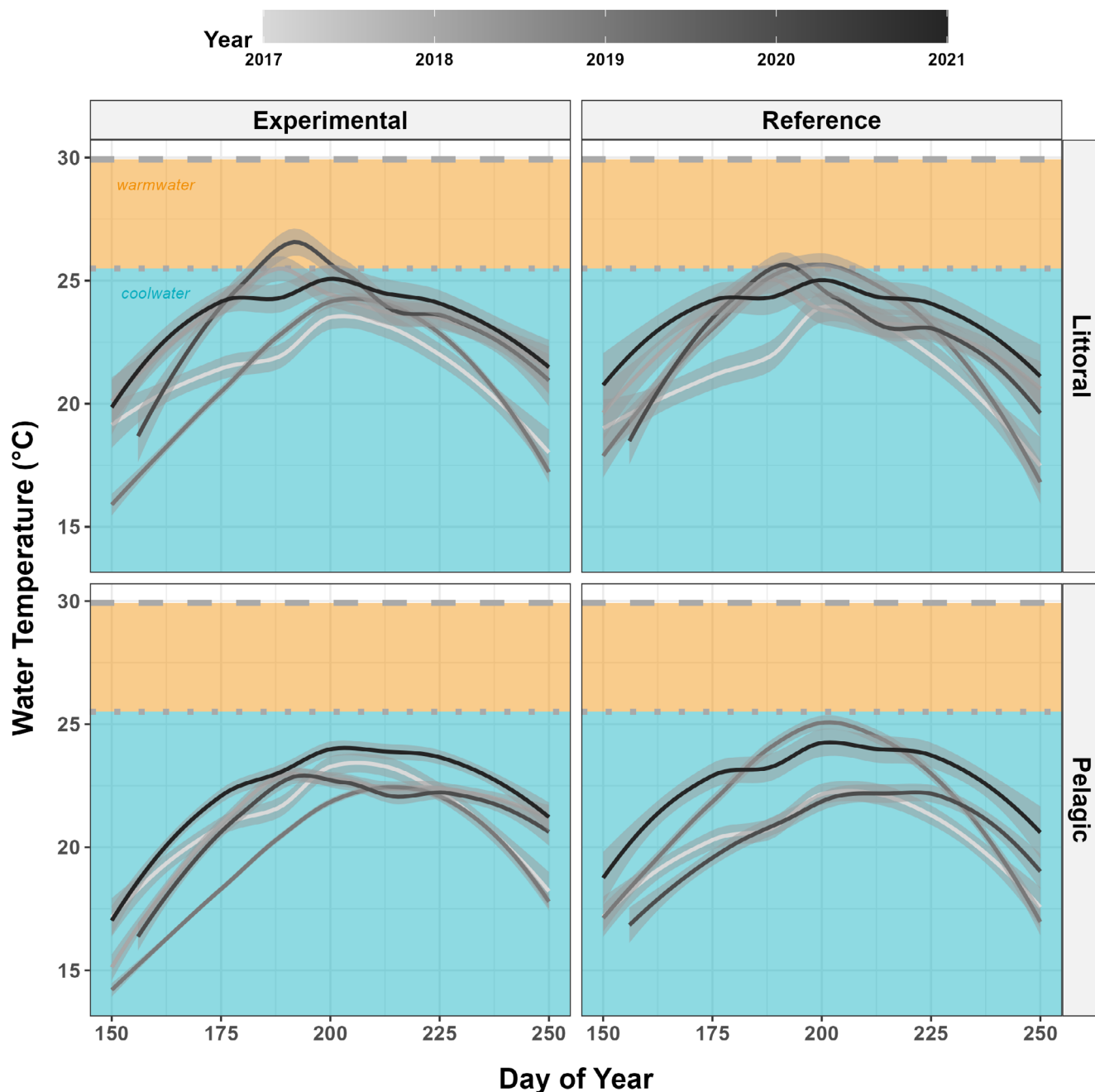


FIGURE 3 Littoral and pelagic water temperature (in degrees Celsius, 1 m depth) for the experimental and reference lakes taken May–September (day of the year 150–250) from 2017 to 2021. Horizontal dotted and dashed lines correspond to the mean optimal maximum water temperature (in degrees Celsius) estimated by Mandeville et al. (2019) for warmwater (orange) and coolwater (blue) fishes.

the only significant change in prey reliance observed was a 0.4 decline in yellow perch trophic position from $TP = 3.29$ in 2017 to $TP = 2.89$ in 2021 (Figure 7). There was no change in $\delta^{13}C$ for primary consumers or fish species over the study period, indicating no measurable change in fish habitat (e.g., benthic vs. pelagic) reliance.

