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ARTICLE

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# Resisting ecosystem transformation through an intensive whole-lake fish removal experiment

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## Abstract

Lake ecosystems are shifting due to many drivers including climate change and landscape-scale habitat disturbance, diminishing their potential to support some fisheries. Walleye *Sander vitreus* (Mitchill) populations, which support recreational and tribal fisheries across North America, have declined in some lakes. Climate change, harvest, invasive species and concurrent increases in warm-water fishes (e.g. Centrarchidae) may have contributed to declines. To test the utility of an intensive management action to resist walleye loss, an experimental removal of ~285,000 centrarchids from a 33-ha lake over 4 years was conducted while monitoring the fish community response. Centrarchid abundance declined and yellow perch *Perca flavescens* (Mitchill) increased, yet no evidence of walleye recruitment was observed. These findings explore the feasibility of intensive resistance as a management strategy in supporting walleye facing environmental change and provide a platform for management discussions to move beyond resist strategies in the Resist-Accept-Direct (RAD) framework to navigate ecosystem change.

**KEYWORDS**
climate adaptation, climate change, fisheries, fresh water, natural resource management

## 1 | INTRODUCTION

Lake ecosystems are shifting due to unprecedented effects of climate change and landscape-scale disturbances (Carpenter et al., 2011; Lynch et al., 2016). An ecosystem transformation occurs when a system deviates from prior structure, processes and uses by people, with climate often being a dominant driver (Thompson et al., 2021). As global environmental change accelerates and interacts with anthropogenic stressors, such as habitat change and resource overharvest, ecosystems may be pushed across ecological thresholds (Jacobson et al., 2013; Thompson et al., 2021). Freshwater systems are sensitive to these synergistic threats due to their disproportionately high biodiversity and tight human-land-water linkages (Reid et al., 2019). North-temperate lakes, particularly those supporting important fish communities, are transforming at a rapid rate (Carpenter et al., 2011; Lynch et al., 2016). Habitat loss due to climate and land-use change (Christensen et al., 1996; Gaeta et al., 2014; Marburg et al., 2006) in combination with other anthropogenic stressors (e.g. pollution and invasive species) diminish the potential for freshwater ecosystems to support fisheries (Jacobson et al., 2013; Post, 2013).

Walleye *Sander vitreus* (Mitchill), the most sought-after game fish in north-central North America, supports important recreational and tribal fisheries (Nesper, 2002). Walleye populations in Wisconsin have declined in abundance by ~36% over the past two decades (Embke et al., 2019; Hansen et al., 2015a, 2018; Rypel et al., 2018). Walleye recruitment (here defined as non-stocked age-0 relative abundance) failures have been identified as the key bottleneck leading to declines (Gostiaux et al., 2021). Multiple mechanisms have been proposed to explain recruitment failures. Climate change, leading to reduced optimal thermal and optical habitat (Hansen et al., 2019), and habitat degradation (Christensen et al., 1996) have been associated with declines and pose challenges for managers as they are abiotic drivers beyond local control. Other drivers potentially within the control of managers, including harvest (Embke et al., 2019), invasive species (Hansen et al., 2020; Kapuscinski et al., 2010; Mercado-Silva et al., 2007) and shifting ecological interactions resulting in increased competition/predation (Hansen et al., 2015b, 2018; Kelling et al., 2016), have also been implicated in walleye declines. Management interventions have largely sought to resist declines through extended growth fingerling stocking to supplement juvenile populations (Lawson et al., 2022; Sass et al., 2022), regulation changes to limit adult walleye harvest, incentivizing harvest of potentially predatory species (e.g. largemouth bass *Micropterus salmoides* [Lacepède]; Hansen et al., 2015b) and targeted species removals (Tingley et al., 2019, Sikora et al., 2021; Feiner et al., 2022).

Coinciding with walleye declines, black bass and sunfish abundances are increasing (i.e. Centrarchidae species; hereafter centrarchids) leading to speculation that increasing warm-water species abundances may be contributing to walleye declines through increased predation and/or competition, especially during early life stages (Fayram et al., 2005; Hansen et al., 2015b, 2017; Kelling et al., 2016). Removing centrarchids may reduce competition/predation pressure on walleye early life stages, alleviating the recruitment bottleneck observed in many walleye populations (Gostiaux et al., 2021). Managing walleye fisheries in a changing climate will require a better understanding of the role of species interactions as a factor in walleye declines and testing which adaptation options are viable for managers.

The Resist-Accept-Direct (RAD) framework can assist with the process of identifying adaptation options for such transforming ecosystems (Lynch et al., 2021a; Rahel, 2022; Schuurman et al., 2021; Thompson et al., 2021). Decision options in RAD include *resisting* change to maintain historical conditions, *accepting* change without intervention and *directing* the trajectory of change; therefore, it supports decisions that are effective and practically feasible (Lynch et al., 2021b). When one strategy is no longer feasible, the RAD framework can present alternative pathways to determine the viability of other management approaches. Interventions can be tested through targeted monitoring, experimentation and pilot studies to evaluate actions that may be considered at larger scales (Lynch et al., 2021a).

Fisheries managers can use a broad suite of RAD strategies to address transforming aquatic systems (see Lynch et al., 2022, Table 1; Rahel, 2022). Regional management of walleye declines has largely focussed on resistance actions via stocking and harvest regulation, often with limited success (Feiner et al., 2022). One of the few, and most intensive, resist actions that remains untested in its ability to rehabilitate walleye includes centrarchid removal, the efficacy of which could be best tested at the whole-lake scale because they incorporate complex interactions in a natural environment at the appropriate scale for management (Carpenter, 1998; Carpenter et al., 1995; Walters & Holling, 1990). In lakes, the discrete borders and relative ease for sampling provide a useful context to study whole ecosystem shifts in response to disturbance and intervention. Whole-lake manipulations have addressed community and biogeochemical responses to a variety of stressors and increased understanding of the capacity to manage ecosystem change (Carpenter et al., 1995). The focus of these experiments has spanned the effects of eutrophication to large-scale biomanipulations, ultimately informing freshwater policy and management (Bernes et al., 2015; Carpenter et al., 1995; Schindler, 1974). Some whole-lake manipulations have revealed that intervention may need to be continuous, while others have successfully resulted in long-term regime shifts (Mehner et al., 2002). Trade-offs in spatial extent and replication exist in ecosystem experiments; however, there is great value in conducting manipulations in a natural context where the experimental unit includes relevant physical, chemical and biotic processes (Carpenter et al., 1995). Ecosystem experiments can provide incomparable insights regarding system responses to disturbance and the efficacy of a potential management intervention.

