Ecosystem approaches to fisheries management and restoration

by

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Dedication

To Z, my brother from another… I miss you so very much. Your spirit has uplifted, carried, and guided me. I will forever hold our shared experiences and your memory near and dear to my heart.

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GSL WFSU est. 2002; RFE PFW est. 2020 → Rock Pile

"Forward with the plot"

TLDR

Abstract

Ecosystems are abruptly changing due to invasive species and global climate change, threatening their ability to provision ecosystem services. Aquatic ecosystem transformations may occur when the system diverges from previous food web structures, species interactions, processes, and(or) anthropogenic uses. Managing novel ecosystem structures under a single-species framework proves challenging as key ecological processes, habitats, and species interactions leading to the observed system structure may be missed or disregarded. Abruptly changing ecosystems highlight the importance of "food web thinking" or a systems approach when considering management actions. Here, I focused my research on key ecological processes, habitats, and species interactions rather than focusing on removing single stressors or supporting single species. In chapter 1, I review theoretical panarchy and "food web thinking" (i.e., ecosystem-based approaches to fisheries management) to better understand ecosystem dynamics leading to long-term invasive rainbow smelt *Osmerus mordax* dominance or control. I found that success of invasive rainbow smelt control and(or) eradication efforts depended on whether enough rainbow smelt were removed to void their niche space and the empty niche space was filled with desired native species from remnant populations or through stocking. In chapter 2, I apply my "food web thinking" approach in two whole-lake experiments aimed at invasive species control and native species restoration. Here, my experimental lake food webs were purposefully reconfigured to native species dominance following experimental manipulation, mitigating the invasive species driven negative effects. In chapter 3, I used a holistic ecosystem-based analysis to assess Ceded Territory of Wisconsin (CTWI) walleye *Sander vitreus* stability by combining ecologically sensitive production metrics with fisher harvest dynamics. I found that walleye productivity is in decline while fisher harvest is hyperstable; fishers are harvesting the same size slice (harvest) out of an ever-shrinking pie (production). I developed an ecosystem-based vulnerability to harvest index and recommend that exploitation may need to decline to maintain or increase the adaptive capacity of CTWI walleye. In chapter 4, I explored how species seasonal habitat use interacts with sampling gear biases to affect population estimation. I found that species movement is an important ecological consideration that can interact with sampling biases to affect population estimation. These studies demonstrate that our ability to manage and restore aquatic ecosystems, particularly fisheries, can be improved through a food web and ecosystem approach.

Introduction

Freshwater ecosystems and the food webs they support are being increasingly altered by global environmental change, including invasive species expansion, loss of native species, climate change, habitat loss, and overexploitation (Carpenter et al. 2011). From a theoretical panarchy perspective, these perturbations can reduce the ecosystem's stability and cause a release wherein change is imminent as the system moves through the four phases of the adaptive cycle (i.e., release, reorganization, growth, and conservation; Holling 1973; Gunderson and Holling 2002). After transitioning through the adaptive cycle and again stabilizing in the conservation phase, the ecosystem may no longer resemble the former state (dependent on resource availability going into the reorganization phase; Holling 1973; Gunderson and Holling 2002). Here, the alternative ecosystem state contains new and(or) different resources and species, which allow for novel species interactions and subsequent ecosystem structure (Holling and Gunderson 2002). Alternative ecosystem states highlight the importance of "food web thinking" as opposed to traditional fisheries management frameworks, which is often single-species oriented (Kitchell et al. 2000; Pikitch et al. 2004; Vander Zanden et al. 2016). Panarchy theory allows for the incorporation of a systems approach when considering fisheries management actions (i.e., consideration of the ecosystem and food web into fisheries management and restoration). Given the ever-changing global environment, a systems approach (i.e., ecosystem-based fisheries management; Link 2002; Pikitch et al. 2004) is likely critical to the long-term sustainability and management of aquatic food webs.

My research attempts to increase our management capabilities by viewing fisheries management and aquatic restoration in an ecosystem and food web context. In **chapter 1**, I review and document rainbow smelt (*Osmerus mordax*) invasion history, negative ecological effects, and management experiments aimed at control and(or) eradication. I then review and apply panarchy theory to discuss novel control and(or) restoration efforts in a food web context (Mrnak et al. 2023). In **chapter 2**, I apply the Resist-Accept-Direct (RAD) framework to identify an applicable ecological adaptation strategy and panarchy theory as an ecologically-grounded pathway to purposefully direct ecosystem transformation (Lynch et al. 2021, 2022; Mrnak et al. *submitted*). I purposefully leverage panarchy theory during two whole-lake biomanipulations (i.e., intentionally force a release in the adaptive cycle and dictate resource and species availability going into reorganization via manual invasive species removals and native fish reintroductions) to ultimately test whether the control of rainbow smelt and restoration potential of cisco (*Coregonus artedi*) is mediated by the presence/absence of apex predators (i.e., walleye *Sander vitreus*, Muskellunge *Esox masquinongy*, and smallmouth bass *Micropterus dolomieu*). System resilience exists along a gradient and is difficult to assess and quantify in the short-term due to the ecological timescales of regime shifts (Magnuson 1990, Carpenter et al. 1998, Scheffer and Carpenter 2003). Researchers will continue this experimentation through 2029 to adequately test our predator mediation question. Specific objectives for **chapter 2's** aspect of the larger experiment are: 1) testing whether it was possible to reduce the relative abundance and density of invasive rainbow smelt; 2) testing whether it was possible to increase the relative abundance and density of native cisco; and 3) if possible, testing for changes in the relative abundance and density of the native fish community. In **chapter** 3, I take my research beyond historical single-species management frameworks by combining production dynamics and socio-ecological drivers to examine walleye stability across the Ceded Territory of Wisconsin (Mrnak et al. *submitted*). Productivity metrics incorporate key population vital rates (e.g., abundance, recruitment, growth, mortality) that are known to be influenced by environmental change and fisher behaviors (Lynch et al. 2016; Krabbenhoft et al. 2023), including exploitation (Ricker 1946; Embke et al. 2019). My productivity approach that acknowledges the socio-ecological system of walleye fisheries and includes fisheries-dependent and -independent data may represent a more holistic pathway to sustainable fisheries management (Sass et al. 2017; Mrnak et al. 2023; Radinger et al. 2023). In **chapter 4**, I test whether yellow perch seasonal habitat use interacts with sampling gear biases to explore what managers are truly assessing during a survey as species movements and interactions are temporally and spatially dynamic (Mrnak et al. 2021; Bloomfield et al. 2022). Finally, I included **Supplementary Materials** as extensive time, effort, and resources went into spring mark-recapture surveys aimed at estimating the population size of fishes within the experimental lakes. Estimated population size (n) and population biomass (kg) will be combined with ecological data (temperature, forage availability and energy density, diets, isotopic analyses) to contextualize the predator-presence/absence-effect on invasive species control and native species restoration. These studies will further our management capabilities of aquatic food webs and our understanding of how food web processes and interactions shape ecosystems and the inland fish communities they support in a dynamic world.

