

FEATURE

Invasive control and native restoration: Directing ecosystem transformation through purposeful food web manipulations

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A mature Cisco *Coregonus artedii* being measured above a stocking truck holding tank prior to reintroduction into Sparkling Lake, Vilas County, Wisconsin, USA. Photo credit: Amber Mrnak.

ABSTRACT

Ecosystems are abruptly changing due to invasive species and global climate change. In lakes, invasive Rainbow Smelt *Osmerus mordax* can cause negative ecosystem effects through competitive and predatory interactions with native species leading to food web shifts away from native species dominance, altered zooplankton communities, and the decline or extirpation of native cool and coldwater fishes. We conducted two whole-lake removals of invasive Rainbow Smelt and simultaneous introductions of native Cisco *Coregonus artedii* through stocking. About 327 and 1.6 adult Rainbow Smelt/ha were removed and about 45 adult Cisco/ha were stocked over 4 years into the two experimental lakes. In one system, native Yellow Perch *Perca flavescens* relative abundance and density significantly increased by 556% and 143% post-manipulation, respectively. In the other system, native Walleye *Sander vitreus* relative abundance increased by 26% and became consistently present in the pelagic zone post-manipulation (allowing for density estimation). Rainbow Smelt relative abundance and density decreased by >85% in both experimental lakes. The two ecosystems shifted to native species dominance while invasive Rainbow Smelt became insignificant components of the food webs. In these two intensive whole-lake manipulations, we applied the Resist–Accept–Direct (RAD) climate adaptation framework to test an applicable ecological adaptation strategy and used panarchy theory as an ecologically grounded pathway to purposefully *direct* ecosystem transformation. We used this holistic management framework to better understand and manage undesired ecological change—“food web thinking.” In the context of our study, two ecosystems were purposefully *directed* towards native food web structures, species interactions, and processes, which mitigated Rainbow Smelt driven negative effects.

INTRODUCTION

Ecosystems around the globe are abruptly changing (Turner et al., 2020; Vander Zanden, 2005; Weiskopf et al., 2020). Aquatic ecosystems can undergo abrupt change due to invasive species and global climate change (Carpenter et al., 2011; Rahel & Olden, 2008; Reid et al., 2019), among other factors. Ecosystem transformations may occur when the system diverges from previous food web structure, species interactions, processes, and/or anthropogenic uses (Carpenter et al., 2011; Embke et al., 2022; Folke et al., 2004). As global change and species invasions accelerate and interact with other stressors (e.g., overexploitation, land use and habitat change, pollution), ecosystems may cross an ecological threshold, resulting in a novel system structure (Jacobson et al., 2013; Mrnak et al., 2023; Thompson et al., 2021). Given high biodiversity and coupled human–land–water linkages, freshwater ecosystems are highly sensitive to the interacting threats of invasive species and climate change (Reid et al., 2019). North-temperate lake ecosystems are transforming at a rapid rate (Embke et al., 2022; Feiner et al., 2022; Lynch et al., 2016). Invasive species (Bethke et al., 2023; Martin et al., 2023; Perales et al., 2021) and habitat loss (Christensen et al., 1996; Marburg et al., 2006; Sass et al., 2017), in combination with other stressors (e.g., overexploitation, pollution), reduce or weaken the potential for freshwater ecosystems to support sustainable fisheries (Embke et al., 2019; Hilborn et al., 2015; Mrnak et al., 2018; Post, 2013; Walsh et al., 2016).

Invasive species are drivers of ecological change (Vander Zanden et al., 2010; Vitousek et al., 1996). Rainbow Smelt *Osmerus mordax* (Mitchill, 1814), native to the North Atlantic coast, have invaded many north-temperate inland lakes (Evans & Loftus 1987; Hrabik et al., 1998; Mercado-Silva et al., 2007). Rainbow Smelt can cause significant negative community effects via competition and/or predation due to their rapid population growth, early spawning phenology, omnivorous diet, and eurythermal life history (Evans & Loftus, 1987; Grosholz et al., 2021; Sheppard et al., 2012). Thus, Rainbow Smelt interacts (directly or indirectly) with a wide range of native biota at multiple trophic levels. The most well documented negative effects of Rainbow Smelt on native aquatic ecosystems include shifting food webs away from native species dominance, altering zooplankton communities, and the decline or extirpation

of native cool and coldwater fishes (e.g., Yellow Perch *Perca flavescens* (Mitchill, 1814), Walleye *Sander vitreus* (Mitchill, 1818), Cisco *Coregonus artedii* (Lesueur, 1818), Lake Whitefish *Coregonus clupeaformis* (Mitchill, 1818); Evans & Loftus, 1987; Hrabik et al., 2001; Lepak et al., 2023). Mechanistically, declines of cool and coldwater fishes, such as Yellow Perch and Cisco, have been linked to competition and predation, respectively (Hrabik et al., 1998, 2001). A thorough review on the invasion history, biology, and ecology of Rainbow Smelt in North America is presented in Mrnak et al. (2023).

Removing Rainbow Smelt from a north-temperate ecosystem may reduce competition and/or predation pressure on native fishes, potentially alleviating critical population bottlenecks (Gaeta et al., 2015; Krueger & Hrabik, 2005; Lawson et al., 2015; Mrnak et al., 2023). Management to control or eradicate Rainbow Smelt have focused on whole-lake experiments using two approaches, (1) biomanipulation (Gaeta et al., 2015) and (2) the mechanical elimination of suitable oxythermal habitat (Lawson et al., 2015; Mrnak et al., 2023). Both studies resulted in a >90% reduction in invasive Rainbow Smelt abundance (Gaeta et al., 2015; Lawson et al., 2015). However, the devoid niche space following removals was not recolonized by remnant native species (Mrnak et al., 2023). Given the strong compensatory recruitment response invasive Rainbow Smelt may exhibit, these invaders may reach high densities and dominate the fish community again if left unchecked (Mrnak et al., 2023). Invasive Rainbow Smelt control and native species recovery was documented for two lakes in northern Wisconsin (Krueger & Hrabik, 2005). In response to declining native Cisco, Krueger and Hrabik (2005) increased Walleye predation rates through stocking and regulatory protection. Due to selective predation by Walleye on Rainbow Smelt, a competitive and/or predatory release was lifted off the dwindling remnant Cisco population, allowing for their recovery (Krueger & Hrabik, 2005). Mrnak et al., (2023) concluded that Rainbow Smelt control and/or eradication success depends on whether (1) enough Rainbow Smelt were removed to devoid their niche space and (2) devoid niche space became filled with desired native species.

Recent shifts in ecosystem management have increasingly focused on frameworks that account for both the unpredictability and complexity of global environmental and biological

change (Embke et al., 2022; Mrnak et al., 2023). The Resist-Accept-Direct (RAD) framework is a novel management tool designed to help resource managers make strategic decisions in the face of rapid ecological transformations, such as those caused by invasive species and climate change. The RAD framework categorizes responses into three distinct pathways: resisting change to maintain historical conditions, accepting change without intervention, or directing change toward a desired future state (Lynch et al., 2021; Rahel, 2022; Thompson et al., 2021). The RAD approach is particularly useful in addressing the challenges posed by shifting ecosystems, as it offers a structured yet flexible decision-making framework that can adapt to the dynamic and often irreversible transformations ecosystems undergo (Lynch et al., 2021). This framework is vital for managing aquatic ecosystems that are vulnerable to compounding stressors, including invasive species and climate change, which threaten biodiversity and ecological functions (Thompson et al., 2021).