To test the utility of intensive *resist* actions, a whole-lake experimental removal of centrarchids was conducted. More than ~285,000 centrarchids were removed from a 33-ha Northern Wisconsin lake over 4 years, while the walleye population and fish community response in the experimental lake and a reference lake

**TABLE 1** Species-gear-specific age-1+ relative abundance (CPUE; n/gear) for the experimental (McDermott) and reference (Sandy Beach) lakes before (2017) and after (2021) Centrarchidae species were removed from the experimental lake. If no individuals were collected in given gear in 2017, 2018 values are shown. Modelled predictions are presented for statistically significant trends, and empirical estimates are presented for statistically insignificant trends

| Lake | Species | Gear | Pre-removal mean CPUE | Post-removal mean CPUE | % change | Statistically significant |
|---|---|---|---|---|---|---|
| Experimental (McDermott) | Black Crappie | Fyke net | 13.25 | 2.26 | −82.94 | Yes |
| | Bluegill | Cloverleaf Trap | 76.62 | 29.07 | −62.06 | No |
| | | Electrofishing | 1.83 | 1.87 | 2.19 | No |
| | | Fyke net | 43.72 | 21.00 | −51.97 | Yes |
| | | Mini-Fyke net | 20.85 | 3.13 | −84.99 | Yes |
| | Largemouth Bass | Electrofishing | 8.26 | 8.81 | 6.66 | No |
| | Pumpkinseed | Cloverleaf Trap | 1.2 | 0.14 | −88.33 | No |
| | | Electrofishing | 0.32 | 0.49 | 53.13 | No |
| | | Fyke net | 1.61 | 3.30 | 104.97 | No |
| | | Mini-Fyke net | 3.81 | 1.06 | −72.18 | Yes |
| | Rock Bass | Cloverleaf Trap | 0.05 | 0.20 | 294.00 | No |
| | | Electrofishing | 0.19 | 0.03 | −84.21 | Yes |
| | | Fyke net | 1.21 | 0.40 | −66.94 | Yes |
| | | Mini-Fyke net | 0.69 | 0.75 | 8.70 | No |
| | Yellow Perch | Fyke net | 8.9 | 79.11 | 788.88 | Yes |
| Reference (Sandy Beach) | Black Crappie | Fyke net | 9.95 | 38.97 | 291.66 | No |
| | Bluegill | Cloverleaf Trap | 29.34 | 4.63 | −84.22 | No |
| | | Electrofishing | 0.13 | 0.13 | 0.00 | No |
| | | Fyke net | 1.21 | 2.19 | 80.99 | No |
| | | Mini-Fyke net | 2.47 | 2.37 | −4.05 | No |
| | Largemouth Bass | Electrofishing | 0.75 | 1.65 | 120.00 | No |
| | Pumpkinseed | Cloverleaf Trap | 1.2 | 0.40 | −66.67 | No |
| | | Electrofishing | 0.02 | 0.18 | 800.00 | No |
| | | Fyke net | 0.29 | 0.31 | 6.90 | No |
| | Yellow Perch | Fyke net | 17.61 | 38.14 | 116.58 | No |

were monitored. The primary objective of this research was to test whether removing centrarchids would result in quantifiable walleye natural recruitment. Additional study objectives included the following: (a) testing whether it was possible to reduce the abundance and biomass of centrarchids; (b) if possible, test for changes in abundance in the percid (i.e. walleye and yellow perch *Perca flavescens* Mitchill) community; and (c) test for changes in the size structure of the centrarchid community under intensive removal. More broadly, this manipulation was used to understand the role species interactions play in limiting natural walleye recruitment. These findings explore the feasibility of intensive resistance as a management strategy in supporting walleye fisheries facing environmental change and provide a platform for management discussions to move beyond *resist* actions when navigating ecosystem change. It is acknowledged that any fish community responses to the biomanipulation coincided with the removals; therefore, our results represent short-term responses that may be stable or transient over time. Therefore, additional monitoring of the experimental and reference lakes will commence in the future to test for longer-term responses.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Selecting the experimental lake where centrarchid removals occurred was a lengthy process that began with >50 candidate lakes and included extensive consultation with Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) biologists, and public meetings with lakeshore property owners. In addition to gaining necessary public and management support for site locations, the experimental and reference lakes were selected based on a series of abiotic and biotic characteristics. Criteria included the following: a history of self-sustaining, natural walleye recruitment, a population of adult walleye, ample walleye spawning habitat and an increase in centrarchid abundances. The experimental (McDermott Lake; 46.00299280, −90.16081610) and reference (Sandy Beach Lake; 46.10614350, −89.97131020) lakes are in Iron County in Northern Wisconsin. The experimental lake has a surface area of 33.1 ha, mean depth of 3.0 m and maximum depth of 5.7 m. The reference lake has a surface area of 44.5 ha, mean depth of 2.1 m and maximum depth of 4.0 m. Both lakes included a variety of substrates (e.g. rock, gravel and sand) and areas of submerged and emergent vegetation. At the start of the study, the experimental and reference lake fish communities were similar with high centrarchid abundances (e.g. black crappie *Pomoxis nigromaculatus* (Lesueur), bluegill *Lepomis macrochirus* Rafinesque, largemouth bass and pumpkinseed *Lepomis gibbosus* (Linnaeus)), few adult walleye and a history of self-sustaining, natural walleye recruitment. For Wisconsin lakes, natural recruitment of walleye is defined as the relative abundance of non-stocked age-0 individuals collected in fall electrofishing surveys. Natural recruitment was last detected in both lakes in 2003–2004, with higher age-0 catch per unit effort (CPUE) in the reference lake (~6.51 ind/km) compared with the experimental lake (~1.67 ind/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 total length; TL) during the fall of every other year since at least 2011. Other species present included yellow perch, northern pike *Esox lucius* Linnaeus, muskellunge *Esox masquinongy* Mitchill, black bullhead *Ameiurus melas* Rafinesque and golden shiner *Notemigonus crysoleucas* (Mitchill).