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Chapter 1: Applying Panarchy Theory for Aquatic Invasive Species Management: A Case Study on Invasive Rainbow Smelt *Osmerus mordax*

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Abstract

Invasive species are a global concern. After an invasive species establishes, they often disrupt ecosystems leading to new dynamics and species interactions, making management efforts difficult. Panarchy theory is a conceptual framework to account for the dual and seemingly contradictory characteristics (stability and change) of all complex systems across distinct spatial and temporal scales. Panarchy theory has the potential to be applied to gain better insight into invaded system dynamics by creating a framework to characterize complex natural systems. This framework allows for management actions (e.g., whole-lake biomanipulations, invasive species control, native species restoration) to be leveraged against natural and induced ecosystem processes, providing a greater probability of desired outcomes. In this review, panarchy theory is applied to invasive species management using rainbow smelt *Osmerus mordax* as a case study. First, panarchy theory and the invasion history and subsequent ecological effects of rainbow smelt in inland lakes were reviewed. Second, rainbow smelt eradication and control efforts were reviewed to better understand mechanisms that led to long-term success or failure. Last, panarchy theory was applied to discuss future control and(or) native species restoration efforts in invaded lakes. This review found that invasive rainbow smelt cause negative effects on some native ecosystems. The success of invasive rainbow smelt control and(or) eradication efforts depended on whether: 1) enough rainbow smelt were removed to devoid their niche space; and 2) devoid niche space was filled with desired native species from remnant populations or through stocking. This review suggested that the probability of successful invasive species control and(or) native species restoration may be dependent on the four phases of the nested adaptive cycle (i.e., growth, conservation, release, and reorganization) through management intervention during the release phase. The application of panarchy theory should be viewed as a conceptual extension of efforts to restore ecosystems and(or) manage fisheries using a food web and ecosystem context (i.e., "food web thinking", ecosystem-based fisheries management).

Keywords: *panarchy theory; adaptive cycle; invasive species; inland fisheries; management*

1.1 Introduction

Invasive species are a global concern, particularly for aquatic ecosystems (Vander Zanden 2005; Dudgeon et al. 2006; Carpenter et al. 2011). Once established and self-sustaining in a non-native system (thus becoming 'invasive'), invasive species can produce effects that range in degree (negative, positive), magnitude (benign, severe), and scale (individual, ecosystem). Though prevention is the best management practice (Ruesink et al. 1995; Mack et al. 2000; Simberloff 2003), detection often occurs after a species has established and become self-sustaining within a system (Mehta et al. 2007; Vander Zanden et al. 2010; Walsh et al. 2016). Populations of invasive species have created issues by negatively affecting native species and biodiversity (Wilcove et al. 1998; Sala et al. 2000; Courchamp et al. 2017), driving undesired ecological and evolutionary change (Olden et al. 2004; Lodge et al. 2006; Carlsson et al. 2009), and causing severe economic damage (Pimentel et al. 2005; Lovell et al. 2006). Post-invasion, new dynamics and interactions have occurred at multiple and varying degrees and scales (Epanchin-Niell & Hastings 2010; Cucherousset & Olden 2011; Perkins et al. 2013; Lohr et al. 2017). These new dynamics and interactions may create a mismatch (e.g., Cushing 1969, 1990) between existing management frameworks and the current (invaded) regime. Here, the application of panarchy theory is reviewed to gain insight into invaded system dynamics by creating a framework to characterize complex natural systems as a dynamically organized and structured series of nested adaptive cycles (Gunderson & Holling 2002). Incorporating panarchy theory into existing management frameworks (i.e., recognizing and understanding the distinctly scaled and nested adaptive cycles in all ecological systems) may increase our understanding of system trajectory and the likelihood that a purposeful management action will result in a particular outcome (i.e., desired regime; Holling & Meffe 1996). Therefore, panarchy theory under a fisheries management context may allow for improved mitigation of invasive species impacts and(or) native species restoration (Allen et al. 2014; Jacques 2015; Garmestani et al. 2020). This concept may aid in the critical challenge of invasive species management and thus should be implemented as part of deliberate learning experiments.

Panarchy theory is a framework of nature's rules that accounts for the dual and seemingly contradictory characteristics of all complex systems, namely stability and change (Holling 1973; Holling 2001; Gunderson & Holling 2002). Panarchy theory has been used to explain economic, ecological, and institutional systems and their interactions (Gunderson et al. 1995; Holling & Gunderson 2002; Biggs et al. 2021). Panarchy theory in ecology is organized by ecosystem characteristics, fundamental ecosystem dynamics and stages of the adaptive cycle (i.e., growth, conservation, release, and reorganization), properties of the adaptive cycles, and interconnectedness of the adaptive cycles (i.e., levels; Allen et al. 2014; Jacques 2015; Garmestani et al. 2020). These nested adaptive cycles make up the hierarchical structure of the system (i.e., panarchy) and range across temporal and spatial scales (Holling 1973; Holling 2001;

Gunderson & Holling 2002). Panarchy theory describes ecosystem characteristics and dynamics in four ways: 1) that change is episodic, not continuous, gradual, or consistently chaotic; 2) that reorganization of resources across levels is governed by non-linear dynamics; 3) that multiple equilibria are common properties in ecosystems; and 4) that management systems should be flexible to account for these dynamics (Gunderson & Holling 2002). In the context of ecosystem characteristics and invasive species, non-linear dynamics and the existence of multiple regimes may suggest that the colonization, establishment, and ecological effects of invasive species could drive a lake's native community assemblage into an alternative regime (e.g., Scheffer et al. 2001; Scheffer & Carpenter 2003; Hansen et al. 2013). An alternate regime indicates that the system has become self-organizing around a particular (alternative) set of ecosystem processes, structures, and functions (Scheffer & Carpenter 2003; Folke et al. 2004). An alternative invasive species dominant regime is then reinforced by positive feedback loops through predation and competition with native species. Because ecosystems are highly dynamic and capable of multiple regimes, changes via fast and slow variables and(or) management interventions may also lead to a native ecosystem regime or an alternative low impact invasive species regime (Holling 2001; Rooney et al. 2006; Rooney & McCann 2012). A low impact invasive species regime would occur when invasive species are present but exist at low population levels such that negative effects on native species are minimal (Krueger & Hrabik 2005; Hein et al. 2006; Roth et al. 2007; VanMiddlesworth et al. 2017; Perales et al. 2021). Therefore, just as native commercial and recreational fisheries are subject to accidental or unintended collapse and movement to alternate regimes (Roughgarden & Smithtt 1996; Mullon et al. 2005; Pinsky et al. 2011), the control and(or) eradication of invasive species can also be purposefully attempted (Krueger & Hrabik 2005; Hein et al. 2006; Roth et al. 2007; VanMiddlesworth et al. 2017;

Perales et al. 2021). Here, control is defined as a reduction in invasive species abundance such that negative effects are reduced and(or) non-existent. Eradication is defined as elimination of the invasive species from the system. Panarchy theory (particularly the stages of the adaptive cycle; Figure 1) can be leveraged and used purposefully to determine the appropriate timing and scope of invasive species management to increase the probability of a native or low impact invasive species alternative regime for the long-term.

The application of panarchy theory to inland lake invasive species management was reviewed through the lens of rainbow smelt *Osmerus mordax* invasions. Rainbow smelt have successfully invaded many freshwater systems across North America and have had numerous effects through predatory and competitive interactions (Evans & Loftus 1987; Hrabik et al. 2001; Mercado-Silva et al. 2007). Negative effects of rainbow smelt invasions include food webs shifted away from native species dominance, altered zooplankton communities, and the decline or extirpation of native cool- and cold-water fishes (e.g., yellow perch *Perca flavescens*, walleye *Stizostedion vitreum* (Bruner 2021), cisco *Coregonus artedi*, lake whitefish *Coregonus clupeaformis*; (Evans & Loftus 1987; Johnson & Goettl 1999; Beisner et al. 2003; Rooney & Paterson 2009). Certain piscivorous species (e.g., Atlantic salmon *Salmo salar*, lake trout *Salvelinus namaycush*, walleye) have also benefitted from rainbow smelt invasions via increased growth rates (Warner & Fenderson 1963; Maher 1983; Evans & Loftus 1987; Jones et al. 1994; Johnston et al. 2003, 2012; Fincel et al. 2014; Sheppard et al. 2015, 2018). Regardless of the ecosystem effect (i.e., negative, benign, or positive), rainbow smelt are highly successful invaders and efficient at altering native ecosystems due in part to life history advantages (i.e., eurythermal, omnivorous; Evans & Loftus 1987; Hrabik et al. 2001). Thus, this invader interacts with a wide variety of native taxa at multiple trophic levels, though interactions may differ among lakes. Despite differing lake-specific interactions and associated negative ecosystem effects, panarchy theory provides a framework for considering management actions aimed at invasive control and(or) ecosystem restoration.