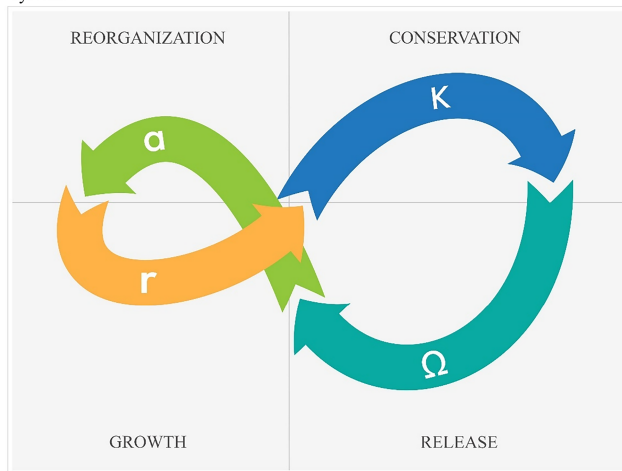
In tandem with RAD, panarchy theory provides a conceptual model for understanding the cyclical nature of ecosystem dynamics through phases of the adaptive cycle; conservation, release, reorganization, and growth (Holling 2001; Mrnak et al., 2023; Figure 1). Panarchy theory describes how systems respond to disturbance and change, acknowledging that ecosystems do not remain static but instead exist in cycles of

stability and disruption. By recognizing where an ecosystem lies within this cycle, managers can better tailor their interventions to either resist unwanted transformations or direct the system toward desirable outcomes. For example, applying panarchy theory to invasive species management involves identifying opportunities to trigger a release phase—such as through the removal of an invasive species from the community—and then guiding the system through reorganization toward a more resilient, native-species-dominated state (Mrnak et al., 2023). Combined with RAD, panarchy theory offers an ecologically grounded framework for proactive and adaptive management that is essential in dealing with the increasing rate of undesired ecological transformation (Gunderson & Holling, 2002; Mrnak et al., 2023).

Shifting species dominance as a form of ecosystem transformation may be a powerful and beneficial strategy, promoting resilience and restoring ecological balance in systems destabilized by invasive species and environmental change (Bouska, 2020; Carpenter et al., 2011; Folke et al., 2004; Sundstrom et al., 2018). Two whole-lake experimental removals of invasive Rainbow Smelt and stockings of native Cisco were conducted and guided by the RAD framework and panarchy theory to test the applicability of shifting species dominance from invasive to native species. Fish community responses in the two experimental lakes and two reference lakes were monitored. Our objectives were to: (1) test whether it was possible to reduce the relative abundance and density of invasive Rainbow Smelt through intensive removals and native Cisco introductions and (2) test for changes in the relative abundance and density of the native fish community.

(α) phase: resources release, ecosystem structure and interactions renew. Reorganization and recovery of the inland fishery if release is strong enough to reset system.

(K) phase: nutrient and biomass growth declines and becomes stored in ecosystem structure, interactions between species become bound and rigid. Inland fishery in a stable ecosystem regime.



(r) phase: abundantly available resources, ecosystem structure and interactions increasing. New ecosystem structure allows for novel interactions within the inland fishery.

(Ω) phase: disturbance/perturbation to the ecosystem where chaos ensues. Stored biomass (ecosystem structure) and interactions weaken and breakdown.

Figure 1. Four phases of a single nested adaptive cycle of a panarchy. Conservation phase—invasive Rainbow Smelt dominant; Release phase—invasive Rainbow Smelt removed and native Cisco *Coregonus artedii* stocked; Reorganization and Growth phases—monitored following experimental food web manipulations to test whether the resulting Conservation phase of native species dominance was achieved (Mrnak et al., 2023). Reprinted and adapted with permission from J. T. Mrnak, L. W. Sikora, M. J. Vander Zanden, and G. G. Sass.

METHODS

Study area

Experimental (Crystal Lake, 37.6 ha, 46.000878°, −89.612474°; Sparkling Lake, 63.5 ha, 46.007317°, −89.700080°) and reference (Trout Lake, 1,563 ha, 46.033541°, −89.673653°; Anderson Lake, 10 ha, 46.170762°, −89.344326°) lakes are located in Vilas County, Wisconsin, USA (Figure 2) and

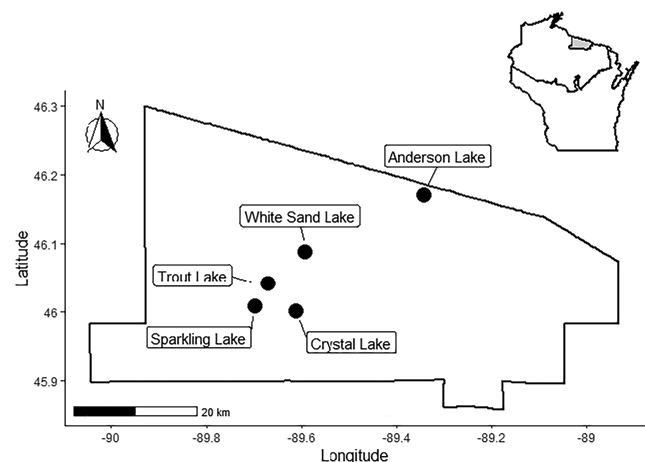


Figure 2. Map of Vilas County, Wisconsin, USA showing experimental (Crystal Lake, Sparkling Lake), reference (Anderson Lake, Trout Lake), and Cisco donor (White Sand Lake) systems.

Table 1. Fish community composition for experimental (Crystal and Sparkling lakes) and reference (Trout and Anderson lakes) systems highlighting current dominant predators and pelagic forage fishes (e.g., Cisco, Lake Trout, Lake Whitefish *Coregonus clupeaformis*, Largemouth Bass *Micropterus nigricans*, Muskellunge, Rainbow Smelt, Smallmouth Bass, Walleye, and Yellow Perch).

	Lake			
	Crystal (experimental)	Sparkling (experimental)	Trout (Cisco reference)	Anderson (Rainbow Smelt reference)
Dominant predators	None	Muskellunge, Smallmouth Bass, Walleye	Lake Trout, Walleye	Muskellunge, Largemouth Bass, Smallmouth Bass
Dominant pelagic forage fishes	Cisco, Rainbow Smelt, Yellow Perch	Cisco, Rainbow Smelt	Cisco, Lake Whitefish	Rainbow Smelt

have similar lake characteristics but different fish communities (Shay et al., 2024). At the beginning of our experiment in 2020, Crystal Lake contained invasive Rainbow Smelt, no native Cisco, and no top predators, while Sparkling Lake contained invasive Rainbow Smelt, native top predators in Walleye, Muskellunge *Esox masquinongy* (Mitchill, 1824), and Smallmouth Bass *Micropterus dolomieu* (Lacepede, 1802), and no remaining native Cisco (Table 1). Invasive Rainbow Smelt abundances were at historically low levels in Crystal and Sparkling lakes at the beginning of our experiment (Magnuson et al., 2024) likely due to a whole-lake water column mixing experiment aimed to exceed the thermal tolerance of Rainbow Smelt (Lawson et al., 2015) and a prior Rainbow Smelt physical removal experiment (Gaeta et al., 2015), respectively. Trout Lake’s fish community is dominated by native Cisco and contains no invasive Rainbow Smelt, while the Anderson Lake fish community is dominated by invasive Rainbow Smelt with no native Cisco present (Mrnak et al., 2023; Parks & Rypel 2018; Table 1). Crystal Lake experienced marked declines in the Yellow Perch population following Rainbow Smelt invasion in 1985 (Hrabik et al., 1998, 2001; Lawson et al., 2015; Mrnak et al., 2023). Following Rainbow Smelt invasion in Sparkling Lake in 1982, Cisco were extirpated from the system (Hrabik et al., 1998; Mrnak et al., 2023) and Walleye recruitment (i.e., relative abundance of nonstocked age-0 Walleye collected in fall electrofishing surveys) declined (Gaeta et al., 2015). Similar to other imperiled Walleye populations across the Midwest USA, Sparkling Lake has been stocked with extended growth fingerling Walleye (~150–220 mm TL) during the fall of odd years since 1997 (see Elwer et al., 2023). Due to this standard practice occurring consistently for the past 26 years, we reasoned that stocking would be independent of any observed responses in the Walleye population following experimental manipulation (see also Elwer et al., 2023; Lawson et al., 2022).