## 2.2 | Fish sampling

### 2.2.1 | Standardised surveys

During 2017–2021, standardised monitoring surveys were conducted using numerous sampling techniques to test for changes in the fish communities of both lakes. Sampling began immediately after ice-out (~mid-April) with the deployment of five fyke nets (1.2 m × 1.8 m frames, 1.9 cm bar mesh) for one week at nonrandom locations in lakes 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; and (2) to estimate relative abundances (fish per net night) of black crappie and yellow perch. During these surveys, all collected walleye were measured (TL; mm), sexed, checked for a uniquely coded passive integrated transponder (PIT) and implanted with a PIT if one was not present. Adult (mature) walleye were defined either as all fish ≥381 mm or for which sex could be determined by extrusion of gametes (regardless of length). Walleye of unknown sex <381 mm were classified as juvenile (immature). Both study lakes have had walleye population estimates previously conducted by the WDNR. Therefore, WDNR protocols were followed where the goal was to mark 10% of the anticipated spawning population (based on previous population estimates; Cichosz, 2017). Marking continued until the target number was reached or spent females began appearing in fyke nets. Tagged walleye were recaptured using night-time AC boat electrofishing within one week (typically 1–4 days) after netting and marking were completed (Beard et al., 1997). In each lake, the entire shoreline was electrofished. All walleye were measured and examined for PITs. Population estimates (PEs) were calculated using Chapman's modification of the Petersen estimator (Chapman, 1951; Cichosz, 2017). To determine black crappie and yellow perch relative abundances, all individuals were counted and a subsample of 30 fish per species per day for each lake was measured (TL; mm).

A combination of standardised surveys was performed to quantify centrarchid relative abundances of species other than black crappie (i.e. bluegill, largemouth bass, pumpkinseed and rock bass *Ambloplites rupestris* [Rafinesque]). In early summer (May, water temperatures = 13.0–21.0°C), surveys began with an AC boat electrofishing. During June–August, fish were sampled once monthly when lake surface water temperatures were ≥13.0°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 and cloverleaf traps). 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 night-time boat electrofishing (Wisconsin-style; AC; 2.0–3.0 amps, 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-m × 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 early afternoon, fished overnight and retrieved the following afternoon (~24-h soak time). All catches were standardised according to gear-specific effort. For boat electrofishing, CPUE was calculated as the number of individuals captured per hr. 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, multiple gears were used, including ichthyoplankton surface trawls, micromesh 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 about every 7 days beginning 2 weeks after the presumed walleye spawn until June (Isermann & Willis, 2008). In late July/early August, four vertical gillnets (46-m × 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 and at depths ranging from 0 to 5 m. Set duration ranged from 1 to 2 h to minimise bycatch (Boehm et al., 2020). In late August, 0.24-m-long beach seines with 0.64-cm mesh were pulled at five sites in each lake. Sites were chosen to represent a variety of habitat types and based on ability to effectively use the seine. Seining sites remained fixed for the duration of the study. Seines were used during daylight hours on each lake. Catch per unit effort was calculated as the number of individuals per seine haul. When water temperatures fell below 21°C (early September), age-0 walleye were sampled using night-time boat electrofishing of the entire shoreline of each lake (Wisconsin-style; AC; 2.0–3.0 amps, 200–350 V, two netters). Surveys were conducted prior to walleye fingerling stocking, meaning any collected age-0 walleye were produced via natural recruitment.

### 2.2.2 | Removal efforts

In addition to standardised 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 from May 14 to June 7 and in 2019, from May 9 to June 27. During 2018 and 2019, fyke netting ended when centrarchid catches started to decline. 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, and sites were rotated to maximise centrarchid catches. Collected fish were identified to species, and up to 30 individuals per species per gear were measured daily (TL, mm). Centrarchid species were retained, while other species were returned to the lake. Species removed included black crappie, bluegill, green sunfish *Lepomis cyanellus* Rafinesque, pumpkinseed, rock bass, largemouth bass and smallmouth bass *Micropterus dolomieu* Lacepède (Figure 1). Removed centrarchids were used for ageing purposes (see below) or donated to local wildlife health centres.

### 2.2.3 | Fish processing

To understand demographic changes of the centrarchid and yellow perch populations in the experimental and reference lakes, up to 20 individuals per ~25 mm interval were retained for analyses from each lake. In the laboratory, individuals were dissected and species, TL (mm) and weight (g) were recorded. Sagittal otoliths were removed to determine whether an individual was age-0 or age-1+. Ages were estimated using a combination of whole and thin-sectioned otoliths.