This review details panarchy theory and the invasion history and subsequent ecological effects of rainbow smelt in inland Wisconsin lakes and the surrounding Laurentian Great Lakes region. This review is focused on the context of rainbow smelt as an undesirable, invasive species. Eradication and(or) control efforts with varying degrees of success are then reviewed to better understand mechanisms that may contribute to effective rainbow smelt control. Last, panarchy theory is leveraged to discuss novel control and(or) restoration efforts based on previous knowledge with the focal panarchy being composed of species-, community-, and inland lake-level nested adaptive cycles (Figure 2). Understanding and mitigating invasive species effects are of primary interest to managers and ecologists alike. The objective of this paper is to provide an updated review on ecosystem effects of rainbow smelt invasions in inland lakes (e.g., Evans & Loftus 1987; Rooney & Paterson 2009) and then document subsequent ecosystem responses with emphasis on native fish populations and ecosystem regime shifts (e.g., Scheffer et al. 2001; Scheffer & Carpenter 2003; Hansen et al. 2013). Panarchy theory was applied *a priori* to gain more insight into system dynamics, successes, and failures, and to discuss its application for invasive species management.

1.2 Panarchy theory to control rainbow smelt or other invasive species

According to panarchy theory, ecosystem dynamics are governed by four phases of the adaptive cycle; growth, conservation, release, and reorganization (Holling 2001; Gunderson & Holling 2002; Figure 1). In the growth phase, populations rapidly expand within available niche space. This phase contains abundantly available resources where ecosystem structure and interactions among species increase in frequency and magnitude. The conservation phase is characterized by competitive processes leading to the dominance of a few species for some period of time. Here, nutrient and biomass growth declines and becomes stored in ecosystem structures while interactions among species become bound and rigid. The rigidity of these food web interactions is believed to make the system more susceptible to change or perturbation because energy and nutrients are either effectively bound in biomass or successfully captured by the dominant species along tightly coupled food web connections (McCann 2000; Holling 2001; Holling & Gunderson 2002). In turn, this renders the system more vulnerable to disturbance cascading across the system (Holling 1973; McCann 2000). The release phase is characterized by nutrient and biomass decline, which may be caused by a myriad of perturbations such as disease, establishment of other competitors or invaders, exploitation, a change in environmental conditions, or a purposeful biomanipulation. Regardless of the type of disturbance, stochasticity ensues throughout the system during the release phase and stored biomass (ecosystem structure) and interactions between species across the food web break down. Community reorganization occurs when selection allows certain species to survive despite mechanisms causing a release. Now, freshly released resources provide new opportunities for species to establish themselves and interactions between species to again develop. This may result in a system that is similar in configuration to the previous one (i.e., no change in regime), or the transition from the release to the reorganization phase may result in entirely new configurations, with the system reorganizing around different structures and functions (i.e., a shift to an alternative regime; Holling 2001; Scheffer & Carpenter 2003; Garmenstani et al. 2009). Invasive species often become dominant in an ecosystem (conservation phase) through bottom-up, top-down, and(or) competitive interactions with native species (Sakai et al. 2001; Vander Zanden & Olden 2008; Seebens et al. 2021). Regardless of how invasive species become dominant, their duration as the dominant species during the conservation phase may be shortened and(or) altered through deliberate management actions (e.g., physical removals, exploitation, stockings), disease, and(or) slow variables (e.g., climate change, habitat degradation). If, in fact, adaptive cycles represent different dynamic phases of systems like lakes, then it may be possible to use this to our advantage and apply purposeful management actions to trigger the collapse of an undesirable conservation phase (i.e., one dominated by invasive species), followed by other management actions that try to direct the trajectory of system reorganization (i.e., around desirable native species). Management to elicit an ecosystem release and shift from an undesired to a desired regime should be conducted such that desired resources (native species) are present and(or) stocked, while undesired resources (invasive species) are eliminated or reduced as much as possible prior to the reorganization phase. This should allow for the desired remnant and(or) stocked native species (i.e., novel structures) to form interactions not observed during the previous invasive dominated regime (Scheffer and Carpenter 2003; Folke et al. 2004). Over time, the desired structure and interactions should increase, and the ecosystem should ultimately move into the conservation phase. Given the desired resources going into this transition (and lack of undesired resources), the newly bound and rigid regime should be one with low or no invasive species impact. Due to hysteresis, coercing regime shifts is often difficult, if not impossible, due to the ability of a system to self-organize into multiple dissimilar regimes around the same system structures, processes, and functions (Scheffer et al. 2001; Scheffer and Carpenter 2003; Scheffer et al. 2012). Though a no invasive species impact regime is ideal, a low invasive species impact regime is more realistic and usually acceptable to managers and stakeholders. Further management interventions during the low invasive species impact regime using this proposed framework may also be considered if the goal of invasive species management is complete eradication; however, eradication of invasive species has proven challenging (Parkes & Panetta 2009; Green & Grosholz 2021) and control may be the most viable and feasible option.

Panarchy theory describes the three dynamic properties of the adaptive cycle (Holling 2001; Gunderson & Holling 2002; Holling & Gunderson 2002); potential, connectedness, and resilience. Potential describes the bounds of what future ecosystem regime options are possible based upon available resources and potential species interactions. Connectedness is defined by internal controls (e.g., food web connections, species interactions) that dictate maintenance of a regime (which may also include positive feedback loops) that are independent of external controls. Resilience is the ability of an ecosystem to tolerate perturbations and remain in the same regime, while either staying within the conservation phase or by reorganizing around the same regime-defining structures, processes, and functions in a new conservation phase (Holling 1973; Gunderson 2000; Angeler & Allen 2016). Weakened or low resilience to disturbances and perturbations may lead to collapse and a new ecosystem regime (Holling 2001). Interconnectedness among the levels (i.e., food web components) of panarchy theory in ecology are important to describe some ecosystem dynamics (e.g., multiple and nested spatial and temporal scales, large and slow versus small and fast variables; Rooney et al. 2006; Rooney & McCann 2012). Thus, this consideration may be critical for aquatic invasive species management (Vander Zanden et al. 2004), which typically encompasses a local and whole-lake spatial scale (i.e., whole-lake, single management unit). Therefore, an understanding of local scale ecosystem dynamics (i.e., whole-lake; Figure 2) of aquatic invasive species management may be relevant to broader spatial scales of management (i.e., the Ceded Territory of Wisconsin, Upper Midwest north-temperate inland lakes; e.g., Jacques 2015). Because invasive species are typically managed at a local scale, potential for changes in the dominant ecosystem regime should theoretically be more feasible because the number of options are limited (i.e., narrow range of species can persist in the system; invasive species dominated regime, low impact invasive species regime, native species dominated regime). Further, connectedness within these inland lake ecosystem regimes should be relatively low because of the small spatial scale of the management unit (whole-lake; less diverse and complex than larger systems), particularly for invasive species in simple fish communities driving biodiversity reductions (Wilcove et al. 1998; Sala et al. 2000; Courchamp et al. 2017). Lastly, system resilience exists along a gradient and is difficult to assess and quantify due to the ecological timescales of regime shifts (Carpenter et al. 1998; Scheffer et al. 2001; Scheffer and Carpenter 2003). Yet, invasive species embedded in diverse fish communities may be weakly resilient to a change in ecosystem regime because invasive species drive biodiversity declines (Wilcove et al. 1998; Sala et al. 2000; Courchamp et al. 2017) while species interaction strengths (i.e., consumer-resource interactions) may be inversely related to the number of interactions, thus reducing food web stability (e.g., Figure 2a in McCann 2000). Therefore, invasive dominated regimes often have fewer consumer-resource interactions than native regimes, ultimately reducing food web stability (McCann 2000). Despite this, invasive dominated regimes are still capable of being highly resilient (Peterson et al. 1998; Folke et al. 2004; Gaeta et al. 2015; Lawson et al, 2015). Nevertheless, native species dominant regimes where invasive species are present but impacts are minimal do exist (Krueger & Hrabik 2005; Hein et al. 2006; Roth et al. 2007; VanMiddlesworth et al. 2017; Perales et al. 2021). Overall, panarchy theory in ecology suggests that principles governing ecosystem regimes and dynamics (i.e., four phases of the nested adaptive cycles; growth, conservation, release, reorganization) may be leveraged to inform invasive species management efforts to increase the probability of desired outcomes (Table 1) whereby consideration of alternative regimes and the use of perturbations can be used to move between undesired (invaded) and desired (native, low-impact invasive) regimes.