Experimental manipulation

Native species introduction efforts

Native Cisco introductions into the experimental lakes occurred in November of 2020 and 2021. Before Cisco could be moved across the landscape, the donor lake (White Sand Lake, 306 ha; Vilas County, Wisconsin, USA; 46.083402°N, –89.587942°W; Figure 2) Cisco population needed to test negative for viral hemorrhagic septicemia and whirling disease by Wisconsin Department of Natural Resources fish veterinarians (Figure 3A; negative results acquired on November 2,

2020). Donor Cisco were captured from White Sand Lake during peak spawn via AC boat electrofishing when water temperatures were 4–6 °C (November 4–November 13; Figure 3B). All captured Cisco were enumerated and a subset ($n = 50$) were measured for total length (TL) and sexed (by visual expression of gametes) to estimate the male:female ratio (Figure 3C). All Cisco were mature and running. Captured Cisco were moved from the electrofisher livewell to an insulated hatchery truck containing oxygenated water from the recipient lake (i.e., Crystal or Sparkling Lake; mitigate invasive species spread; Figure 3D and E). Based on a summer 2020 population estimate and conversations with the local fishery biologist, the 2020 Cisco introduction goal was 14.8 adult Cisco/ha into Crystal and Sparkling lakes. These densities equated to 587 and 962 adult Cisco being stocked into Crystal and Sparkling lakes, respectively, in November 2020. After an additional Cisco population estimate on White Sand Lake in summer of 2021, introduction efforts were doubled in fall of 2021. The 2021 Cisco introduction goal was 29.6 adult Cisco/ha into Crystal and Sparkling lakes. These densities equated to 1,167 and 1,887 adult Cisco being stocked into Crystal and Sparkling lakes, respectively, in 2021. There were no observed Cisco mortalities on the night of the transfer or on the following day after circumnavigating each lake’s shoreline.

Invasive species removal efforts

Intensive Rainbow Smelt removal efforts started in spring of 2021 in the experimental lakes using mini fyke nets (0.6 × 1.2 m, 0.65-cm bar mesh) and continued through 2023 (Figure 4A). About 2 weeks before ice-out (April 1–April 26), a chainsaw and/or spud bar was used to break ice perpendicular to shore for mini fyke net deployment (~3 × 10-m rectangle; Figure 4B and C). The number of mini fyke nets initially deployed was dictated by ice or environmental conditions but ended at 8 nets/lake by the end of the Rainbow Smelt spawn (shortly after ice-out). Mini fyke net locations were chosen based on observed Rainbow Smelt spawning habitat (gravel, cobble) and previous research (Lischka & Magnuson, 2006). Mini fyke nets were checked daily with all fish identified to species and up to 30 individuals per species were measured (TL; nearest mm), weighed (nearest g), and sexed by visual expression of gametes (Figure 4D). Invasive Rainbow Smelt were separated and donated to an animal rehabilitation facility to be used for recovering animal food, while all other fish were returned to the lake (Figure 4D). In addition to our intensive Rainbow Smelt removal method (pre-ice-out mini fyke nets during Rainbow Smelt spawn), Rainbow Smelt were also

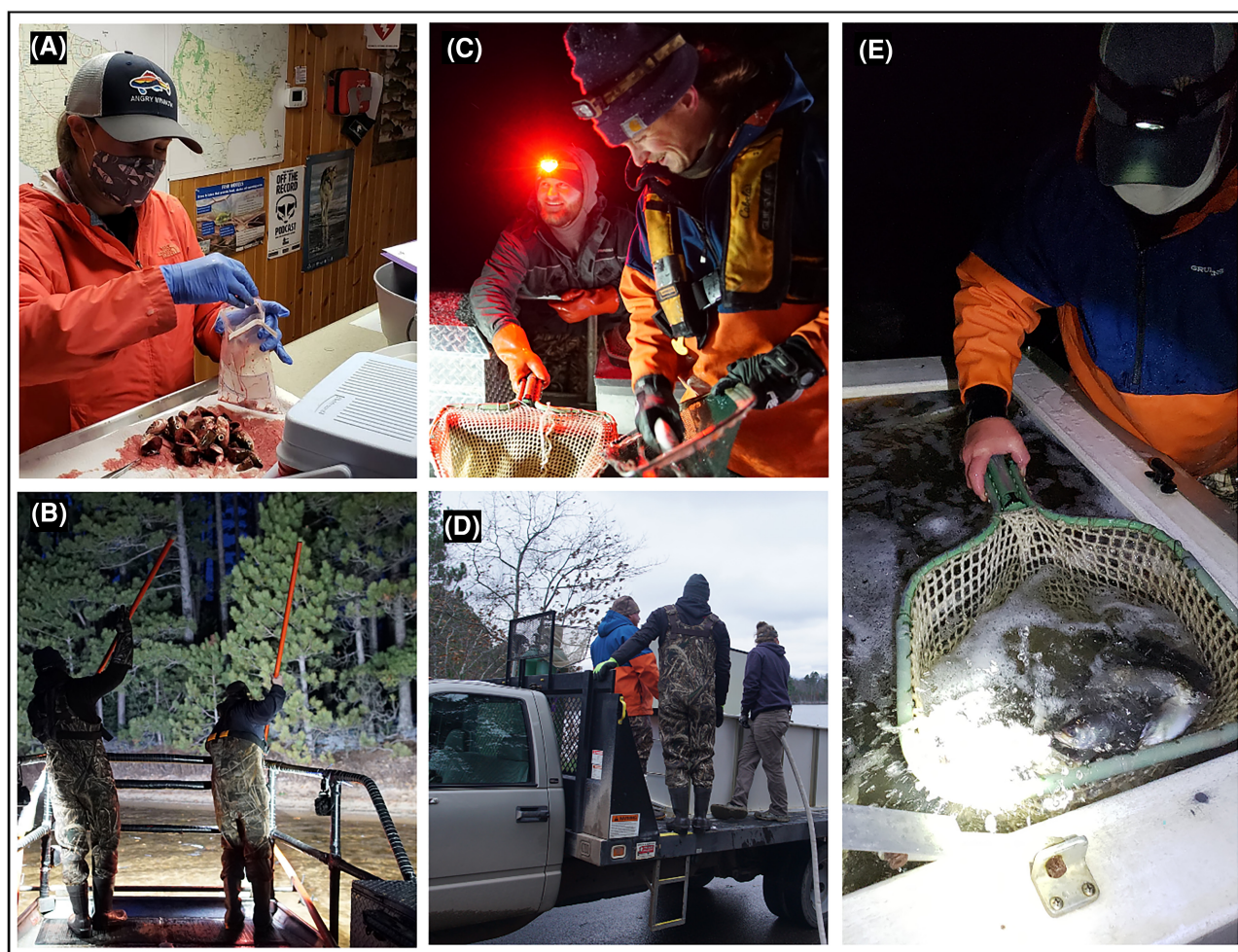


Figure 3. Photographs of the Cisco stocking efforts for the experimental manipulation. (A) Wisconsin Department of Natural Resources Senior Aquatic Veterinarian preparing Cisco samples for viral hemorrhagic septicemia and whirling's disease testing. (B) Researchers capturing Cisco via boat electrofishing on the donor lake (White Sand Lake; Vilas County, Wisconsin USA). (C) Researchers processing captured Cisco for demographic information prior to transfer into the stocking truck. (D) Stocking truck being filled with recipient lake water (Crystal or Sparking lakes; Vilas County, Wisconsin USA). (E) Researcher netting Cisco out of the stocking truck to be stocked into the recipient lake (e). Photo credits: Joe Mrnak (A & E), Amber Mrnak (B–D).

removed from the experimental lakes when captured in our summer vertical gill net monitoring surveys (see below).