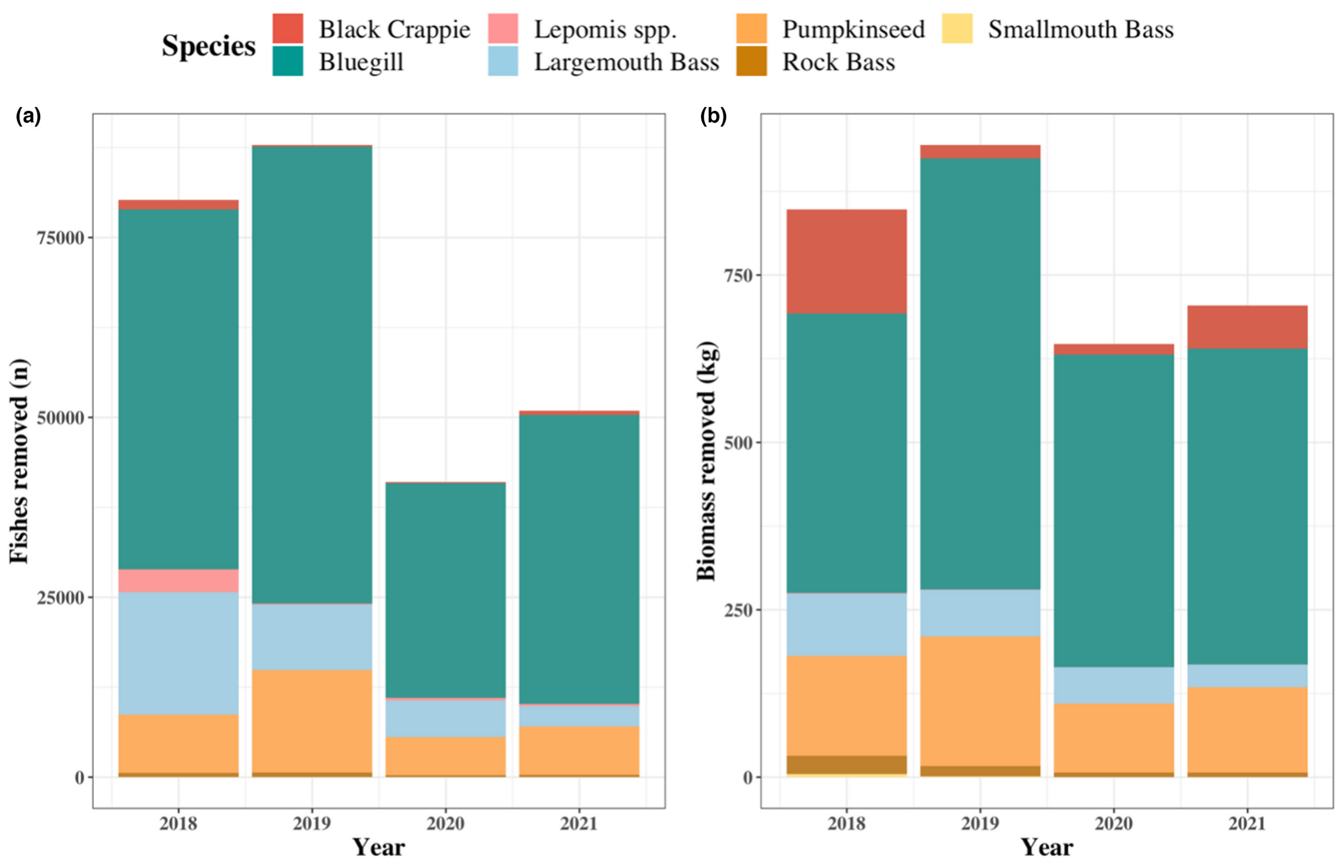


**FIGURE 1** Centrarchidae species removed from the experimental lake, McDermott Lake, Wisconsin, during 2018–2021. Panel A shows the abundance (n) of fishes removed, and panel B shows biomass (kg) of fishes removed. Colours indicate species

To generalise 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 using a Nikon DS-Fi2 or DS-Fi3 colour camera connected to Nikon NIS-Elements software (Schramm & Doerzbacher, 1985). 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 assigned 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.

### 2.3 | Data analyses

The total biomass of centrarchids removed from the experimental lake over the study period was estimated via extrapolation of lengths and weights to unmeasured fish based on the measured samples. A subset of measured fish lengths (daily maximum = 30 per species per gear) was used to assign total length (mm) to unmeasured individuals. Available fish lengths were sampled with replacement and used to assign lengths to unmeasured fish according to the total number of individuals collected. To estimate centrarchid biomass (kg) removed from the experimental lake, species-specific weight-length regressions were developed for each year within each lake to predict weights (g) of fishes that were not weighed. Length (mm) was $\log_e$ transformed prior to analysis. Once all sampled fish had an assigned weight, centrarchid weights were summed from the experimental lake for years 2018–2021 to calculate total biomass removed from the lake.

Examination of temporal trends in the relative abundance and removed biomass of species focussed on the species 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 the abundance (n) and biomass (kg) of centrarchids removed from the experimental lake. Standardised survey CPUE 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 CPUE was used, whereas boat electrofishing survey CPUE was used for largemouth bass, as these surveys best reflect adult relative abundance shifts. Further, once lengths had been assigned for all sampled fish during spring electrofishing surveys, largemouth bass <203 mm were removed, as they were not fully recruited to the sampling gear.

Bluegill, pumpkinseed and rock bass were susceptible to multiple gears throughout the sampling season. Therefore, gear-specific CPUE from each standardised survey gear (cloverleaf trap, mini-fyke net, fyke net and boat electrofishing) was used. This research was primarily interested in understanding adult population dynamics of these species while avoiding the influence of highly variable age-0 recruitment dynamics. Therefore, otolith age data from 2017 to 2020 were used to develop lake-species 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+ 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, mean CPUE was calculated for each lake-gear-species combination. For all data, Shapiro–Wilk tests were run to test whether CPUE was normally distributed. Based on findings, CPUE data were $\log_e$-transformed prior to analysis. To test for differences in mean annual CPUE and mean length before and after the experiment, a one-way ANOVA was used. Gear-specific $\log_e$(CPUE) or total length (mm) was compared before and after the experiment. An $\alpha = 0.05$ (adjusted for multiple comparisons) was used for all statistical analyses. All calculations and statistical analyses were performed in R version 4.0.3 (R Core Team, 2021). All data and accompanying metadata are freely available to the public supported by the U.S. Geological Survey (USGS) Climate Adaptation Science Centers (DOI in prep).

## 3 | RESULTS

Seven centrarchid species were among the ~285,100 fishes (~3190 kg) removed from the experimental lake during 2018–2021 (Figure 1). Most individuals removed were bluegill (*n* = 197,152) and largemouth bass (*n* = 35,168), while the majority of biomass removed was bluegill (~64% of all removed biomass), in addition to black crappie and pumpkinseed (Figure 1). Over the study duration, removal efforts in the experimental lake comprised 107 h of electrofishing, 717 net nights of fyke nets, 908 net nights of mini-fyke nets and 6942 traps nights of cloverleaf traps. When spread across individual nights, this effort totalled ~23 years of individual nightly effort.

After 2 years of centrarchid removals, adult walleye abundance temporarily increased in the experimental lake when ~120 (95%CI = 54–342) adults were estimated, but in the most recent sampling year (2021) abundance decreased to pre-removal levels (~30–40 [95%CI = 26–98] individuals; Figure 2). In contrast, adult walleye abundance decreased in the reference system until the most recent year (2021) when the population increased to ~112 (95%CI = 64–474) individuals (Figure 2). Both lakes were stocked with extended growth walleye fingerlings (mean TL ~164 mm) in late September 2017, 2019 and 2021. Specifically, the experimental lake was stocked with ~840 individuals each stocking year and the reference system was stocked with ~1110 individuals each stocking year.

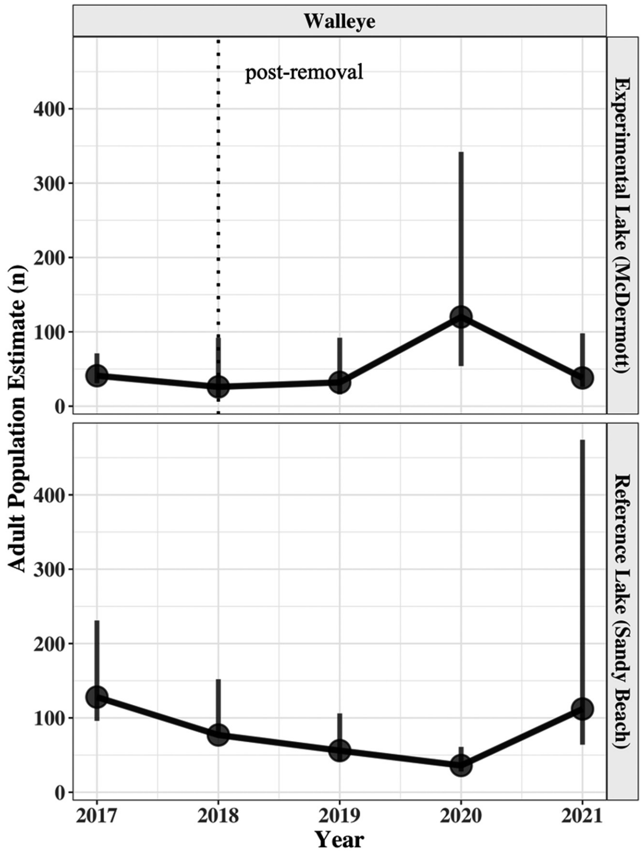


FIGURE 2 Adult walleye (*Sander vitreus*) population estimates (n) for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017–2021. The upper row corresponds to the experimental lake, and the lower row corresponds to the reference lake. Error bars represent 95% confidence intervals. The vertical dotted line indicates when Centrarchidae species removals began from the experimental lake in 2018

No age-0 walleye were collected in either lake, indicating that no detectable natural recruitment had occurred during the study period.