In addition to habitat and prey reliance, we also quantified fish species diet compositions (Appendix S1: Figure S3). Regardless of thermal guild, fish diets were dominated by benthic items (i.e., benthic invertebrates,

crayfish) and fishes in both lakes, emphasizing the importance of benthic resources in supporting higher trophic levels as well as fishes as links between benthic and pelagic habitats (Figure 7; Appendix S1: Figure S2; Vander Zanden et al., 2011; Vander Zanden & Vadeboncoeur, 2002). In the experimental lake, warmwater fishes were highly omnivorous, with largemouth bass showing the highest variability in diet (Figure 7; Appendix S1: Figure S2). Of the two coolwater species, yellow perch were omnivorous (5-year mean = 36% benthic

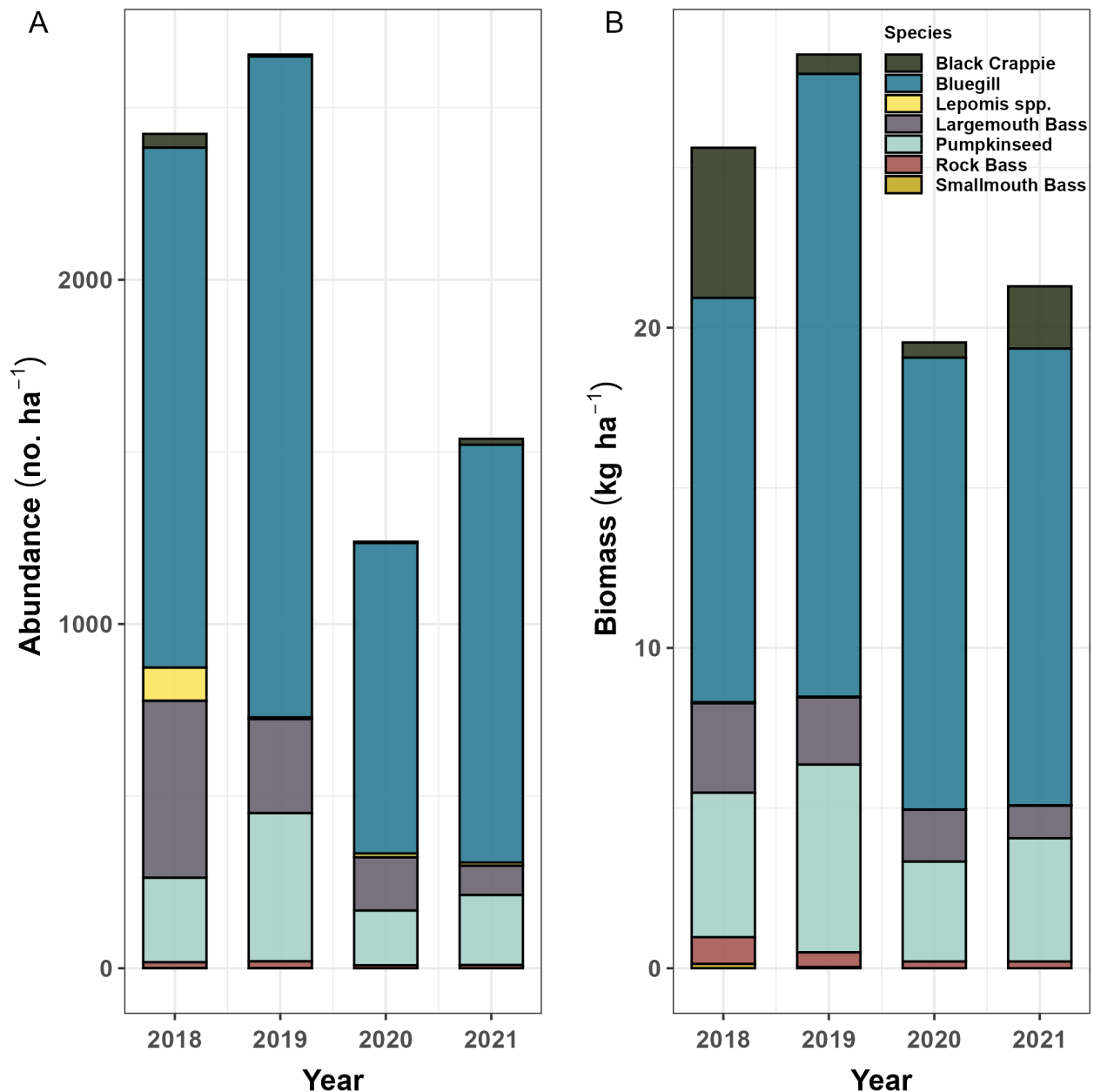


FIGURE 4 Warmwater fish guild (e.g., Centrarchidae) (A) abundance and (B) biomass removed from the experimental lake from 2017 to 2021. Color indicates species removed.

invertebrates, 7% crayfish, 31% fishes, 4% terrestrial invertebrates, 14% vegetation, 12% zooplankton; Appendix S1: Figure S3) and had a 5-year mean trophic position of 3.10 in the experimental lake (Figure 5). In the reference lake, yellow perch was also omnivorous, but showed lower reliance on benthic (e.g., crayfish) prey items in 2021 compared to yellow perch in the experimental lake (Appendix S1: Figure S3). Walleye were more piscivorous (5-year mean = 27% benthic invertebrates, 65% fishes, 8% terrestrial invertebrates; Appendix S1: Figure S3) and had a 5-year mean trophic position of 3.93. Reliance on zooplankton decreased over time for most species, although

very small individuals (<100 mm) were not well represented in diet samples, which likely comprised the largest consumers of zooplankton; therefore, overall zooplankton consumption may have been underestimated (Appendix S1: Figure S3). We recognize there are biases in fish diet analyses, as certain items, including benthic invertebrates and fishes, have longer residency times in fish digestive systems or are easier to identify in stomach contents, and are therefore more likely to be detected in samples (Preston et al., 2017).

Changes in the fish community cascaded to lower trophic levels in the experimental lake, where we observed