Fish sampling Standardized surveys

During 2020–2023, standardized monthly vertical gill net sampling and bimonthly hydroacoustic surveys were conducted post-stratification (mean date during study among lakes was June 15) to test for changes in the fish communities among lakes. For all lakes, hydroacoustic data were collected with a BioSonics DTX echosounder and downward facing 70- kHz split-beam transducer mounted 1 m below the water surface. Thresholds for data collection were set to exclude raw echoes < -100 dB for backscattered (S_v) data to exclude weak signals that were likely to be noise or nontarget objects (e.g., small particles, bubbles) and -70 dB for target strength data to focus on echoes that represented relevant fish targets (e.g., ≥ 75 mm TL) with a transmitted pulse duration of 0.4 ms. Hydroacoustic surveys were conducted at least 30 min beyond nautical twilight to minimize the likelihood of backscattering

via fish schooling behavior and followed standardized and replicable whole-lake transects at a mean vessel speed of ~ 9 km/h. All whole-lake transects surveyed habitat > 3 m in depth. Prior to each year's sampling, we calibrated our hydroacoustic system using a tungsten carbide sphere (38.1 mm in diameter; Mrnak et al., 2021). Across all years, observed target strength fell within acceptable limits of the nominal target strength.

All hydroacoustic data was analyzed using Echoview software (v12.1). The top 2 m of the water column were excluded from analysis, including the 1 m transducer depth and twice the transducer nearfield range (0.49 m). A 0.25-m bottom exclusion line was applied to raw data to delineate returns from the benthic acoustic dead zone. Data criteria followed the Great Lakes Standard Operating Procedure for acoustic data (Mrnak et al., 2021; Parker-Stetter et al., 2009); target strength threshold of -55 dB, 0.5 minimum and 1.5 maximum normalized pulse length, 6 dB maximum beam compensation, and 1° minor- and major-axis angles.

To inform species composition from hydroacoustic data, we conducted 24-h vertical gill net surveys to apportion



Figure 4. Photographs of the invasive Rainbow Smelt *Osmerus mordax* removal efforts for the experimental manipulation. (A) Crystal Lake (Vilas County, Wisconsin USA) at the beginning of the Rainbow Smelt removal efforts in 2022. (B) Researcher stepping over a set mini fyke net after clearing a 3 m × 10 m area of >30 cm thick ice on Rainbow Smelt preferred spawning habitat (rock, gravel). (C) Researcher maintaining ice around a mini fyke net. (D) Researcher processing removed Rainbow Smelt for demographic information prior to transport to a local animal rehabilitation facility. Photo credits: Joe Mrnak.

species-specific hydroacoustic estimates using gill net count and fish length data. We followed standardized North Temperate Lakes Long-Term Ecological Research protocols (Feucht et al., 2023; Magnuson et al., 2024) and deployed seven monofilament gill nets in the deep basin of each lake from surface to bottom. After 24 h, vertical gill nets were picked and all fish were identified to species, enumerated, measured (TL; nearest mm), and weighed (nearest g). Gill nets were 3 × 30 m and had stretched mesh sizes of 19, 25, 32, 38, 51, 64, or 89 mm. Species-specific mean TL was then transformed into a target strength following the multispecies model developed in Love (1971). Species classes were then assigned using mean target strength and then assigned a proportion of total biomass, derived from gill net catches. Two individuals of the same species needed to be captured in the gill nets for that species to be represented in the hydroacoustic data and ensuing density estimate. We used single target analyses to estimate sigma values (excluding targets > -55 dB), which were then applied to S_v data (i.e., backscattered sound) to estimate pelagic density for each 200-m segment along whole-lake transects. A 200-m segment length was chosen because correlation analyses have shown that this segment length is generally not spatially correlated with others (Mrnak et al., 2021). Each 200-m transect was treated as a replicate such that whole-lake density and associated 95% CI could be estimated. Passive vertical gill net sampling provided relative abundance estimates (catch-per-unit-effort, CPUE; number fish/net night), while active hydroacoustic surveys provided whole-lake density estimates

(number fish/ha). To estimate whole-lake biomass (kg) before and after experimental manipulation, we multiplied the annual mean weight for each species captured in our vertical gill net surveys by the annual mean density estimate and then by lake area.

Data analyses

The biomass of Rainbow Smelt removed from the experimental lakes was estimated by extrapolating lengths and weights to unmeasured fish based on the measured sample. A subset of measured Rainbow Smelt (daily maximum = 30 Rainbow Smelt/gear type) were used to assign TL (mm) to unmeasured fish. Available fish lengths were sampled with replacement and used to assign lengths to unmeasured fish based on the total number of individuals collected. To estimate total Rainbow Smelt biomass removed, weight-length regressions were created for each lake-year combination to predict weights (g) of fish that were not weighed. Length was $\log_e$ transformed prior to analysis. After all sampled Rainbow Smelt had an assigned weight, Rainbow Smelt weights were summed for the experimental lakes during 2020–2023 to calculate total biomass removed (kg). Note that pre-fall 2020 was a baseline monitoring year and Rainbow Smelt removed from experimental lakes in 2020 came from standardized vertical gill net monitoring surveys and not intensive fyke net removals.

Testing for fish community changes focused on summer of 2020 (baseline, pre-manipulation) and 2023 (post-manipulation) vertical gill net (relative abundance, CPUE)

and hydroacoustic (density) data. Our research was focused on understanding adult population dynamics of these species, while avoiding the stochastic variability of age-0 recruitment dynamics. Thus, a 75-mm cutoff was used to designate Cisco, Rainbow Smelt, and Yellow Perch as age-1+ (adult) or age 0 (young-of-year; Hrabik et al., 2001; Mrnak et al., 2021). Only adult Walleye were present in vertical gill net and hydroacoustic surveys. Only adult (i.e., ≥ 75 mm) fish were used in CPUE and density analyses. A Shapiro–Wilk test indicated that CPUE and density data were nonnormally distributed; thus, CPUE and density data were log_e + 1 transformed prior to analysis. To test for differences in mean annual CPUE or density of Cisco, Rainbow Smelt, Yellow Perch, and Walleye before (2020) and after the experiment (2023), a one-way ANOVA was used. Hypothesis tests were considered significant at $\alpha \leq 0.05$.

RESULTS
Experimental manipulation

A total of 12,311 adult invasive Rainbow Smelt were removed from Crystal and Sparkling lakes during 2021–2023 (Figure S). Over 95% of all removed Rainbow Smelt came from spring mini fyke net surveys, with 390 individuals being removed via vertical gill nets during 2020–2023. Spring mini fyke net removal efforts ranged from 48 net nights on Crystal Lake in 2021 to 175 net nights on Sparkling Lake in 2023 and was dictated by water temperature and ice-out. Mean TL and weight of Rainbow Smelt captured during spring fyke net removals increased over time. In Crystal Lake, mean ($\pm$ SD) TL and weight was 169.9 mm (± 10.9) and 30.4 g (± 6.2), 198.2 mm (± 10.3) and 43.4 g (± 7.6), and 202.3 mm (± 12.8) and 50.5 g