1.3 Invasion history of rainbow smelt in North America

Anadromous rainbow smelt are indigenous to the eastern North American coast from New Jersey to Labrador (Scott & Crossman 1998). Native landlocked populations exist in numerous lakes in New Hampshire, Maine, New Brunswick, Nova Scotia, Insular Newfoundland, Labrador, Québec, and eastern Ontario. Rainbow smelt (16.4 million) were intentionally introduced into Crystal Lake (Benzie County, Michigan) in 1912 where they first became established outside of their native range (Creaser 1925; Nellbring 1989). From this inland lake, rainbow smelt soon spread to the Laurentian Great Lakes of Michigan, Huron, Ontario, Superior, and Erie in 1923, 1925, 1929, 1930, and 1935, respectively (Nellbring 1989; Rooney & Paterson 2009). Specifically, rainbow smelt were first captured in Lake Michigan off the east shore near Frankfort, Michigan in 1923 (Van Oosten 1937) and a year later in Big Bay de Noc, an arm of Green Bay in Michigan (Becker 1983). In 1928, rainbow smelt were captured in gillnets in Little Sturgeon Bay (Door County, Wisconsin). In 1929, a few rainbow smelt were collected in Lake Michigan off Gill’s Rock and the Sturgeon Bay Canal. A year later they were captured in Manitowoc, Port Washington, and Racine, Wisconsin. In 1931, rainbow smelt were caught in Kenosha, Wisconsin and Michigan City, Indiana. Today, rainbow smelt inhabit all of Lake Michigan and are found in the lower reaches of many of its tributaries (Lyons et al. 2009).

Abundances have declined due to non-native Pacific salmonid stocking initiated to control alewife *Alosa pseudoharengus* in the 1960s and associated predation on rainbow smelt (Dettmers et al. 2012; Bunnell et al. 2014). In Lake Superior, rainbow smelt were first observed in Whitefish Bay, and then captured in Keweenaw Bay in 1936. By the late 1930s, rainbow smelt reached the Wisconsin waters of Lake Superior and today inhabit all of the lake and the lower reaches of many tributaries (Hansen et al. 1994; Pratt et al. 2016). In Lake Superior, rainbow smelt have comprised a major part of the fish community since the 1950s (Gorman 2007; Gamble, Hrabik, Stockwell, et al. 2011; Gamble, Hrabik, Yule, et al. 2011). Like Lake Michigan, Pacific salmonid stocking in Lake Superior has led to variable rainbow smelt abundances over time (Pratt et al. 2016). Native lake trout in Lake Superior also consume rainbow smelt (Ray et al. 2007).

Currently, rainbow smelt populations occur in all major basins in Wisconsin. Rainbow smelt were first observed in Little Bass Lake (Vilas County) in 1967, and "inadvertently" introduced to the Fence Lake system (Vilas County) in 1968 (Becker 1983) and have expanded to its creeks and channels (Hrabik & Magnuson 1999). Other populations have originated from a combination of purposeful or accidental introductions and the species' natural expansion capabilities through waterways connecting lakes (Evans & Loftus 1987; Hrabik & Magnuson 1999). The further expansion of rainbow smelt in Wisconsin waters was predicted to be incipient (Hrabik & Magnuson 1999; Mercado-Silva et al. 2006). In the Bear River and Manitowish River drainages, Hrabik and Magnuson (1999) modeled the dispersal of rainbow smelt into new ecosystems as a consequence of stream connections among lakes and watersheds, their survival based on physical and chemical attributes of lakes, and the influence of human introductions. Hrabik and Magnuson (1999) predicted that at current rates of expansion within this watershed, half of all lakes suitable for rainbow smelt would be invaded after 200 years. Using models based on physical habitat and chemical characteristics of lakes inhabited by rainbow smelt in their native range of distribution in southern Maine (e.g., lake maximum depth, lake surface area, water transparency), Mercado-Silva et al. (2006) concluded that 553 lakes in Wisconsin could adequately harbor invasive rainbow smelt. Evans and Loftus (1987) and Hrabik and Magnuson (1999) suggested that human transport was one of the main causes of rainbow smelt invasions. Rainbow smelt were present in at least 26 inland lakes in Wisconsin as of 2006 (i.e., Table 1 in Mercado-Silva et al. 2007). Predictions of rainbow smelt spread in Wisconsin inland lakes have not materialized and no new invasions have been documented since 2006 (Lyons et al. 2015; Renik et al. 2020) likely as a result of banning all inland lake netting of rainbow smelt and(or) invasive species educational outreach campaigns (Vander Zanden & Olden 2008).

Outside of Wisconsin, rainbow smelt have spread to several northern Minnesota inland lakes including the Rainy River system (Franzin et al. 1994), various water bodies along the Mississippi River from Minnesota to Louisiana (Suttkus & Conner 1980; Mayden et al. 1987), and the Missouri River basin including Lakes Oahe and Sakakawea in South Dakota, North Dakota, and Montana (Mayden et al. 1987; Nellbring 1989; Franzin et al. 1994). Invasive rainbow smelt are present and well-studied in numerous inland lakes of Ontario and Manitoba, Canada including Lake Winnipeg and its tributaries (Evans & Loftus 1987; Franzin et al. 1994; Rooney & Paterson 2009; Olynyk et al. 2017). Rainbow smelt were first reported in the Hudson Bay basin in 1962 in Little Eagle Lake, Ontario. Rainbow smelt have since been captured in numerous lakes in the Hudson Bay drainage basin (Remnant et al. 1997) and are now reported in

Hudson Bay (Rooney & Paterson 2009). When left unchecked, rainbow smelt are efficient at rapid dispersal and establishment across these north-temperate landscapes.