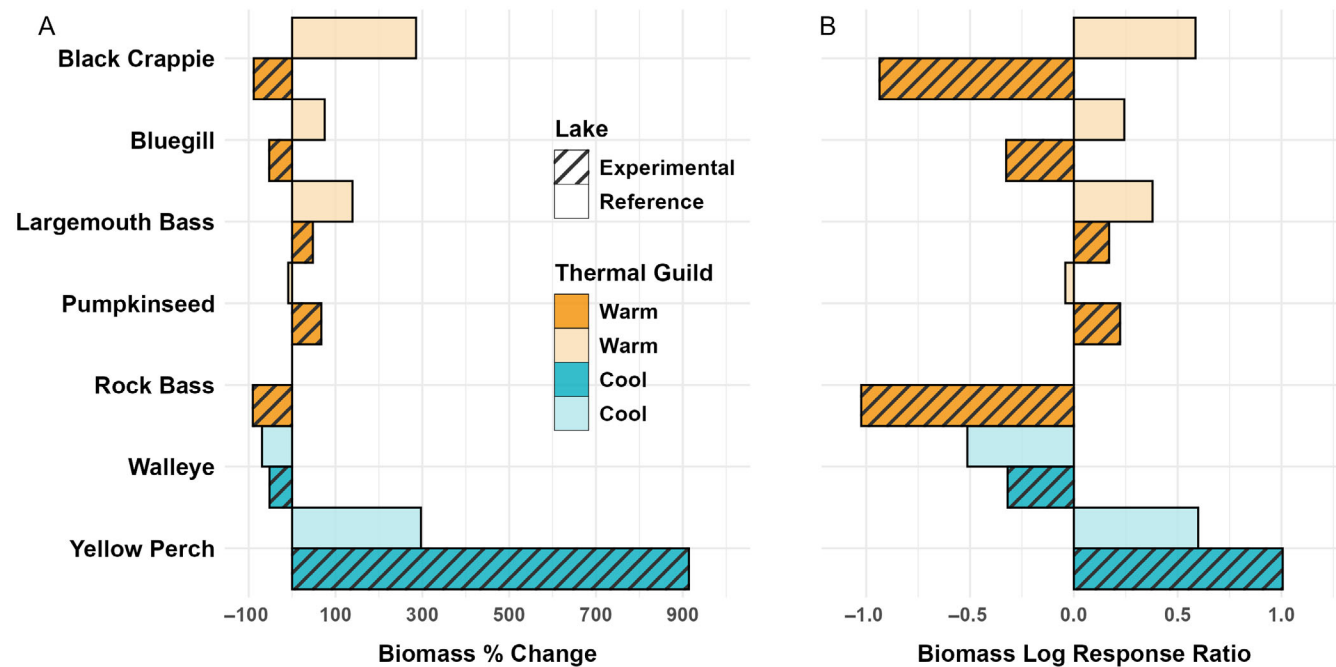


FIGURE 5 (A) Percent (in percentage) change and (B) log response ratio in biomass per unit effort (BPUE; in kilograms per gear) for warm- and cool-water fishes in the experimental and reference lakes from 2017 to 2021 following the removal of warmwater fishes. For walleye *Sander vitreus*, percent change in total population biomass (in kilograms per hectare) is presented.

significant declines in dominant zooplankton taxa abundance (i.e., Calanoida, Cyclopoida, *Daphnia*, $p < 0.001$; Figure 8A), potentially in response to increased predation by yellow perch. In contrast, dominant zoobenthos taxa abundance (i.e., Chironomidae, Gastropoda, Sphaeriidae) significantly increased over time ($p < 0.001$; Figure 8B), potentially due to predation release from declining warmwater littoral species.

DISCUSSION

Despite removing ~285,000 warmwater fishes, centrarchid biomass declined just 23%. The minimal change in the biomass of warmwater centrarchid fishes in response to removal indicates high population resilience and possibly strong density-dependent growth and reproduction (Mittelbach, 1986; Weber et al., 2016; Zipkin et al., 2008). Furthermore, it reveals a persistent challenge in trying to control fish populations when density-dependent effects are pronounced (Beard & Essington, 2000). Coolwater fish adult biomass showed sharply contrasting responses during the study period; walleye recruitment and biomass did not respond, but yellow perch biomass increased nearly 10-fold. Perch length (in millimeters) information (Embke et al., 2022) indicates this response may have been driven by a strong year-class emerging soon after initial removals. It is unclear whether the

year-class explosion of yellow perch was tied to release from predation by centrarchids at early life stages, an abundance of new food resources, or a combination of these and other factors. Further, we found that the relative dominance of cool- and warm-water fishes shifted following warmwater fish removals in the experimental lake. Notably, the biomass of coolwater yellow perch increased to 2–5 times that of warmwater fish, though this effect was short-lived (Figure 6). Overall, our findings supported the hypothesis that removing warmwater fishes may benefit coolwater species; however, responses varied among species within thermal guilds (Jarvis et al., 2024). Continued monitoring will be critical to disentangling the effects of species interactions driving yellow perch population dynamics. This whole-lake experimental removal of warmwater species highlights the importance of biotic interactions in regulating species with similar thermal constraints.

Thermal habitat variability indicated that although these lakes currently provide suitable thermal conditions for coolwater species in some habitats (i.e., pelagic), others (i.e., littoral) are becoming too warm to support the life cycle of coolwater species (Figure 3), a trend predicted to continue with climate change (O'Reilly et al., 2015). Overall, changing thermal regimes in the study lake are consistent with others on the landscape that are increasingly warming (O'Reilly et al., 2015). As climate change accelerates (Woolway & Maberly, 2020),