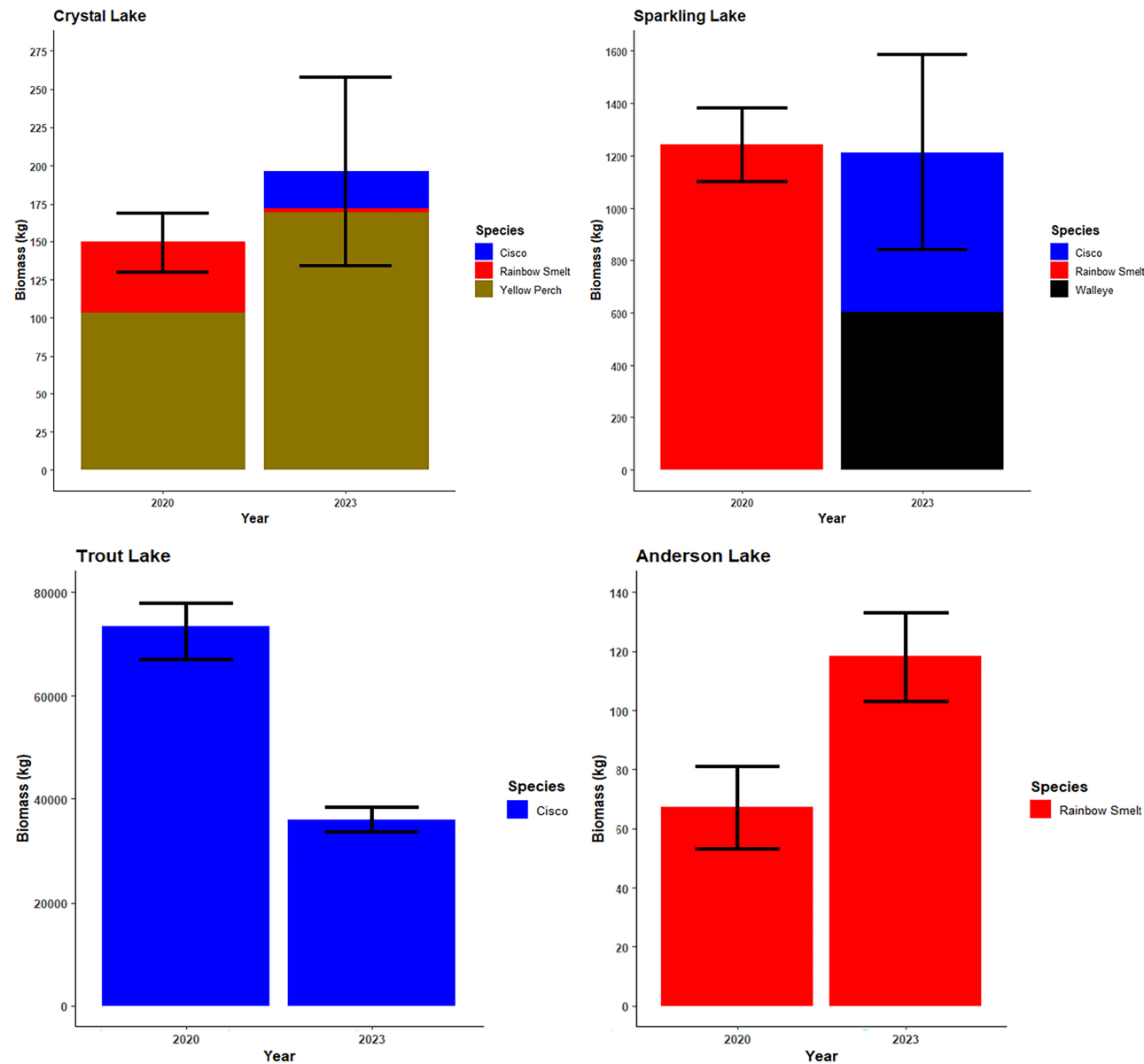


Figure 5. Whole-lake fish biomass ($\pm$ SE) estimates derived from vertical gill net and hydroacoustic surveys for experimentally manipulated (Crystal Lake, Sparkling Lake; top) and reference (Trout Lake, Anderson Lake; bottom) lakes from 2020 (pre-manipulation) and 2023 (post-manipulation). Invasive Rainbow Smelt are shown in red. Native Cisco, Yellow Perch, and Walleye are shown in blue, gold, and black, respectively. Error bars represent 1 SE for the cumulative whole-lake biomass estimate.

Table 2. Species-survey-specific relative abundance (vertical gill net [VGN] CPUE; fish/net night) and density (hydroacoustic estimates; fish/ha) for the experimental (Crystal Lake, Sparkling Lake) and reference (Trout Lake, Anderson Lake) lakes before (2020) and after (2023) Rainbow Smelt removals and Cisco introductions. Spaces with a (–) indicate that the species was not observed in that survey-year combination.

Lake	Species	Survey type	Pre-manipulation mean CPUE or density	Post-manipulation mean CPUE or density	Percent change	F-statistic	Statistically significant ($P \leq 0.05$)
Crystal (experimental)	Rainbow Smelt	VGN	65.00	7.67	–88.2	$F_{1,5} = 27.2$	Yes
		Hydro	48.28	1.73	–96.4	$F_{1,8} = 634.2$	Yes
	Cisco	VGN	–	6.67	–	–	–
		Hydro	–	1.90	–	–	–
	Yellow Perch	VGN	84.00	550.76	555.7	$F_{1,5} = 14.2$	Yes
		Hydro	64.54	156.79	142.9	$F_{1,8} = 28.2$	Yes
Sparkling (experimental)	Rainbow Smelt	VGN	8.00	1.00	–87.5	$F_{1,4} = 126.4$	Yes
		Hydro	1312.32	–	–	–	–
	Cisco	VGN	–	8.67	–	–	–
		Hydro	–	54.40	–	–	–
	Walleye	VGN	1.33	1.67	25.6	$F_{1,4} = 0.5$	No
		Hydro	–	14.14	–	–	–
Trout (Cisco reference)	Cisco	VGN	173.00	401.25	131.9	$F_{1,4} = 9.3$	Yes
		Hydro	1082.55	712.06	–34.4	$F_{1,5} = 4.3$	No
Anderson (Rainbow Smelt reference)	Rainbow Smelt	VGN	10.50	80.33	665.0	$F_{1,3} = 5.8$	No
		Hydro	208.82	461.62	121.1	$F_{1,7} = 21.9$	Yes

(± 12.4) in 2021, 2022, and 2023, respectively. In Sparkling Lake, mean ($\pm$ SD) Rainbow Smelt TL and weight increased from 110.5 mm (± 0.7) and 7.5 g (± 0.7) in 2021 to 112.3 mm (± 6.5) and 7.6 g (± 1.1) in 2022. One individual Rainbow Smelt was captured on Sparkling Lake during the 2023 spring fyke net removal survey (TL and weight of 108 mm and 5 g). In total, 391.5 and 2.2 kg of invasive Rainbow Smelt were removed from Crystal and Sparkling lakes, respectively.

4,594 adult Cisco were successfully captured from White Sand Lake and transferred into Crystal and Sparkling lakes (Figure 5). Across stocking years, mean length of introduced Cisco was 242 mm (range 208–276 mm) and the male:female sex ratio was 4.6. All Cisco handled were mature and expressing gametes.

Fish community responses

After two Cisco stocking events and three intensive Rainbow Smelt removals, the Crystal and Sparkling Lake fish communities shifted from invasive to native species dominance (Table 2; Figure 5). Invasive Rainbow Smelt vertical gill net CPUE (number fish/net night) and hydroacoustic density estimates (number fish/ha) significantly declined in both experimental lakes (all $p < 0.001$; Table 2). Crystal Lake's Rainbow Smelt CPUE and density were lower in 2023 compared to 2020 by 88.2% and 96.4%, respectively (Figure 6). Native Yellow Perch exhibited a significant positive response with CPUE and density being 555.7% and 142.9% greater in 2023 than 2020, respectively (all $p \leq 0.01$; Table 2; Figure 6). Sparkling Lake's Rainbow Smelt CPUE was 87.5% lower in 2023 compared to 2020 and Rainbow Smelt did not show up in the 2023 hydroacoustic density estimates due to inadequate sample sizes in vertical gill net surveys ($n < 2$; Figure 7). There was no statistical change in CPUE of Walleye after the experimental manipulation ($p = 0.51$; Table 2). Walleye were present in the 2022 and 2023 hydroacoustic surveys after not being observed during 2020–2021 estimates (Figure 7).

Cisco were not observed in any survey on Crystal or Sparkling lakes in 2020. Following the stocking events in 2020 and 2021 on Crystal and Sparkling lakes, adult Cisco were present in all 2023 vertical gill net and hydroacoustic surveys (Table 2; Figures 6 and 7). Mean ($\pm$ SD) TL and weight of Cisco captured in vertical gill nets on Crystal and Sparkling lakes in 2023 was 318 mm (± 18.4) and 338 g (± 67.1) and 266 mm (± 14.6) and 177 g (± 29.8), respectively. There was a single Cisco natural recruit (108 mm TL, estimated to be an age 1) captured in vertical gill nets from Crystal Lake on 17, September 2021 (see Feucht et al., 2023) and two Cisco natural recruits (90 and 91 mm TL, estimated to be age 1) captured in vertical gill nets from Sparkling Lake on August 8, 2024 (post-manipulation monitoring).