As fish were removed in the experimental lake, age-1+ CPUE decreased for most centrarchid species (Table 1, Figure 3). Black crappie relative abundance significantly declined following the first year of removal efforts and has remained at lower relative abundances in subsequent years, with an overall decline in CPUE from pre-removal to 2021 of ~83% (CPUE change from ~13.25 to ~2.26 ind/net, $p < 0.01$; Table 1, Figure 3). Adult largemouth bass relative abundance remained relatively constant throughout the study (Table 1, Figure 3). Bluegill were the most abundant species in the lake, with pre-removal CPUE in most gears of ~55 ind/net or per trap (mean CPUE from cloverleaf traps, fyke nets and mini-fyke nets; Table 1, Figure 3). Bluegill showed the largest declines through 2020, concurrent with an increase in adult walleye, but bluegill CPUE was higher in the most recent sampling year (2021; Figures 2 and 3). Cloverleaf traps, which sample smaller individuals (Sullivan et al., 2019a), showed the most variability (Figure 3). Cloverleaf catches initially declined ~89% from pre-removal-2020 CPUE (CPUE change from 75 to 8.5 ind/trap), but then increased ~241% from 2020 to 2021 CPUE (CPUE change from 8.5 to 29.1 ind/trap; Figure 3). Other gears sampling larger bluegill relative abundances including fyke nets and mini-fyke nets significantly declined throughout the study period ($p < 0.01$, Table 1, Figure 3). Overall, pumpkinseed CPUE significantly declined in most gears aside from electrofishing (which remained relatively constant) throughout the study period ($p < 0.01$, Table 1, Figure 3). The CPUE of rock bass significantly declined after the first year of removal efforts, with overall declines of ~75% ($p < 0.01$, Table 1, Figure 3). Fishes in the reference lake varied in CPUE over time, with no statistically significant trends (Table 1, Figure 3). Yellow perch showed the most marked response to removal efforts, with a significant and steady CPUE increase in 788% following fish removals (CPUE change from ~8.9 to ~79.11 ind/net, $p < 0.001$; Table 1, Figure 3). Although not statistically significant, yellow perch CPUE also increased by ~116% in the reference lake over the study period (CPUE change from ~17.61 to ~38.14 ind/net; Table 1, Figure 3).

Yellow perch mean length significantly changed in both lakes over the study period, but in opposite directions ($p < 0.001$, Table 2, Figure 4). In the experimental lake, yellow perch mean length increased by ~17.9% from 156 mm to 184 mm ($p < 0.001$, Table 2, Figure 4). In the reference lake, yellow perch mean length slightly decreased by ~4% ($p < 0.001$, Table 2, Figure 4). In the experimental lake, all centrarchid species except for black crappie significantly decreased in mean length with overall declines of ~6–33% ($p < 0.01$, Table 2, Figure 4). Rock bass showed the largest decrease in mean length from 133 mm to 89 mm over the study period ($p < 0.01$ Table 2, Figure 4). In the reference lake, bluegill significantly increased by 14% in mean length from 77 mm to 87 mm ($p < 0.01$ Table 2, Figure 4).

## 4 | DISCUSSION

### 4.1 | Whole-lake manipulation to resist walleye decline

An ecosystem experiment was performed where ~285,000 centrarchids were removed from a 33-ha north-temperate lake to understand the role of centrarchid species interactions in limiting walleye populations. Although intensive effort was applied and relative abundances of most centrarchids significantly declined by ~74% over the study period, adult walleye abundance did not appreciably change and there was no evidence of natural recruitment (Table 1). These findings indicate walleye were less influenced by centrarchid interactions (e.g. predation and competition) and may be more influenced by other drivers, such as climate and habitat change. However, in the experimental lake yellow perch relative abundance and mean length significantly increased by ~788% and ~18%, respectively, demonstrating that yellow perch may be more sensitive to reduced competition/predation and thus intervention (Figure 3).

The whole-lake experiment that was conducted was used to test the efficacy of resistance as a management approach in sustaining walleye populations given climate change and other disturbances.