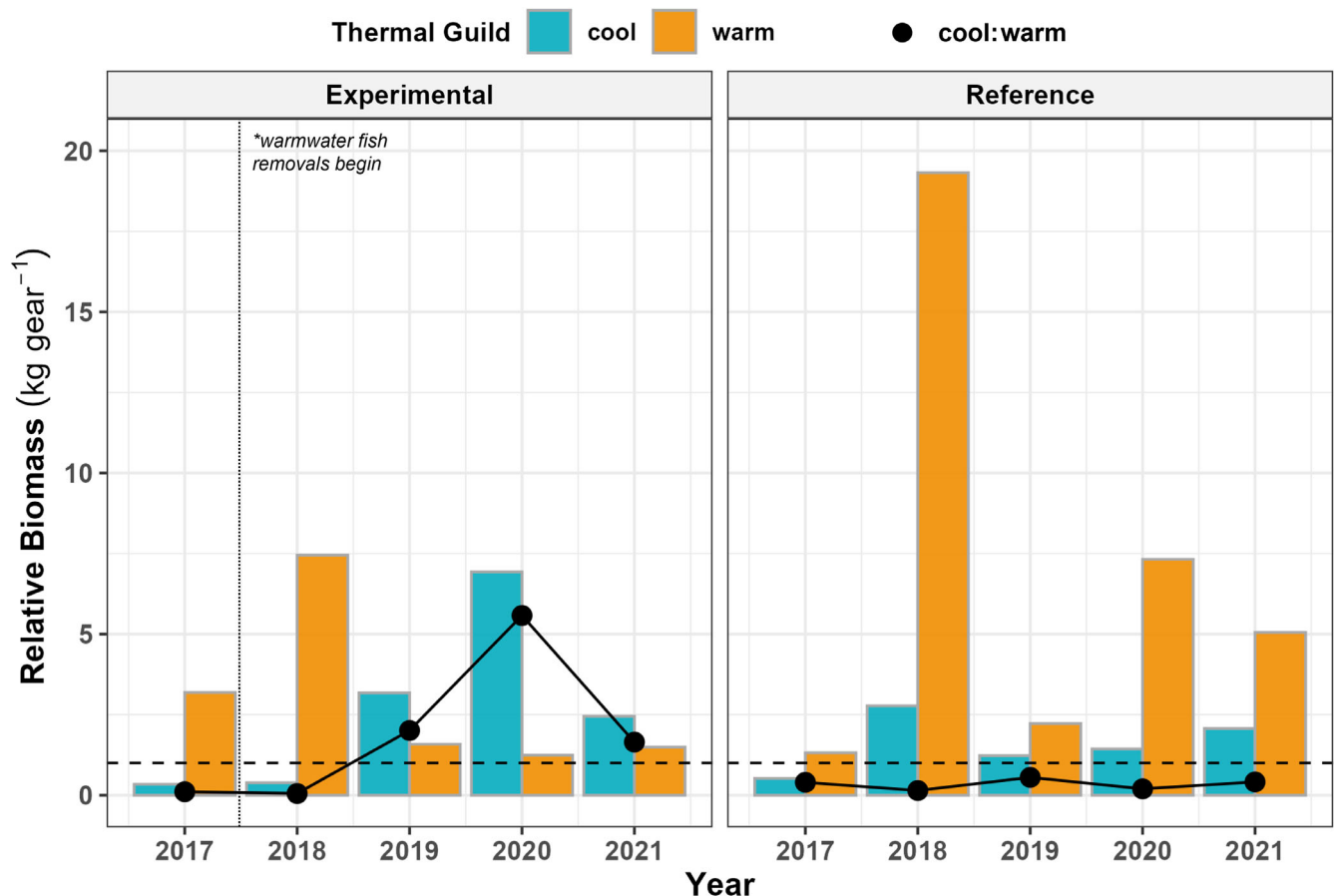


FIGURE 6 Relative biomass (in kilograms per gear effort) of warm- (orange) and cool-water (i.e., yellow perch *Perca flavescens*; blue) fishes measured in the experimental and reference lakes from 2017 to 2021. Black dots show the ratio between cool- and warm-water fish biomass for a given year. The horizontal dashed line at 1 indicates the switch between warm- and cool-water fishes dominance, where <1 corresponds to a year with more warmwater species and >1 corresponds to a year with more coolwater fishes. The vertical dotted line in the experimental lake panel indicates the time at which warmwater fish removals began in 2018.

it is likely more lake habitats will resemble these study lakes, becoming more limiting for coolwater species while also more suitable for warmwater species.

Community structure shifts in fish consumers cascaded to induce changes at lower trophic levels, where we observed a 0.4 trophic level decrease in yellow perch trophic position (indicating increased reliance on lower trophic levels), decreases in zooplankton abundance, and increases in zoobenthos abundances. Thus, increasing yellow perch abundance and biomass may be associated with increased planktivory, leading to declining zooplankton abundances, highlighting the importance of intermediate consumers in regulating food web dynamics. Further, species feeding strategies can influence an organism's ability to adapt to change, with more omnivorous species having more flexibility (Wootton, 2017). Therefore, the flexibility of the yellow perch feeding strategy (i.e., omnivory) in comparison to walleye (largely a piscivore) may have contributed to

the yellow perch ability to adapt to varying ecological conditions.