Reference populations

Trout Lake's reference Cisco population density was similar before and after the experiment ($p = 0.09$; Table 2; Figure 8). Cisco vertical gill net CPUE for Trout Lake was 131.9% greater in 2023 compared to 2020 ($p = 0.03$; Table 1; Figure 8). Anderson Lake's reference Rainbow Smelt population density was 121.1% lower in 2020 compared to 2023 ($p < 0.01$; Table 2; Figure 9) while vertical gill net CPUE did not significantly change ($p = 0.09$; Table 2; Figure 9).

DISCUSSION

Whole-lake manipulations to direct an ecosystem

The food webs of Crystal and Sparkling lakes were purposefully and successfully reconfigured (directed) to native species dominance (Figure 5). Intensive and directed removal efforts targeted at the adult spawning stock of the Rainbow Smelt populations resulted in ecosystem-wide declines in relative abundance and density of this invader. Adult Cisco were successfully reintroduced into the experimental lakes and appeared to have colonized the recently devoid Rainbow Smelt

preferred habitat, as observed by consistent Cisco presence in standardized surveys. Removing adult invasives and introducing adult natives should undermine the reproductive potential of Rainbow Smelt, while increasing the probability of successful Cisco reproduction (Maunder & Punt, 2013; Myers et al., 1999; Thorson, 2020). Though a more long-term lens is needed to adequately assess ecosystem transition, resilience, and persistence (Carpenter et al., 1985; Holling, 2001; Mrnak et al., 2023; Trisos et al., 2020), short-term biotic responses indicated that a predatory and/or competitive hold has been lifted off Yellow Perch in Crystal Lake, as observed by a significant increase in their relative abundance, density, and biomass following the experimental manipulation. Given previous research on Crystal Lake (Hrabik et al., 2001), we reason that thermal and diet overlap between the two species was reduced following our large-scale Rainbow Smelt removal, thus allowing for the strong and rapid Yellow Perch response. We also observed a more consistent presence of Walleye in the pelagic zone of Sparkling Lake beginning in 2022. This may be indicative of a cost-benefit species-interaction change where Walleye may be shifting from littoral resources to select for the novel native pelagic resource provided by Cisco reintroduction (Krueger & Hrabik, 2005; Martin & Vander Zanden, 2023). Additional diet and isotopic analyses will be needed to support or refute this hypothesis.

Diminished abundances of Rainbow Smelt in Crystal and Sparkling lakes should lead to reduced or mitigated negative effects on the native food webs of the lakes (Evans & Loftus, 1987; Mercado-Silva et al., 2007; Mrnak et al., 2023). At the conclusion of our study, native species that have coevolved together represented the dominant biomass in Crystal and Sparkling lakes. At reduced abundances and densities, the Rainbow Smelt negative ecosystem effect strength will be mitigated (Gaeta et al., 2015; Hrabik et al., 1998, 2001; Krueger & Hrabik, 2005; Lawson et al., 2015; Mercado-Silva et al., 2007; Mrnak et al., 2023). We hypothesize that the presence of top predators (e.g., Walleye, Muskellunge, Smallmouth Bass) will mediate the interactions between native Cisco and Yellow Perch and invasive Rainbow Smelt (Abrams, 1987), and that these interactions will influence the long-term efficacy of native species restoration and invasive species control (Mrnak et al., 2023). Over the long-term (>10 year), we hypothesize that there will be greater Cisco reintroduction success (i.e., relative increase in population growth rate and equilibrium population size) and invasive Rainbow Smelt control in Sparkling Lake (contains top predators) than in Crystal Lake (contains no top predators) as predators will aid in the biological control of juvenile and subadult Rainbow Smelt not vulnerable to removal gears. Due to the relatively pristine habitat conditions of Crystal and Sparkling lakes (Magnuson et al., 2024), we hypothesize less need for subsequent invasive species removal and native species introductions to maintain a native species dominated ecosystem, compared to degraded systems that may be more vulnerable to invasive species dominance (Carpenter et al., 2011; Folke et al., 2004). Continual monitoring and assessment of these experimental and reference lakes will be necessary to test for the persistence of the current native-species-dominated ecosystem states of Crystal and Sparkling lakes and whether future interventions are needed.

There are no identical reference systems for whole-lake manipulations, except in cases where a lake basin is divided in two (Sass et al., 2006). Trout and Anderson lakes served as reference systems because they contained Cisco or Rainbow Smelt, respectively. Trout and Anderson lakes are broadly characterized as deep, well oxygenated, oligotrophic, north-temperate lakes, similar to Crystal and Sparkling lakes (Mrnak et al., 2023; Shay et al., 2024). Rainbow Smelt decline in the experimental lakes and a corresponding increase in Anderson Lake suggested that regional factors (e.g., weather, precipitation, disease) did not drive these divergent trajectories among lakes and that the response was a result of the manipulation (Carpenter et al., 1998; Krueger & Hrabik, 2005). Trout Lake Cisco relative abundance and density increased during 2020–2022 and then declined in 2023. This was not surprising, as inland Cisco population dynamics are highly variable (Martin & Mrnak, 2024; Martin et al., 2023; Parks & Rypel, 2018) and largely driven by predator–prey interactions with the native Lake Trout *Salvelinus namaycush* (Walbaum, 1972) population in Trout Lake (Martin & Vander Zanden, 2023). We do not believe the reduction in Trout Lake Cisco relative abundance in 2023 was attributed to regional factors, but, rather, represents natural population fluctuation. Regardless of causal mechanisms, invasive Rainbow Smelt biomass decreased in both experimental lakes and increased in Anderson Lake, while native Cisco biomass increased in both experimental lakes and decreased in Trout Lake (Figure 5). This suggests that our whole-lake experiments potentially overcame natural ecosystem processes and dynamics, evidenced by contrasting species-specific trends between experimental and reference systems.

Experimental limitations and considerations

Whole-lake experiments are critical for understanding ecosystem shifts in response to perturbation or management intervention (Embke et al., 2022; Sikora et al., 2021, 2022). Whole-lake manipulations have addressed biotic and abiotic responses to a variety of drivers ultimately resulting in an increased understanding and ability to manage resources sustainably (Carpenter et al., 1985, 1998). Whole-lake experiments do have tradeoffs in their design, namely spatial extent and replication. Yet, great power remains in conducting experimentation in a natural context where relevant physical, chemical, and biological processes are occurring (Carpenter et al., 1985, 1998). And, replicated ecosystem experiments have resulted in the same responses to manipulation of a key variable (Sass et al., 2006).

There was a substantial decline in Sparkling Lake's Rainbow Smelt summer pelagic densities during 2020–2021. This response occurred following minimal summer vertical gill net monitoring removals in 2020 ($n=24$ Rainbow Smelt removed) and directed spring mini fyke net removals in 2021 ($n=4$ Rainbow Smelt removed). We believe this drastic reduction in Rainbow Smelt density following minor removals can be attributed to a hyperabundant population of minnows (i.e., Cyprinidae, Leuciscidae) throughout Sparkling Lake, most notably Emerald Shiner *Notropis atherinoides*. Irrespective of nearshore or offshore location in 2020, Emerald Shiners were visually present throughout the lake. This more than likely