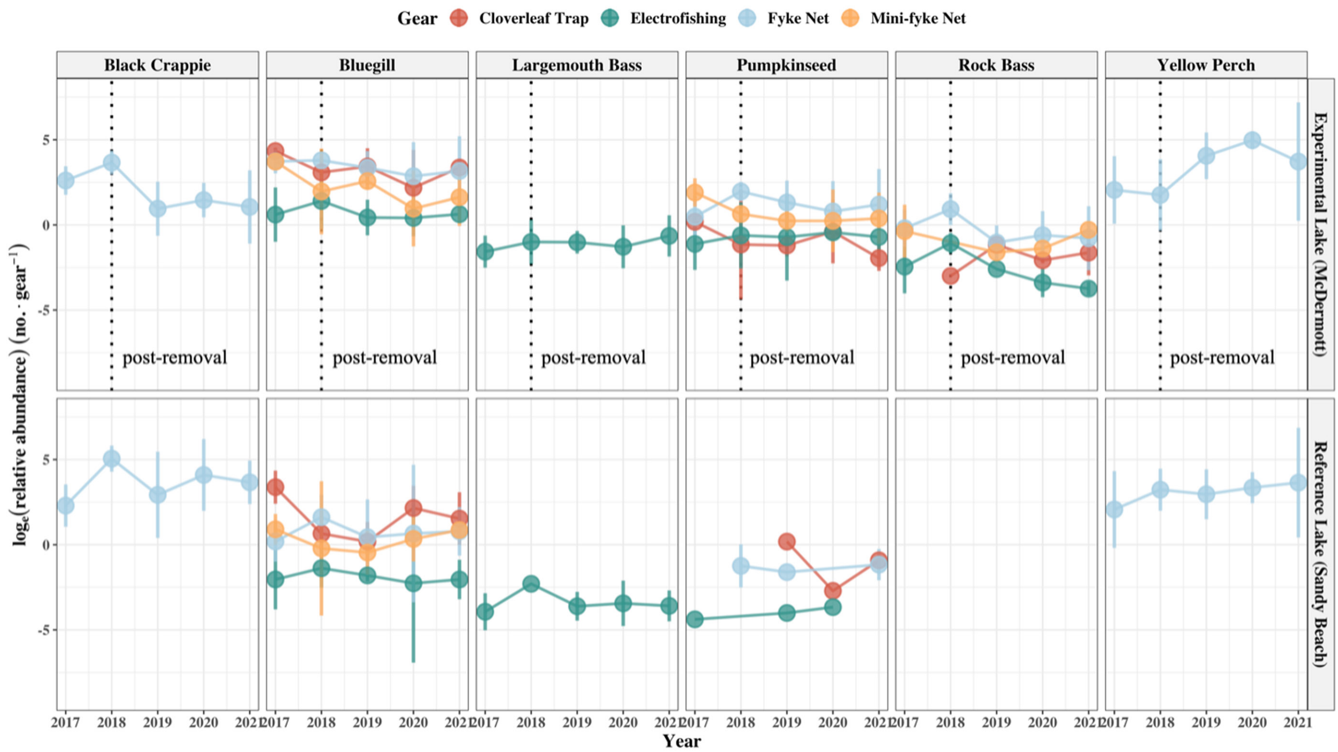


**FIGURE 3** Species-specific relative abundance log$_e$(age-1+ catch per unit effort) (n/gear) for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017–2021. Columns correspond to species, with names identified at the top. The upper row corresponds to the experimental lake, and the lower row corresponds to the reference lake. Error bars represent 95% confidence intervals. Point and line colour correspond to gear type. Vertical dotted lines indicate when Centrarchidae species removals began from the experimental lake in 2018

**TABLE 2** Species-specific annual mean length (mm) for the experimental (McDermott) and reference (Sandy Beach) lakes before (2017) and after (2021) Centrarchidae species were removed from the experimental lake. If no individuals were collected in given gear in 2017, 2018 values are shown. Modelled predictions are presented for statistically significant trends, and empirical estimates are presented for statistically insignificant trends

| Lake | Species | Pre-removal mean length (mm) | Post-removal mean length (mm) | % change | Statistically significant |
|---|---|---|---|---|---|
| Experimental (McDermott) | Black Crappie | 196.78 | 196.38 | −0.20 | No |
| | Bluegill | 75.21 | 70.89 | −5.74 | Yes |
| | Largemouth Bass | 248.65 | 218.30 | −12.21 | Yes |
| | Pumpkinseed | 99.55 | 78.62 | −21.02 | Yes |
| | Rock Bass | 133.48 | 88.78 | −33.49 | Yes |
| | Yellow Perch | 156.14 | 184.03 | 17.88 | Yes |
| Reference (Sandy Beach) | Black Crappie | 202.32 | 203.67 | 0.67 | No |
| | Bluegill | 76.83 | 87.44 | 13.81 | Yes |
| | Largemouth Bass | 419.86 | 355.00 | −15.44 | No |
| | Pumpkinseed | 107.62 | 75.91 | −29.46 | No |
| | Yellow Perch | 167.09 | 160.51 | −3.94 | Yes |

Further, the value of management experiments was demonstrated as the removal helped to define the extent to which managers can intervene in response to shifting ecosystems. Despite intensive effort (more than 23 years of net nights, trap nights and electrofishing), a historical ecosystem condition restoring natural recruitment in the experimental lake was not achieved during the study time frame. These results demonstrate that resistance may not be a viable option in certain contexts, specifically in warming, centrarchid-dominated lakes where fish community composition is also influenced by other non-climate change factors (e.g. voluntary release of centrarchids by anglers, Figure 5; Gaeta et al., 2013; Hansen et al., 2015b; Shaw & Sass, 2020). As resistance efforts may be futile in certain contexts, transitions to different approaches will be critical to adapt to transforming ecosystems (Lynch et al., 2022).

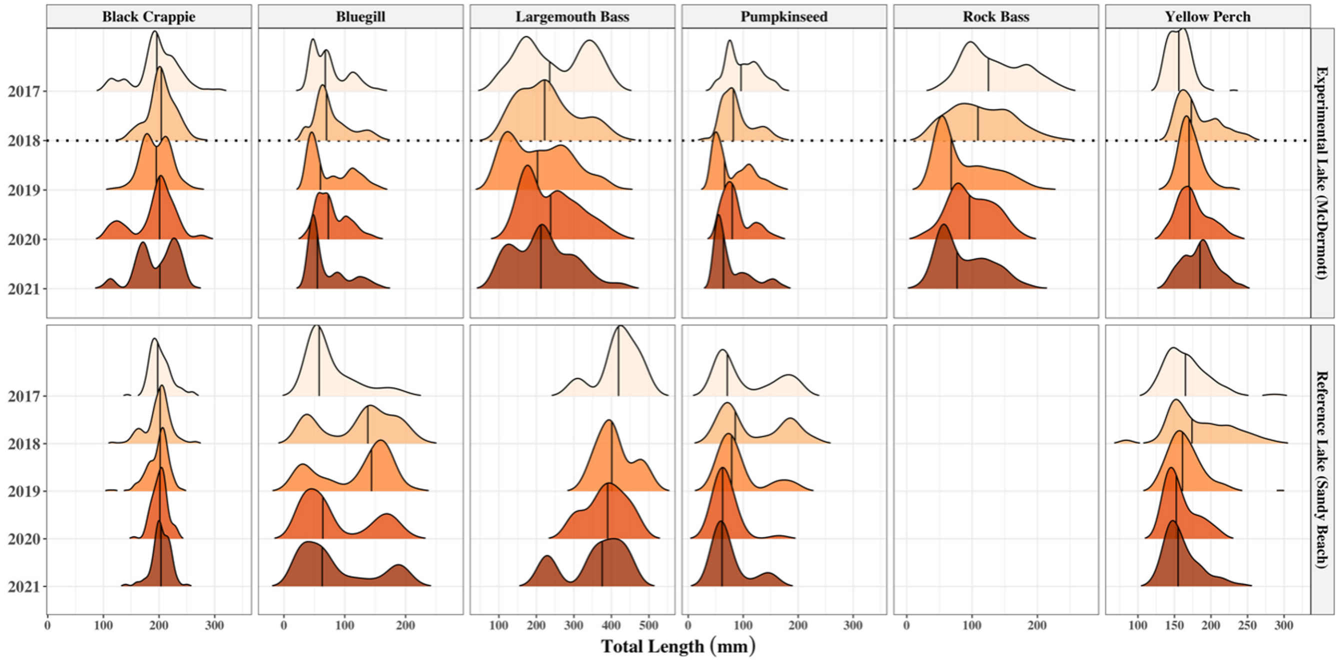


FIGURE 4 Species-specific total length (mm) density distributions for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017–2021. Columns correspond to species, with names identified at the top. The upper row corresponds to the experimental lake, and the lower row corresponds to the reference lake. Vertical black lines in each distribution correspond to the median value. Colour corresponds to year. Horizontal dotted lines indicate when Centrarchidae species removals began from the experimental lake in 2018