We observed strongly contrasting responses of two coolwater fishes during our experimental removal of warmwater fishes in a north-temperate lake, whereby walleye abundance did not change (e.g., held steady) while yellow perch increased. Although both species have similar thermal niches (Christie & Regier, 1988), walleye are more sensitive to light (Lester et al., 2004), take longer to reach maturity (average age-at-maturity = 4–5 years for walleye vs. 2–3 years for yellow perch; Brandt et al., 2022; Cichosz, 2017), and have more specific spawning requirements (Christie & Regier, 1988). Given their flexibility, yellow perch may have a greater adaptive capacity (Thurman et al., 2022) to respond to reduced predation/competition. We found yellow perch biomass increased to be 2–5 times greater than warmwater fish biomass following fish warmwater fish reductions in the experimental lake. However, we

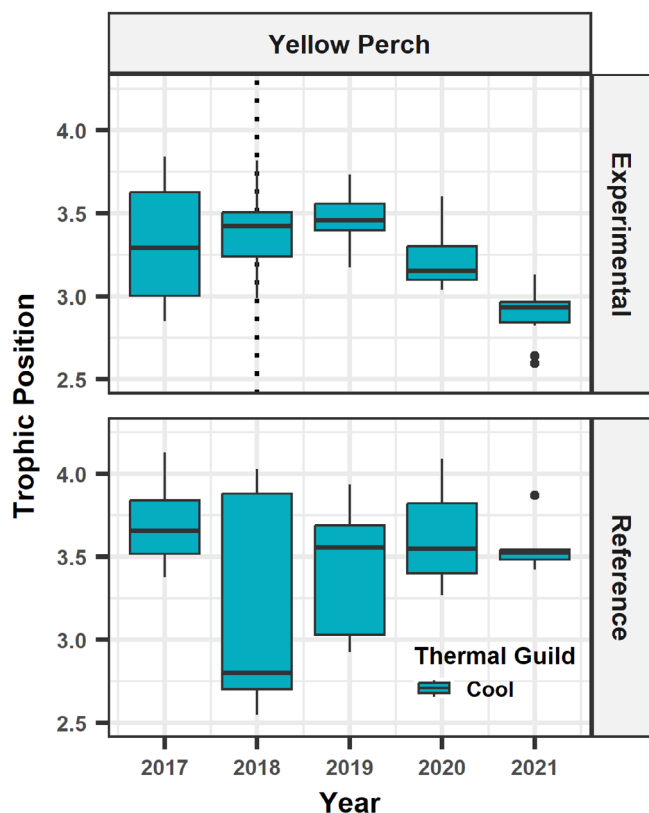


FIGURE 7 Trophic position of yellow perch (*Perca flavescens*) for the experimental and reference lakes from 2017 to 2021. The dotted vertical line indicates the time at which warmwater fishes began to be removed from the experimental lake. Statistically significant changes in trophic position occurred in the experimental lake following warmwater fish removals in 2020–2021.

acknowledge the coolwater fish compensation for warmwater fish losses may not always be the case given variable fish life history strategies and requirements. In our case, warmwater species were dominated by bluegill, which demonstrate similar life history to yellow perch (i.e., both omnivorous broadcast spawners), but this may not be the case for species with different life histories (e.g., northern pike). Further, we recognize ecological changes may not have been detected due to response time-lags, especially for slow-growing species like walleye; therefore, continued monitoring will be key to understanding long-term responses. Our work emphasizes that the relative importance of abiotic and biotic drivers for coolwater species is not uniform but depends on many factors including species life history, biological constraints, and food web interactions.