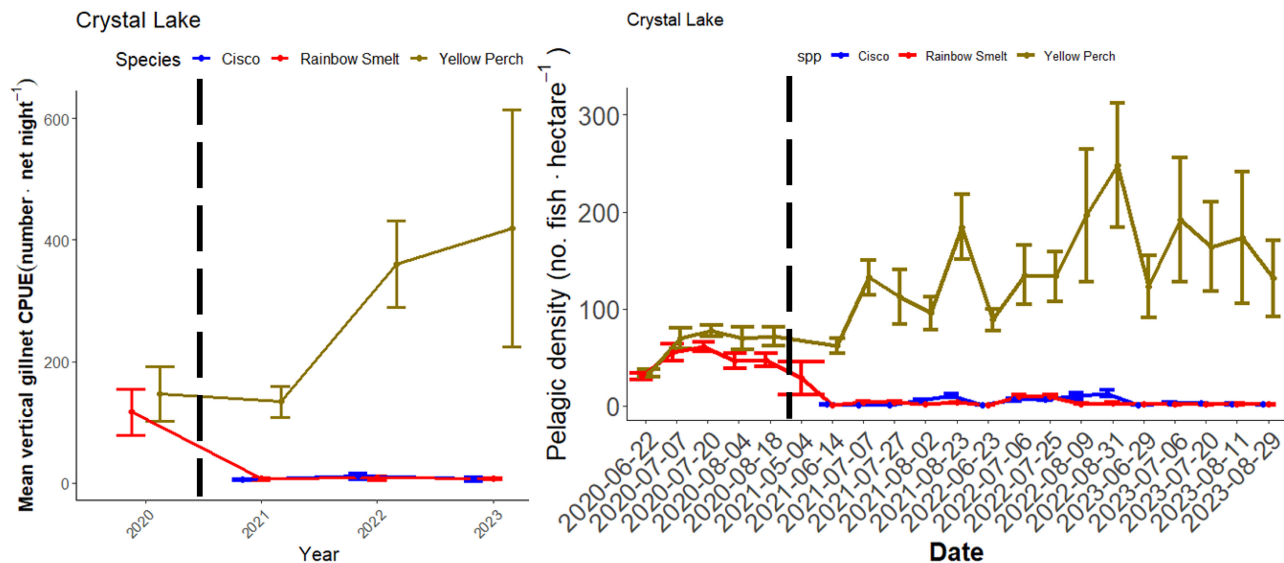


Figure 6. Trends in vertical gillnet catch per unit effort (fish/net night) and mean $\pm$ SE pelagic density estimates (fish/ha) from hydroacoustics for Cisco, Rainbow Smelt, and Yellow Perch in the Crystal Lake experimental manipulation, 2020–2023. Zeros have been removed for clarity. Vertical dashed line indicates the beginning of the experimental manipulation.

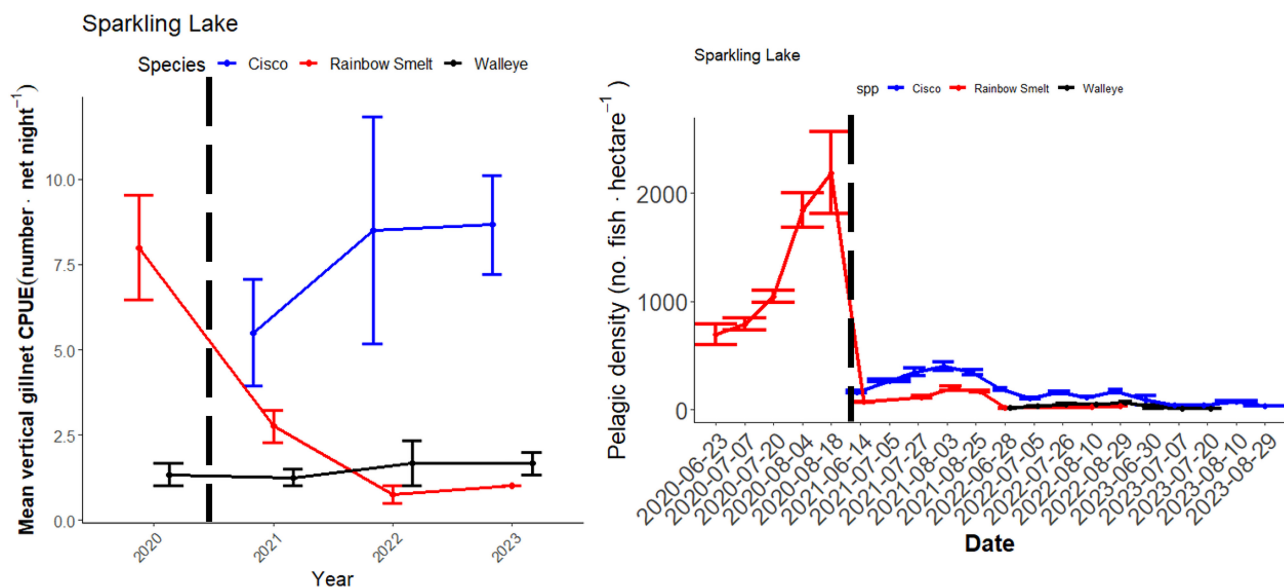


Figure 7. Trends in vertical gill net catch per unit effort (fish/net night) and mean $\pm$ SE pelagic density estimates (fish/ha) from hydroacoustics for Cisco, Rainbow Smelt, and Walleye in the Sparkling Lake experimental manipulation, 2020–2023. Zeros have been removed for clarity. Vertical dashed line indicates the beginning of the experimental manipulation.

caused backscattered returns to the hydroacoustic unit and thus inflated pre-removal density estimates of Rainbow Smelt (Dillon et al., 2020; DuFour, Kocovsky, et al., 2021a; DuFour, Qian, et al., 2021b). Despite this, the passive sampling approach of vertical gill nets also indicated that Rainbow Smelt relative abundance has been in decline since 2020. Beginning in 2021, Cisco were at greater abundances and represented the dominant pelagic biomass in Sparkling Lake.

Food web thinking

Our experiments were performed to test the applicability of purposefully reconfiguring food webs to reduce or eliminate

the negative ecosystem effects of a dominant invasive fish and were guided by panarchy theory and the Resist-Accept-Direct (RAD) framework (Lynch et al., 2021; Mrnak et al., 2023). The RAD climate adaptation framework provides a pathway towards identifying ecological adaptation options for transforming ecosystems (Rahel, 2022; Schuurman et al., 2022; Thompson et al., 2021). Adaptation options in RAD include *resisting* the undesired ecological change to maintain historical food web structure, species interactions, processes, and/or anthropogenic uses, *accepting* the change without intervention, or *directing* the ecosystem's transformation trajectory (Lynch et al., 2021; Thompson et al., 2021). Directing the ecosystem

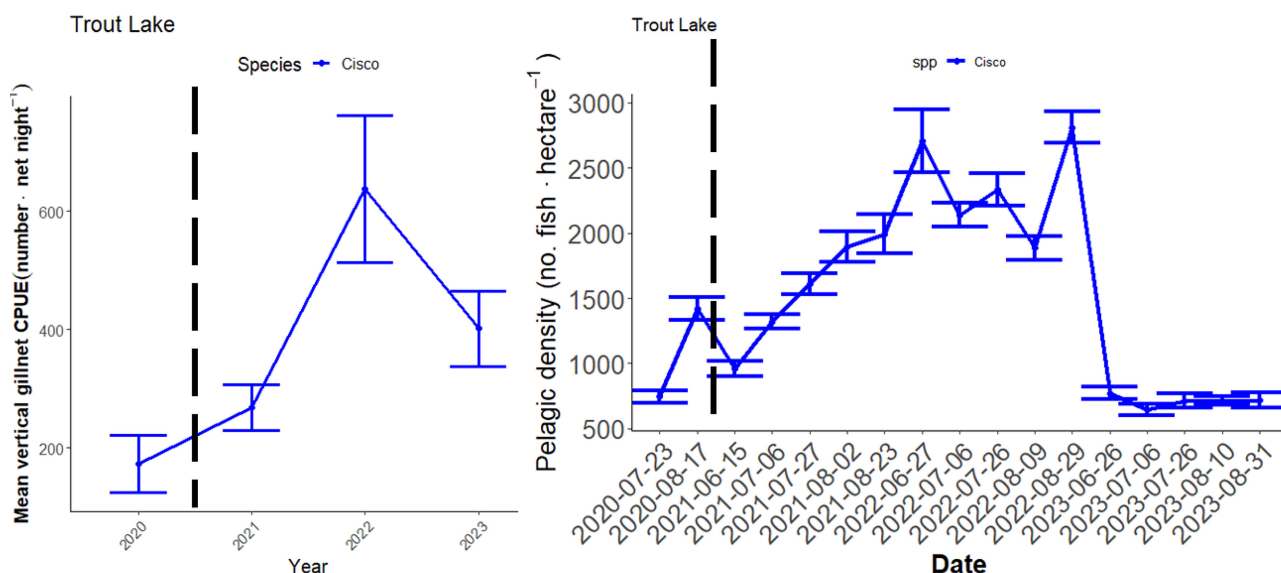


Figure 8. Trends in vertical gillnet catch per unit effort (fish/net night) and mean $\pm$ SE pelagic density estimates (fish/ha) from hydroacoustics for Cisco in Trout Lake (Cisco reference), 2020–2023. Vertical dashed line indicates the beginning of the experimental manipulation on Crystal and Sparkling lakes.