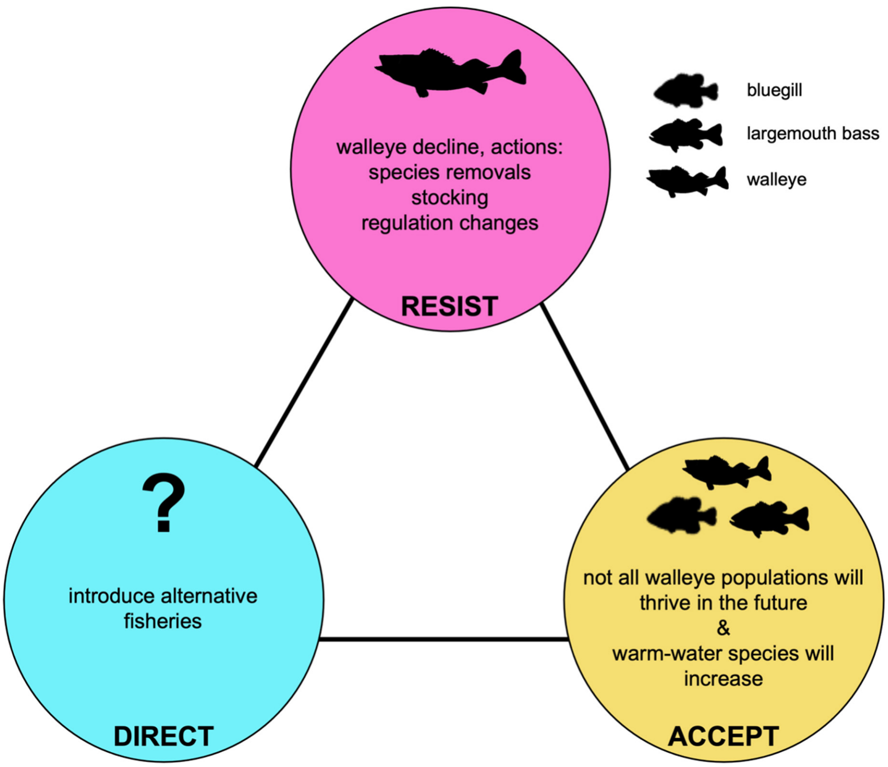


FIGURE 5 Conceptual diagram illustrating potential Resist-Accept-Direct decision pathways for managers reconciling ecosystem transformation in heterogeneous lake districts, such as Northern Wisconsin, USA

## 4.2 | Fish species responses to the whole-lake fish removal experiment

In the experimental lake, an increase in adult walleye abundance was observed in 2020 relative to 2017–2019 and 2021 abundances, but this finding cannot be attributed to any detectable natural recruitment. Given the increasing adult walleye population response in 2020, stocked individuals from previous years may have contributed to the adult fishery at that point, but this response may have been short-lived given the most recent (2021) return to pre-removal abundances. In contrast, after declining for four consecutive years, the reference lake walleye population showed increases in 2021 possibly due to a variety of factors including stocking, harvest variability and natural population fluctuations.

The majority of dominant centrarchid species decreased in relative abundance in the experimental lake, except for largemouth bass, while no significant changes occurred in the reference lake throughout the study period. Black crappie and rock bass showed the largest declines following the first year of removals and have remained at relatively low relative abundances in subsequent years, indicating that these species may be effectively reduced through a single year of intensive removal efforts. Notably, rock bass mean length significantly decreased following removals, indicating compensatory recruitment may have occurred wherein remaining individuals reproduced and grew faster given increased resources (Ali et al., 2003; Gaeta et al., 2015; Sass & Shaw, 2018; Sass et al., 2021a). Pumpkinseed showed slight declines in relative abundance and mean length over time, while largemouth bass showed no change in abundance but a decrease in mean length, illustrating that these species may be more resistant to removal efforts. Largemouth bass, especially juveniles, are difficult to sample in lakes therefore gear evasion may have played a role in the ability to remove this species. Others have shown the limitations of largemouth bass removals via harvest (Gabelhouse, 1987; Sullivan et al., 2019b); therefore, controlling largemouth bass abundance may currently be beyond the reach of management efforts.

The most abundant fish species in the lake, bluegill, showed relative abundance declines in response to fish removals, especially for gears sampling smaller fishes; however, this trend was reversed in 2021. Large-bodied bluegill relative abundance, best indicated by fyke net CPUE, declined throughout the study period, until remaining consistent in 2021. In combination with smaller-bodied bluegill CPUE increases in 2021, increasing bluegill relative abundances and reduced mean length potentially indicating a density-dependent compensatory response occurred. Prior to fish removals, the bluegill population was characterised by many small-bodied individuals (i.e. a stunted population); therefore, it is not entirely surprising that reduced population densities resulted in increased abundances and reduced mean length (Beard & Essington, 2000). However, it is notable that this potential compensatory response did not occur until ~228,000 fishes had been removed from the lake. In contrast, bluegill in the reference lake showed a ~14% increase in mean length. Overall, with the decline in abundance of younger age classes (i.e. smaller fishes) due to removals, it is unsurprising older ages (i.e. larger fishes) also declined over the study period, until a compensatory response was observed. As is emphasised by these results, bluegill are a highly resilient species with remarkably flexible life-history characteristics making them challenging to control in predictable ways (Beard & Essington, 2000; Mittelbach, 1986).

Yellow perch significantly increased in relative abundance and mean length following the first year of fish removals and maintained high levels for the remainder of the study period, overall increasing in abundance by ~788% and in length by ~18%. Although the ecosystem was not pushed back to its historical state supporting natural walleye recruitment, centrarchid relative abundances were reduced such that a window may have been opened for yellow perch to increase and maintain high relative abundances and increase in mean length. It is possible this response was driven by a very strong year-class emerging soon after initial removals; therefore, monitoring will be critical to disentangle the effect of species interactions driving yellow perch population dynamics. Yellow perch are a highly popular cool-water gamefish in north-temperate lakes and a close taxonomic relative to walleye (Brandt et al., 2022; Embke et al., 2020; Feiner et al., 2020). Based on these findings and others (Sikora et al., 2021), yellow perch may be more responsive to changes in community dynamics, revealing potential management intervention avenues to support self-sustaining populations in the future (Figure 5). Increased yellow perch relative abundances present potential fishery opportunities that may satisfy resource user needs given climate change limitations for walleye.