Despite highly intensive removal efforts, warmwater centrarchids were not easily controlled, highlighting a capacity for these species to adapt to high rates of harvest and withstand mortality. Centrarchids can spawn throughout the summer and are thus relatively

independent of abiotic spawning limitations, increasing their capacity to reproduce despite climate variability (Beard & Essington, 2000). Further, centrarchids have nest spawning behavior and some parental care; therefore, they can reduce competition/predation of their offspring (Mittelbach, 1986; Winemiller & Rose, 1992); however, this parental investment may require increased energy expenditure. Centrarchid reproductive strategies are in direct contrast to coolwater broadcast spawners with short, sensitive spawning strategies (Winemiller & Rose, 1992). For these reasons, bluegill and other centrarchids are notoriously resilient to harvest, and populations will rarely go extinct; however, size structure can be strongly impacted (Beard & Kampa, 1999; Rypel et al., 2016). Our study supports these findings, as the size structure of centrarchids shifted toward smaller individuals, but abundances never dropped to levels threatening extirpation (Figure 5; Embke et al., 2022). Instead, a compensatory response was observed, consistent with other centrarchid removal studies (Weber et al., 2016; Zipkin et al., 2008). This resilience is also evident in previous work where fish reductions led to strong year-classes of smallmouth bass (Weidel et al., 2007). Biomanipulation efforts have shown mixed results in altering species interactions; for example, bullhead removals improved walleye recruitment (Sikora et al., 2021), while other studies found that biomanipulations can impact water quality (McQueen et al., 1989). However, the efficacy of biomanipulation depends heavily on lake morphometry and habitat availability, with planktivore removals in shallow lakes often leading to more stable, long-term changes (McQueen, 1998). Overall, warmwater species such as centrarchids appear more resilient to climate change than coolwater species, suggesting that maintaining coolwater populations in habitats dominated by warmwater fishes may not be a viable climate adaptation strategy (Feiner et al., 2022).

Understanding the relative importance and interactions between thermal conditions and biotic drivers in regulating fish dynamics will become increasingly important as we try to navigate climate change and develop climate adaptation approaches (O’Gorman et al., 2023). Others have identified the critical importance of biotic interactions in regulating population dynamics in a changing climate (Hellmann et al., 2012; Suttle et al., 2007), however, our understanding of these relationships in freshwaters is limited. In developing management strategies, it will be key to consider species habitat requirements as well as biotic interactions and indirect food web implications of these shifts. Further, species life history strategies will likely play a key role in a species’ ability to adapt to climate change (Rypel, 2023). For