1.4 Biology of rainbow smelt invasions

Invasive rainbow smelt typically inhabit deep, oligo- or mesotrophic lakes, with pH > 6.0, water temperatures between 6 – 14°C, and across a wide range of salinity (Evans & Loftus 1987; Nellbring 1989; Mercado-Silva et al. 2006). Except for spawning, adult rainbow smelt typically inhabit hypolimnetic waters near the thermocline during daylight hours but expand to other areas of lakes in wintertime and during the night (Hrabik et al. 1998, 2001). Mercado-Silva et al. (2006) determined that lakes deeper than 9 m, with surface areas larger than 21 ha and relatively high transparency (Secchi depth > 6.1m), were best suited for invasive rainbow smelt. Johnson et al. (1977) also suggested lakes with low productivity as typical rainbow smelt lakes. Evans and Loftus (1987) suggested that rainbow smelt can occur in waters with pH > 6.0, and in their native region (Maine), they have been reported from lakes with pH ~ 7.2 (Mercado-Silva et al. 2006). Rainbow smelt appear to be plastic in their pH tolerance, although Evans and Loftus (1987) suggested that rainbow smelt eggs could be subject to lethal pH depressions (< 6.0) in poorly buffered lakes. Rainbow smelt are adapted for a variety of salinity conditions. Anadromous rainbow smelt larvae have been found in salinities as high as 30‰ (Laprise & Dodson 1989), and in Wisconsin waters, are found in waters with little to no salinity (~0‰; Mercado-Silva et al. 2006). Rainbow smelt in Crystal and Sparkling lakes (Vilas County, Wisconsin) prefer waters with mean dissolved oxygen concentrations of ~ 7 – 10mg/L (Mrnak *unpublished data*). Suitable adult rainbow smelt oxythermal habitat can also be characterized as similar to that of inland cisco and lake whitefish (Lyons et al. 2015, 2018; Renik et al. 2020).

Rainbow smelt are anadromous spawners in their native range. Following introduction to inland lakes, their spawning behavior has adapted to the new environments and conditions by using littoral areas with sand, gravel, and groundwater inputs for spawning slightly before or after ice-out at night in spring (Lischka & Magnuson 2006; Gaeta et al. 2015). Once established, rainbow smelt in inland lakes can demonstrate rapid, exponential population growth and reach high densities (~18,000/ha, Figure 3; Arim et al. 2006; Sass et al. 2010; Grosholz et al. 2021). Lending to their success as an invasive species, rainbow smelt are omnivorous feeders consuming zooplankton (copepods and cladocerans) and benthic invertebrates as young-of-year and juveniles (< 150 mm) and start incorporating juvenile and small fishes into their diets as adults (Becker 1983; Hrabik et al. 2001; Roth et al. 2010; Sheppard et al. 2012). Further, rainbow smelt have a eurythermal life history where the species will occupy most available habitats within a lake over its life cycle (Evans & Loftus 1987; Hrabik et al. 1998, 2001). As young-of-year, rainbow smelt occupy the warm, near shore littoral areas of a lake. During the juvenile stage, rainbow smelt select for cooler metalimnetic areas before moving to cold hypolimnetic habitats as adults. Due to their ability to reach high abundances quickly (i.e., compensatory recruitment response and cultivation effects; Walters & Kitchell 2001; Grosholz et al. 2021), omnivorous feeding habits, and eurythermal life history, rainbow smelt interact with a wide spectrum of native inland lake fishes across multiple trophic levels and habitats.

1.5 Ecological effects of rainbow smelt invasions

Colonization of invasive rainbow smelt in inland lakes and waterbodies has resulted in negative, benign, or positive effects on native fish species. In Evans and Loftus (1987), ~70% of the case studies where rainbow smelt invaded lakes with non-coevolved species resulted in negative effects. The most well-documented negative effects of rainbow smelt on native fishes include extirpations (without intervention, stocking) of walleye, yellow perch, cisco, and lake whitefish. Rainbow smelt have negatively influenced walleye natural recruitment in invaded inland lakes of Wisconsin (Mercado-Silva et al. 2007). In this study, young-of-year walleye density was lower in rainbow smelt invaded lakes than uninvaded lakes in 17 of the 18 years examined. Three of the Mercado-Silva et al. (2007) study systems had pre- and post-invasion data and indicated about a 70% decline in young-of-year walleye densities following rainbow smelt establishment. Support for Mercado-Silvia et al. (2007)'s evidence for the negative interaction between invasive rainbow smelt and walleye recruitment comes from the fact that all invaded lakes included in their study required stocking to sustain the walleye populations at the conclusion of the research (Wisconsin Department of Natural Resources *unpublished data*). Negative effects of rainbow smelt on walleye recruitment have been reported for other systems (Schneider & Leach 1977; Colby et al. 1987; Jones et al. 1994; Johnson & Goettl 1999). Although these studies did not identify causal mechanisms, reduced zooplankton abundance and adult rainbow smelt predation on young-of-year walleye were suggested.

Negative effects of invasive rainbow smelt on native forage fish (e.g., yellow perch, cisco) populations are well documented (Evans & Loftus 1987; Rooney & Paterson 2009). Hrabik et al. (1998) examined thermal preferences, diet characteristics, and interactions between rainbow smelt and yellow perch and cisco and found a strong negative effect of rainbow smelt invasions on native fishes. For example, in Sparkling Lake (Vilas County, Wisconsin), adult rainbow smelt and cisco were found to use similar thermal habitats, but adult cisco feeding success was not reduced via competitive interactions (Hrabik et al. 1998). Adult rainbow smelt predation on young and(or) juvenile cisco forced by life history to occupy cold epi- or hypolimnetic habitats were proposed to have led to the observed cisco recruitment failures (Hrabik et al. 1998). Ultimately, this resulted in the extirpation of cisco from Sparkling Lake eight years after rainbow smelt were detected (Figure 3). Conversely, in Crystal Lake (Vilas County, Wisconsin), no predation effects were found between adult rainbow smelt and yellow perch (Hrabik et al. 1998). Unlike young and(or) juvenile cisco, yellow perch that occupied similar thermal habitat as adult rainbow smelt were too large to be consumed. Despite a lack of direct interactions, thermal overlap and similar prey resources resulted in reduced feeding success and condition for juvenile and adult yellow perch in Crystal Lake (Hrabik et al. 1998). These competitive effects resulted in the Crystal Lake yellow perch population decline four years after rainbow smelt were detected (Figure 4). Due to a lack of spatial overlap between adult rainbow smelt and young yellow perch (Hrabik et al. 1998), Hrabik et al. (2001) tested for interactions between age-0 yellow perch and rainbow smelt in a follow up study on Crystal Lake. During this two-year study, age-0 yellow perch and rainbow smelt hatched at similar times, had similar spatial distributions, and showed similar prey preference (Hrabik et al. 2001). This suggested that resource competition between age-0 yellow perch and rainbow smelt likely reduced the chance for strong yellow perch year-classes where age-0 rainbow smelt co-occur. Direct evidence for a competitive advantage of age-0 rainbow smelt over other age-0 fishes is limited in the inland lake literature (Evans & Loftus 1987; Rooney & Paterson 2009). Inference of competition between age-0 rainbow smelt and other age-0 fishes can be circumstantially drawn from habitat and diet data (Garvey & Chipps 2012). For example, as with most exogenously feeding age-0 fishes (Holt 2011), age-0 rainbow smelt preferentially select for small zooplankton (e.g., *Cyclops* spp., *Diaptomus* spp., copepod nauplii, diatoms, and rotifers; Evans and Loftus 1987, Hrabik et al. 2001). Though this does not definitively conclude competition between age-0 rainbow smelt and other native fishes, it is suggestive given the early spring (i.e., sometimes before ice-out; Gaeta et al. 2015) spawning of rainbow smelt (3 – 10 °C; O'Brien et al. 2012). Early spring spawning and subsequent hatching appears to provide age-0 rainbow smelt with a strong competitive advantage over other age-0 fishes in the system. Invasive age-0 rainbow smelt are provided an unexploited planktonic resource by being the first species to spawn and hatch. In turn, this allows for a faster ontogenetic diet shift towards larger zooplankton and ultimately piscivory, further accelerating individual growth rates and population establishment (i.e., feedback loops).