## 4.3 | Approach limitations and considerations

This experiment was performed on a single lake; therefore, the results may not adequately represent the variety of conditions and suite of responses when scaled up to other locations with variable habitat or species assemblages. For example, Sikora et al. (2021) found remarkable rebounds in natural walleye recruitment following single-year intensive bullhead (*Ameiurus* spp.) removals in north-temperate lakes, indicating predator/competitor life-history strategies greatly influence intervention success (Weidel et al., 2007). Further, a significant reduction in centrarchid abundance may not align with a comparable ecological effect for walleye. Perhaps the threshold where enough resources are released for walleye to become dominant was not reached, and therefore, any observed responses may be short-lived. It is acknowledged that a critical threshold may not have been passed but future research may show if the manipulation achieved a new state of the food web as well as if the intensive removal and ongoing stocking could shift the walleye population from depensation to compensation (Mehner et al., 2002; Sass et al., 2021b; Walters & Kitchell, 2001). Therefore, despite uncertainty with regard to reaching a critical threshold, these findings still indicate it is unrealistic to use this intensity of removal efforts as a management measure in broader contexts.

Although the experimental lake did have a history of natural walleye recruitment, no natural recruitment has been detected since 2004. It is possible the experimental lake was never a robust natural population; therefore, this lake may represent a more marginal population like many of those in the region. However, the research presented here represents a highly intensive removal effort for centrarchid species and, therefore, is likely representative of the efficacy of less-intensive management approaches that may be undertaken. Large-scale management experiments such as this are necessary to understand which approaches are feasible given ecological, economic and social constraints (Lynch et al., 2021b).

This study was performed over 5 years, and many organisms including walleye are slow-growing (average age-at-maturity = 4 years for males, 5 years for females; Cichosz, 2017); thus, changes underway may not have been detected due to response time-lags. Yellow perch relative abundance increased in both lakes; however, the magnitude of increase in the experimental lake was significant and suggestive of a centrarchid removal manipulation effect. Given the abundance and mean length response of yellow perch to the centrarchid removal, it is possible that walleye natural recruitment and adult abundance responses may be lagged. Yellow perch are a major prey item of walleye (Forney, 1974), and indices of yellow perch abundance have been shown to be significant predictors of walleye recruitment (Beard et al., 2003; Hansen et al., 1998). Monitoring will be essential to track the ecosystem trajectory and detect when/if the system reaches a new state, specifically if reduced centrarchid populations rebound once removal efforts subside or if walleye and other species, such as yellow perch, further increase.

### 4.4 | Alternative management approaches and future thoughts

Given the effects of global environmental change, it is necessary to consider alternative strategies to *resisting* ecosystem transformation (Lynch et al., 2022). Alternative *accept* and *direct* approaches can be used simultaneously. In this context, managers could *accept* that walleye fisheries may not persist in all ecosystems where they once thrived, especially in warming, centrarchid-dominated systems (Figure 5). At the same time, managers could identify ecosystems most likely to support walleye in the future (e.g. lakes with lower centrarchid abundances; Tingley et al., 2019) and allocate management resources accordingly (Figure 5; Dassow et al., 2022). However, for north-temperate lakes with multi-species fisheries, acknowledging expected walleye declines in certain systems has great implications for the management of other species and human expectations (Hansen et al., 2015b, Tingley et al., 2019; Feiner et al., 2022). For example, when resistance is no longer feasible and managers *accept* that some ecosystems may turn to centrarchid dominance, they could then *direct* certain fisheries towards different species to provide alternative ecologically viable, socially acceptable opportunities (Figure 5). Overall, lake districts—regions with many lakes such as those in Northern Wisconsin—provide the option to distribute RAD approaches across the landscape. For instance, some walleye population managers can *resist* transformation by limiting invasive species or removing bullheads or other predators, while others can *accept* warm-water fisheries that emerge, or others may *direct* the systems by introducing new fisheries (Figure 5).

The heterogeneity of lakes on the landscape provides a great context to apply the RAD decision framework. Management decision pathways such as these will be necessary to manage transforming ecosystems that are likely unable to transition back to historical states given changing climates (Dassow et al., 2022; Feiner et al., 2022). Further shifts to inland systems are likely as complex lake food webs yield to a changing climate (Jackson, 2021). As observed in the large-scale experiment, ecosystem responses are unpredictable and non-stationary. Even in the reference system which was only influenced by abiotic effects and current management approaches (e.g. stocking and harvest regulations), community responses were non-stationary. To effectively manage transforming ecosystems, decisions must consider the inherent uncertainty in future outcomes to account for unexpected shifts (Lynch et al., 2021b). For inland recreational fisheries, several assessment methods exist that consider stochastic dynamics and critical thresholds (Cahill et al., 2021; Carpenter et al., 2017; Embke et al., 2019). To increase management resilience to ecosystem transformation, it will be vital to use approaches such as these that directly consider system thresholds in combination with iteratively evaluating management options in the RAD framework to move beyond traditional resistance when this approach is no longer viable.

## 5 | CONCLUSION

Global environmental change is transforming ecosystems at unprecedented rates. Freshwater systems and the fisheries they support are particularly vulnerable to these changes given their sensitivity to anthropogenic stressors. Although some fishes are negatively influenced by climate change and have declined in some areas (e.g. walleye), others are positively affected and abundances have increased (e.g. centrarchids). These shifting community dynamics present novel challenges for natural resource managers, who have generally resisted change by attempting to maintain historical conditions. The RAD framework provides alternative decision pathways to consider, especially when resistance is no longer an ecologically, economically or socially feasible option (Lynch et al., 2021a; Schuurman et al., 2021; Thompson et al., 2021). The efficacy of resistance as a strategy in supporting self-sustaining walleye populations was tested through a whole-lake centrarchid removal experiment. Although centrarchid abundances were reduced and yellow perch abundance significantly increased, natural walleye recruitment was not detected indicating resistance may not be a viable approach in warming, centrarchid-dominated systems also influenced by other drivers. Managers may need to consider alternative *accept* and *direct* pathways, which open the door to new fishery opportunities (e.g. centrarchids and/or yellow perch in the region of this study). Large-scale management experiments such as the one undertaken here are vital to better understand the capacity to manage ecosystem change. To increase resilience to ecosystem transformation, managers can incorporate uncertainty into assessments while iteratively evaluating management options within the RAD framework.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interests.

## DATA AVAILABILITY STATEMENT

All data and accompanying metadata are freely available to the public supported by the U.S. Geological Survey (USGS) Climate Adaptation Science Centers (https://www.sciencebase.gov/catalog/item/573f4df1e4b04a3a6a24ae6b).

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