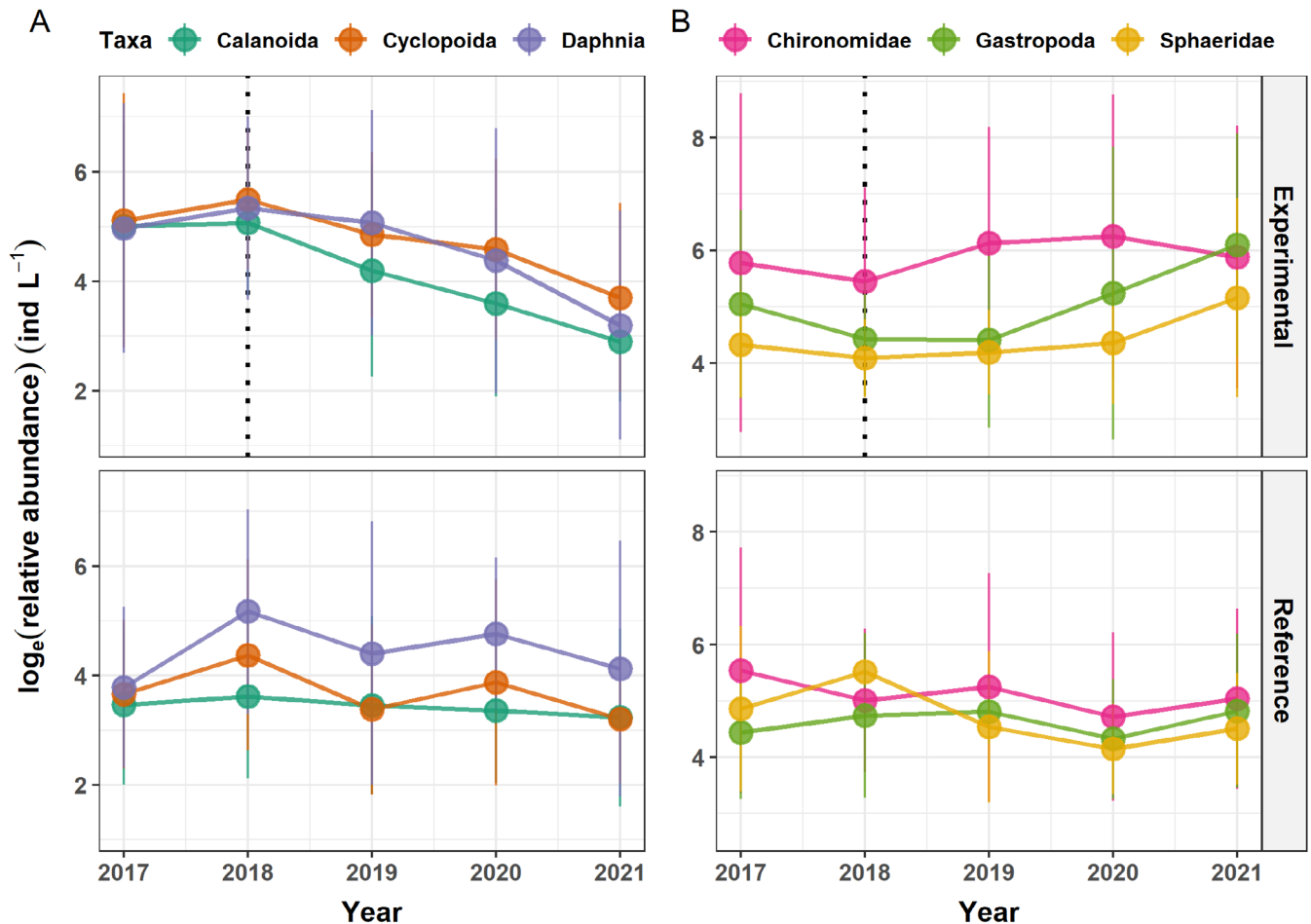


FIGURE 8 The $\log_e(\text{abundance})$ of (A) key zooplankton taxa and (B) zoobenthos taxa in the experimental and reference lakes from 2017 to 2021 (mean $\pm$ 2 SD). Vertical dotted lines indicate the time at which warmwater Centrarchidae removals began from the experimental lake in 2018. Only taxa with statistically significant responses are displayed.

example, particularly sensitive species such as walleye may require different adaptation approaches than other coolwater species such as yellow perch, despite similar thermal tolerances. In ecosystems projected to shift toward suboptimal conditions under climate change, it will be critical to consider the governing influence of species interactions in fragile ecosystems. We found that responses are flexible to a degree for some species but may also depend on factors such as the life history strategies of both the warmwater and coolwater species.

Species interactions are notoriously complex and may be largely beyond the control of managers, especially when thermal habitat availability becomes increasingly limited (Carpenter et al., 2017). We highlight that climate change strongly favors warmwater species, which are resilient and flexible, while coolwater fishes may be more sensitive and dependent on specific habitat characteristics. However, species responses were not uniform within thermal guilds. Because climate change will have unmanageable impacts on important coolwater species, it may be necessary to consider a portfolio of adaptation