Invasive rainbow smelt are highly adapted to freshwater environments. Fast population growth, an omnivorous diet, and an eurythermal life history allows this invasive species to interact (directly and indirectly) with a wide range of native biota at multiple trophic levels. Indeed, a process-based model used to simulate food-web interactions leading to rainbow smelt dominance in Sparkling Lake corroborated this (Roth et al. 2010). Roth et al. (2010) found that rainbow smelt may dominate Sparkling Lake under multiple dissimilar scenarios. Although invasive rainbow smelt driven ecosystem effects can be negative, benign, or positive, our synthesis and that of Evans and Loftus (1987) and Rooney and Patterson (2009) conclude that invasive rainbow smelt generally lead to ecosystem effects that are viewed as undesirable from the perspective of inland lake stakeholders.

1.6 Rainbow smelt control and(or) eradication

Management experiments

Given that rainbow smelt have negatively influenced native fish species in inland lakes, management to control and(or) eradicate this invasive species have focused on whole-lake experiments. These studies were deliberately conducted to methodically undermine the role of invasive rainbow smelt in native food webs of inland lakes such that any positive outcomes would be broadly transferable for applied management in other invaded systems. Rainbow smelt control and(or) eradication in inland lakes has been attempted using two approaches: 1) biomanipulation; and 2) the mechanical elimination of suitable oxythermal habitat.

Rainbow smelt were first observed in Sparkling Lake in 1982 (Gaeta et al. 2015; Figure 3). After colonization, rainbow smelt rapidly increased in abundance and functionally extirpated cisco and yellow perch, and would likely have extirpated walleye without stocking interventions (Gaeta et al. 2015; Steve Gilbert *pers. comm.*). In spring 2002, a whole-lake rainbow smelt removal/control biomanipulation study was initiated on Sparkling Lake that included the identification of spring spawning locations (Lischka & Magnuson 2006), physical removals of adult rainbow smelt during spawning, stocking of adult and extended growth fingerling walleye, and protection of the walleye population through conservative harvest regulations (711 mm minimum length limit with a daily bag limit of one fish). During 2002 -2003, Lischka and Magnuson (2006) determined that rainbow smelt in Sparkling Lake preferred to spawn on gravel-cobble substrates and that the presence of groundwater inputs were unimportant for spawning site selection. From 2002 – 2009, adult rainbow smelt were physically removed during spring spawning using fyke nets and electrofishing (Gaeta et al. 2015). During the physical removal portion of the study, over 4,170 kg of adult rainbow smelt were removed with up to 93% of adults removed annually. Previous research suggested that walleye preferentially consumed rainbow smelt over cisco (Krueger & Hrabik 2005), therefore adult and extended growth fingerling walleye were stocked into Sparkling Lake to increase predation pressures on remaining rainbow smelt. Conservative recreational angler harvest regulations and a cessation of the tribal spearfishery for walleye (e.g., Mrnak et al. 2018) in Sparkling Lake were implemented during the study to protect and conserve the walleye population. Significant reductions in the adult rainbow smelt population were observed during the biomanipulation; however, declines in abundance were short-lived after the manipulation ceased in 2009 due to strong, compensatory recruitment responses (Figure 3; e.g., Grosholz et al. 2021). Several hypotheses were implicated as potential mechanisms leading to the ineffectiveness of the biomanipulation. These include strong, compensatory recruitment responses of rainbow smelt at reduced stock sizes, a failure to achieve walleye biomass and consumption rates necessary to exert sufficient top-down control (Krueger & Hrabik 2005; Roth et al. 2010), the absence of cisco and(or) yellow perch to fill the empty niche space (due to functional extirpations), and(or) the confounding influence of a co-occurring invasive rusty crayfish *Faxonius rusticus* removal experiment on Sparkling Lake (Hein et al. 2006; Perales et al. 2021)

Rainbow smelt were first observed in Crystal Lake in 1987. About five years after first being detected, rainbow smelt were the dominant species in Crystal Lake and yellow perch persisted at low levels (Figure 4). Crystal Lake had a very simple fish community dominated by yellow perch prior to rainbow smelt colonization. Given the oxythermal habitat conditions required by adult rainbow smelt, Crystal Lake was experimentally mixed to eliminate thermal stratification during the summers of 2012 and 2013 in an attempt to elevate water temperatures above their thermal tolerance threshold (Gaeta et al. 2012; Lawson et al. 2015). In response to whole-lake mixing, rainbow smelt exhibited behavioral shifts, showed intra-population divergence in body condition, and were significantly reduced in abundance (~95%; Lawson et al.

2015). Despite a significant reduction in rainbow smelt abundance, smaller individuals within age classes tended to survive the elevated temperatures achieved in the lake. Thus, the population was reduced, but not eliminated. Behavioral plasticity, the inability to control summer temperature and associated whole-lake water temperature, and intra-population variation in thermal tolerances were implicated in the persistence of rainbow smelt following the manipulation (Lawson et al. 2015). Nevertheless, the reduction in rainbow smelt abundance and associated increases in lake water levels following a long-term drought in northern Wisconsin (Gaeta et al. 2014) appeared to weaken competitive and predatory constraints on the remaining yellow perch population. Yellow perch abundance increased during and after the mixing experiment to the lower bounds observed prior to rainbow smelt colonization (Figure 4). Given the strong compensatory recruitment response rainbow smelt typically exhibit and the available niche space left in Crystal Lake (Figure 4), there is reason to believe that rainbow smelt may again reach high densities and dominate the fish community if left unchecked.

Invasive rainbow smelt long-term control was achieved on two lakes in one northern Wisconsin study (Figure 5). A whole-ecosystem biomanipulation experiment to eradicate invasive rainbow smelt was conducted on the Lac Du Flambeau chain of lakes (i.e., Fence and Crawling Stone lakes, Vilas County, Wisconsin) in response to declines in native cisco abundance (Krueger & Hrabik 2005). The biomanipulation focused on increasing walleye abundance and biomass, and thus predation pressure (i.e., consumption rates) on rainbow smelt through protective fishing regulations (recreational and tribal) and walleye stocking (Krueger & Hrabik 2005). During the biomanipulation, walleye biomass increased from 3.2 and 3.1 $kg{\cdot}ha^{-1}$ to 9.7 and 25.4 $kg{\cdot}ha^{-1}$ in Fence and Crawling Stone lakes, respectively (Figure 5). Using a bioenergetics approach, Krueger and Hrabik (2005) determined that these biomass estimates corresponded to rainbow smelt consumption rates of 12 and 58 kg·ha·year^{-1} for Fence and Crawling Stone lakes, respectively. Diet data indicated that walleye selectively consumed rainbow smelt over cisco (Krueger & Hrabik 2005; Figure 6). Increased walleye biomass resulted in rainbow smelt abundance declines and a parallel increase in cisco abundance (Figure 5). Krueger and Hrabik (2005) concluded that: 1) rainbow smelt populations may decline to low levels and cisco may recover when walleye consume ≥ 58 kg·ha·year^{-1} of rainbow smelt; and 2) walleye consumption rates of 12 kg·ha·year^{-1} may reduce rainbow smelt to a lesser degree, but still promote a diverse forage base and allow for cisco recovery. Overall, high walleye biomass and consumption rates corresponded with an increase in cisco abundance. Krueger and Hrabik (2005) represent a somewhat rare, successful biomanipulation where changes in the food web, fish community, and low invasive rainbow smelt abundances persisted to date (i.e., the system has self-organized around the native community structure). Achieving high top predator (walleye) abundances, selectivity of walleye consumption on rainbow smelt over cisco, remnant populations of cisco and yellow perch in the system to fill voided niche space, and the overall diversity of fish communities and habitats in the Lac Du Flambeau chain of lakes were implicated in the success and persistence of this whole-ecosystem biomanipulation.