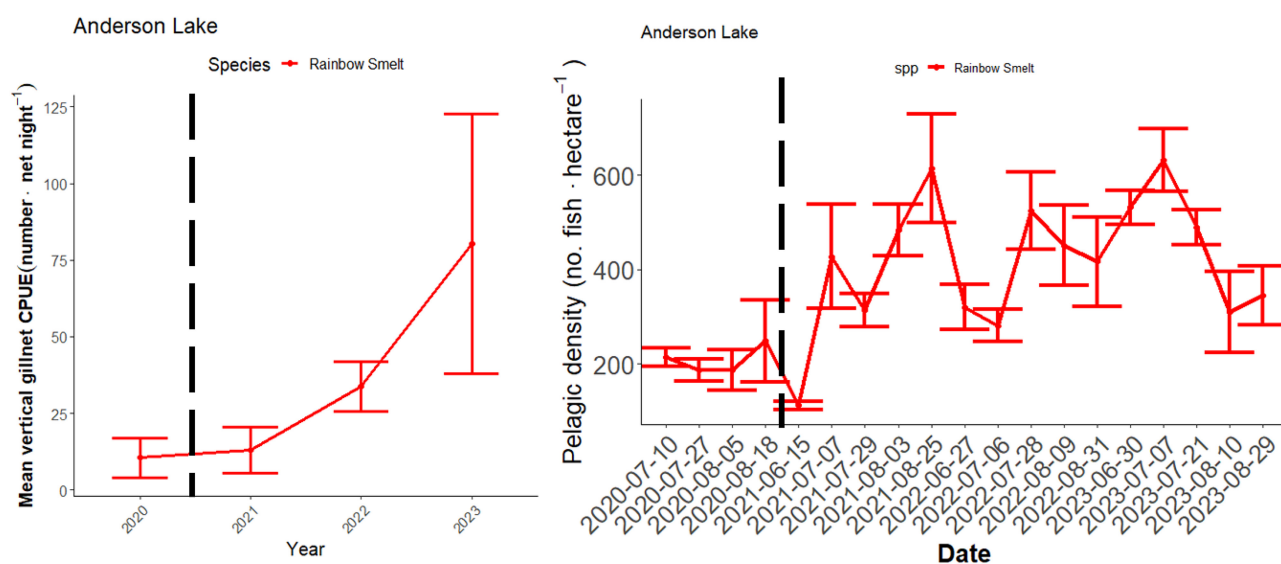


Figure 9. Trends in vertical gillnet catch per unit effort (fish/net night) and mean $\pm$ SE pelagic density estimates (fish/hectare) from hydroacoustics for Rainbow Smelt in Anderson Lake (Rainbow Smelt reference), 2020–2023. Vertical dashed line indicates the beginning of the experimental manipulation on Crystal and Sparkling lakes.

trajectory by purposefully shaping the change in the system towards a preferred configuration has been infrequently used and applied (Lynch et al., 2021, 2022; Embke et al., 2022; Feiner et al., 2022). This study attempted to direct the trajectory of two manipulated lakes by simultaneously removing invasive Rainbow Smelt and introducing native Cisco to a fish community.

Panarchy theory provided a framework of nature's rules that accounts for complex ecosystem dynamics such as stability and change (Holling 1973, 2001; Gunderson & Holling 2002). The probability of successful invasive species control and/or native species restoration may be dependent on the four phases of the adaptive cycle of a panarchy (Figure 1; Mrnak et al.,

2023). Our whole-lake experiments applied panarchy theory to invasive species management (Mrnak et al., 2023). Rainbow Smelt abundances were at historically low levels in Crystal and Sparkling lakes at the beginning of our experiment (Magnuson et al., 2024). Following recent management interventions (i.e., Gaeta et al., 2015; Lawson et al., 2015), the ecosystems were likely in a weakened conservation phase or potentially in the release phase (Mrnak et al., 2023). To further exacerbate these food web shifts and cause or strengthen a release in the ecosystem's adaptive cycle, adult Rainbow Smelt were physically removed from both lakes while adult Cisco were reintroduced. While the systems were believed to be nearing or in a release phase and transitioning towards reorganization, we continued

to influence ecosystem reorganization potential and likelihood through continued Rainbow Smelt removals and Cisco additions. Given our management action to purposefully push these ecosystems to reorganize (Rainbow Smelt removals, Cisco stocking) and the likelihood to self-organize around desirable resources and interactions (continued Rainbow Smelt removals and Cisco stocking), we predict the ensuing growth phase will contain desirable resources and interactions leading to an ecosystem transition that differs from the former Rainbow Smelt dominant regime (i.e., native species/Cisco dominant; Mrnak et al., 2023; Vander Zanden et al., 1999). In this context, panarchy theory created an ecologically grounded pathway to *direct* these ecosystem transformations. Our results also suggest that inducing a release phase (Rainbow Smelt removals) prior to management intervention (Cisco re-introduction) may be critical for increasing the probability of the reorganization and growth phases to manifest in a desirable ecosystem outcome in the conservation phase.

The temporal duration of this *new* regime is unknown and, thus, requires additional monitoring and assessment over the long-term. Regardless, we believe panarchy theory in combination with the RAD climate adaptation framework are useful tools for fish restoration and conservation, where efforts to restore and/or manage fisheries should be viewed in a food web or ecosystem context (i.e., “food web thinking,” ecosystem-based fisheries management). Further, our application of RAD suggests that this framework may be applicable to other aquatic natural resource restoration and conservation initiatives and not solely limited to climate adaptation strategies.

Purposefully applying panarchy theory with a RAD approach brings a new coupled framework to benefit invasive species management and the restoration and conservation of native aquatic resources. Fisheries management is often single-species orientated rather than based in an ecosystem or food web context (Hilborn 2011; Kitchell et al., 2000; Mrnak et al., 2023; Pikitch et al., 2004; Radinger et al., 2023). Across the globe, there is a critical need for “food web thinking” (Mrnak et al., 2023, 2024; Radinger et al., 2023; Vander Zanden et al., 1999). Panarchy theory allows for the incorporation of a systems approach when considering RAD strategy management actions. This systems approach appears critical to the long-term sustainability of aquatic food webs given the current rate of ecosystem transformation.

Management implication

Global change is transforming the environment at an alarming rate. Aquatic ecosystems and the fisheries they support are particularly vulnerable to these changes given their sensitivity to abiotic drivers, anthropogenic stressors, and the limited dispersal ability of fishes (Lynch et al., 2016). Shifting food web dynamics and ecosystem structures present new challenges to natural resource management and conservation that has broadly resisted or accepted ecological change (Lynch et al., 2021, 2022; Rahel, 2022). Purposefully directing ecosystems remains the least-used RAD strategy but offers opportunities for managing undesired ecological change. For example, direct strategies may allow managers to get ahead of (predicted) global change where improvements to habitats can be made that benefit species adapted to a warmer climate

or where changes to regulations can be made to maximize the production potential for novel species favored by climate change (Rahel, 2022). Here, we used a holistic management framework based on panarchy theory and guided by RAD climate adaptation strategies to understand and manage undesired ecological change. In our study, Crystal and Sparkling lakes were purposefully directed towards food web structures, species interactions, and processes dominated by native species (Mrnak et al., 2023). Large-scale ecosystem experiments like ours are necessary to better understand which approaches and frameworks are feasible, practical, and applicable given the fast-changing ecological environment (Carpenter et al., 1998; Lynch et al., 2022).

DATA AVAILABILITY

Data available upon request.

ETHICS STATEMENT

There were no Wisconsin Department of Natural Resources ethical guidelines applicable to this study.

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CONFLICTS OF INTEREST

None declared.

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