approaches (Dudney et al., 2022; Hellmann et al., 2012). There may be a conflict between biotic and abiotic drivers in regulating population dynamics, and these dynamics may provide advantages to certain species under certain conditions. Given this high level of context dependence, it is necessary to develop a better system-specific understanding of climate adaptation approaches. Time scale and context are critically important in understanding the impacts of climate change on certain species. In ecosystems with less than optimal conditions, which will become more common with climate change, species interactions may play a larger role, but that is dependent on species life-history traits and sensitivities. Understanding species adaptive capacity under variable conditions can greatly inform the development of feasible solutions. In a changing climate, coolwater species adaptation may benefit from considering the current and future habitat trajectory of the ecosystem, species assemblage life history strategies, and potential indirect biotic interactions, as all of these factors interact to generate complex and variable outcomes.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design, data analysis, and writing of the manuscript. Giancarlo Coppola, Holly S. Embke, Daniel A. Isermann, Christopher J. Sullivan, and M. Jake Vander Zanden performed data collection. Holly S. Embke maintains raw data and metadata.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All raw data and accompanying metadata for species-specific biomass per unit effort, carbon and nitrogen stable isotopes of primary and secondary consumers, as well as zooplankton and zoobenthos relative abundances (Embke, 2024), are available from the U.S. Geological Survey (USGS) Climate Adaptation Science Centers ScienceBase-Catalog: <https://doi.org/10.5066/P14MU9WM>.

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SUPPORTING INFORMATION

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