Rainbow smelt introductions, control, and(or) eradication have been achieved through the elimination of recreational fishing methods contributing to their spread, educational outreach campaigns, and in a whole-ecosystem study. Rainbow smelt are a popular harvest-oriented species in several of the Laurentian Great Lakes and may have been intentionally introduced in many inland lakes for human consumption. Thereafter, regulations were enacted in Wisconsin inland lakes to ban netting of rainbow smelt to control (gamete and individual) spread after learning of the negative ecosystem consequences. This intervention has likely contributed to the lack of new invasions since 2006 despite the large number of uninvaded inland lakes with suitable oxythermal habitat (Mercado-Silva et al. 2006; Lyons et al. 2018; Renik et al. 2020). Additionally, educational outreach efforts to prevent the spread of invasive species, including rainbow smelt in inland lakes, have been extensive and are likely a contributing factor to the cessation of their spread (Vander Zanden & Olden 2008; Seekamp, McCreary, et al. 2016; Seekamp, Mayer, et al. 2016).

Management lessons learned

Commonalities observed in unsuccessful attempts to control and(or) eradicate invasive rainbow smelt include unexpected behavioral responses to whole-lake mixing, variable sensitivity to elevated temperatures, insufficient top predator abundance and biomass to exert top-down predatory control (e.g., Schmitz & Suttle 2001; Terborgh & Estes 2010; Jones et al. 2020), and a lack of ecologically similar species (i.e., planktivorous and omnivorous fishes) in the system to fill the devoid rainbow smelt niche space. Indeed, rainbow smelt dominance has often resulted in a strongly resilient ecosystem regime. Theoretically, whole-lake mixing would be a viable option for rainbow smelt control and(or) eradication; however, air temperatures will dictate whole-lake water temperatures, *in-situ* rainbow smelt thermal tolerances may not align with lab-derived thermal tolerance due to intra-population variability and behavioral shifts, and broadly applying whole-lake mixing may not be feasible or cost effective, particularly for larger water bodies. Further, whole-lake mixing would select against native *Coregonus* spp. that require similar oxythermal habitat. Therefore, certain aspects and conditions of previous biomanipulations to control and(or) eradicate rainbow smelt may provide more feasible approaches for management (i.e., predator mediated top-down control; Krueger & Hrabik 2005).

Clearly, rainbow smelt control and(or) eradication efforts should be more focused on control rather than eradication to weaken rainbow smelt resilience and negative ecological effects on native aquatic communities (Green & Grosholz 2021).

Lessons learned from previous whole-ecosystem biomanipulation experiments to control and(or) eradicate rainbow smelt suggest that a multi-trophic level invasive species could be controlled by biomanipulating multiple trophic levels simultaneously, including top predator native species. Because rainbow smelt negatively influence inland lakes through competitive and predatory mechanisms, biomanipulations should therefore also focus on the addition of native fish species that may breakdown or decrease resilience of the positive feedback loops that rainbow smelt reinforce for themselves when highly abundant and fill devoid rainbow smelt niche space when abundance is reduced. Perhaps most importantly, control efforts should focus on elevating mortality rates of adult and juvenile rainbow smelt, such that a critical abundance threshold is reached and depensatory recruitment dynamics occur (Walters & Kitchell 2001; Grosholz et al. 2021; Sass et al. 2021). In the context of rainbow smelt control, we reason that successful management (i.e., reduced rainbow smelt effects, native species dominated food web/regime) may be achieved in the long-term in two ways. First, adult rainbow smelt are physically removed by agencies or researchers during spring spawning to reduce adult abundances (species-level adaptive cycle), top predator abundance (e.g., walleye) is maintained through stocking and(or) conservative harvest regulations (species-level adaptive cycle with predation influencing community-level adaptive cycle), and multi-trophic level competitor(s) are added to the system (e.g., cisco, yellow perch; community-level adaptive cycle). Alternatively, adult rainbow smelt are physically removed by agencies or researchers during spring spawning and(or) are at low abundances due to other factors, competitor(s) are still extant in the system, and additional competitive interactions are induced by the recovery of extant and(or) stocked competitor(s). In the former, control is hypothesized to be invoked through top-down predatory control and competition for planktonic resources. In the latter, control is hypothesized to be invoked through competition for planktonic resources and eliminating available niche space for rainbow smelt compensation when they are at low abundance. In both cases, it is encouraged that agencies or researchers conduct the physical removals of rainbow smelt as recreational fisheries for this species likely led to their spread (Evans and Loftus 1987; Hrabik & Magnuson 1999). In either scenario, a key factor increasing the probability of rainbow smelt long-term control may be through leveraging the nested adaptive cycles comprising panarchy theory to initiate biomanipulations when rainbow smelt populations are already compromised.

1.7 Invasive rainbow smelt management experiments leveraging panarchy theory

Two whole-lake experiments are proposed to apply panarchy theory to invasive species management and test the role of apex predators (piscivorous fishes) in mediating the interaction between native cisco and yellow perch with invasive rainbow smelt in a species reintroduction context (Figure 7). Apex predators can regulate community structure and have profound ecological effects that extend to the base of the food web (Pace et al. 1999; Terborgh & Estes 2010). This can include mediating interactions among prey species (Abrams 1987a, 1987b), which has been reported for rainbow smelt-cisco interactions (Krueger & Hrabik 2005). The idea that interactions between native and invasive forage fishes is mediated by the presence of a predator is the foundation of the proposed research.

By reintroducing native cisco into two similar lakes with distinctly different food web configurations (i.e., presence or absence of apex predators), the hypothesis that presence of native apex predators facilitates the reestablishment of cisco by affecting the nature and(or) magnitude of interactions between rainbow smelt and cisco will be tested. Rainbow smelt are at historically low abundances in two core North Temperate Lake Long-Term Ecological Research (NTL-LTER) lakes, Sparkling and Crystal (Figure 3 and 4, respectively). Due to recent interventions (i.e., Lawson et al. 2015; Gaeta et al. 2015), the species- and community-level adaptive cycles are likely in the release phase (Figure 1 and Figure 2), noted by diminishing rainbow smelt vertical gillnet catches and pelagic density estimates in both lakes. Moreover, in Crystal Lake, native yellow perch catches and pelagic density estimates have been increasing in recent years (Figure 4). To further exacerbate these food web shifts and cause a release in the inland lake-level adaptive cycle (i.e., cause more stochasticity, further weakening system structure and interactions), rainbow smelt will be physically removed (i.e., Gaeta et al. 2015) from Sparkling and Crystal lakes during the spring spawning period. Rainbow smelt removals began in the spring of 2021. Native cisco will then be introduced at similar densities into Sparkling and Crystal lakes, both of which contain suitable oxythermal habitat for the species. Cisco introductions began in the fall of 2020. Sparkling Lake has apex predators (walleye, muskellunge *Esox masquinongy*, and smallmouth bass *Micropterus dolomieu*) and will receive additional walleye stocking with the goal of achieving a biomass >10 $kg \cdot ha^{-1}$ and consumption rate > 12 $kg \cdot ha \cdot year^{-1}$ (Krueger & Hrabik 2005). Crystal Lake contains no apex predator and will not undergo predator stocking. In concert, these interventions should increase the probability that the inland lake-level adaptive cycle reorganizes and then self-organizes on the desired (native) set of ecosystem processes, structures, and functions. A relatively long-term approach (5 – 10 years) will be taken in this experiment, as interactions among these species may vary over time in response to differences in generation times or inter-annual variability in recruitment success among these species.

Annual fish population and lake monitoring has been ongoing since 1981 (NTL-LTER) with more directed sampling efforts beginning one year prior to the manipulations (began spring of 2020). These data collection efforts will continue with the aim of generating a decadal or longer time series and allow for a before-after-control-impact design analysis (Stewart-Oaten et al. 1986). Cisco will be captured using electrofishing and transferred from White Sand Lake (Vilas County, Wisconsin). Three reference lakes will be monitored to account for any disease or climate-driven changes (Carpenter et al. 1998; Krueger & Hrabik 2005). Big Muskellunge and Trout lakes (both located in Vilas County, Wisconsin) are two core NTL-LTER lakes that contain cisco and no rainbow smelt. Anderson Lake (Vilas County, Wisconsin) will serve as the third reference system as it contains rainbow smelt and no cisco. Fish populations will be tracked and monitored using multiple gear and survey types over spring, summer, and fall (e.g., fyke net mark-recapture, hydroacoustic and vertical gillnet (i.e., Mrnak et al. 2021), and electrofishing surveys). Diet, growth, and isotopic studies will be conducted to provide a basis for understanding predatory and competitive interactions within the food webs.

It is hypothesized that the presence of apex predators (e.g., muskellunge, smallmouth bass, walleye) mediates the interactions between native and invasive cold-water forage fishes (Abrams 1987a, 1987b), and that these interactions can determine the outcome of native species restoration and invasive species control. Thus, it is expected that there will be greater cisco reintroduction success and invasive rainbow smelt control in Sparkling Lake (contains predators) than in Crystal Lake (contains no predators). In Crystal and Sparkling lakes, adult rainbow smelt will be mechanically removed. Additionally, in Sparkling Lake, predation pressure should further reduce rainbow smelt population size by removing juvenile and young-of-year individuals not susceptible to our mechanical removals. This predation pressure should promote a faster progression through the adaptive cycles (i.e., Figure 1 and Figure 2) and a greater stabilizing force once the ecosystem transitions to the new conservation phase by further mitigating the negative effects of invasive rainbow smelt. By leveraging panarchy theory, there is reason to believe the Crystal Lake biomanipulation will also be successful. That is (as with the Sparkling Lake biomanipulation), purposeful injection of management actions (rainbow smelt removal, cisco stocking) to compromise the current ecosystem regime across the nested adaptive cycles (conservation phase). This should cause the system to release and move into the reorganization phase. Due to the rainbow smelt removals and cisco stocking, newly freed resources will be available for the desired (native) species to utilize. This should generate species interactions (e.g., cisco consuming zooplankton; predators consuming YOY and juvenile rainbow smelt) that will increase the connectivity of the food web during the growth phase. Given the management action to nudge the system to reorganize (rainbow smelt removals) and likelihood to self-organize around desirable interactions (cisco stocking), this growth phase should contain desirable species- and community-level interactions leading to an inland lake-level adaptive cycle that differs from the former rainbow smelt dominated regime. Theoretically, these novel (cisco-based) resources and interactions will develop and build overtime until the system moves into the conservation phase, albeit now under a new ecosystem regime that was dictated by resource and interaction availability during the reorganization phase. This new ecosystem regime should in theory be one with low or no invasive species impact and viewed as much more desirable to managers and stakeholders. The results of this work will be directly applicable to invasive species management and native species restorations.

1.8 Conclusion

This review integrates lessons learned from previous rainbow smelt control efforts and panarchy theory to develop novel experiments for controlling aquatic invasive species. In theory, weakening the conservation phase of an invasive population and causing a release in the adaptive cycle should be initiated prior to further intervention. Release may be caused by a purposeful intervention (e.g., exploitation, physical removals) or can be natural (e.g., disease, climate change). Regardless of mechanism, intervention to promote a new regime should be undertaken during the release phase of the adaptive cycle to guide the reorganization phase towards a new desirable regime (e.g., low impact invasive, native). Interventions during the release phase should then focus on strengthening species interactions (competition, predation) in simple fish communities such that devoid niche space of the invasive species is filled by native species in the absence of a top predator. The addition of a top predator may further increase the probability of changing an invasive species ecosystem state to a desirable ecosystem state by increasing species diversity and the complexity of species interactions.

Purposefully applying panarchy theory will bring new ideas that will benefit invasive species management. Ecosystem and fishery management is too often target species oriented rather than based in an ecosystem or food web context (Kitchell et al. 2000; Pikitch et al. 2004; Vander Zanden et al. 2016). Across the globe, there is a need for ‘food web thinking’ (Vander Zanden et al. 2016). Panarchy theory allows for the incorporation of a systems approach when considering management actions (i.e., incorporation of the ecosystem and food web into fisheries management and restoration). This systems approach (i.e., ecosystem-based fisheries management; Pikitch et al. 2004) is critical to the long-term sustainability of aquatic food webs and future invasive species control and(or) native species restoration experiments.

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1.11 Tables

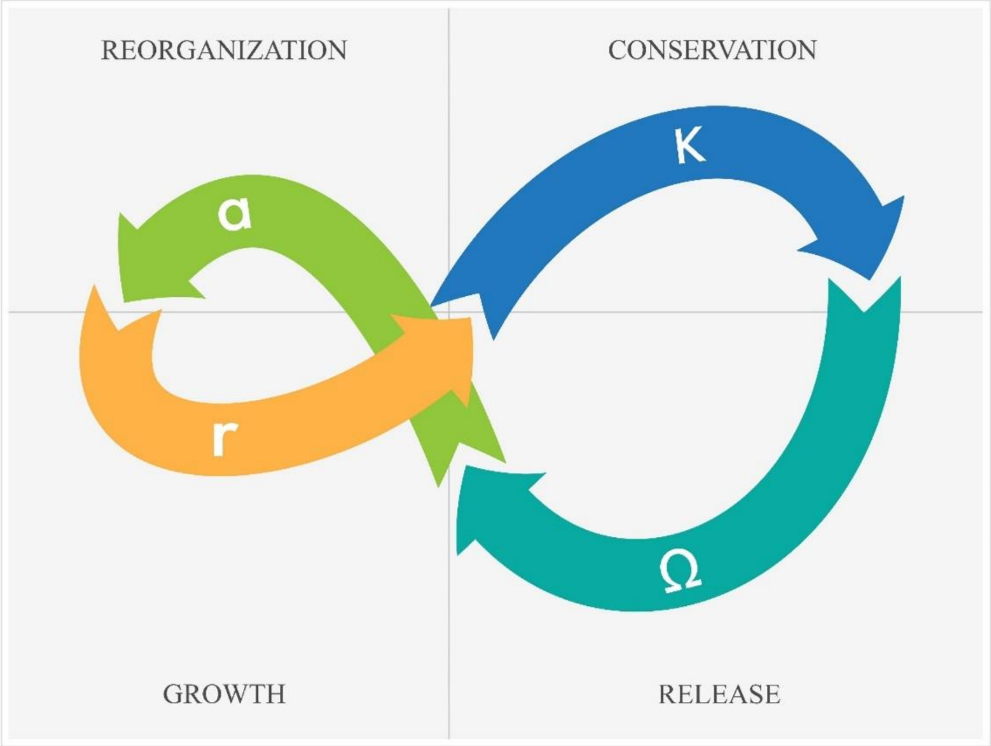
Table 1. Four phases of a nested adaptive cycle of a panarchy for inland aquatic ecosystems.

Adaptive cycle phase	Example	Management response
Growth	Recently formed oxbow lake	1) If invasive and(or) undesired species are present, a rapid removal is required or 2) if a native and(or) desired species are absent, a rapid stocking is required before ecosystem structure and interactions set up and become bound and rigid.
Conservation	Lake with long-term invasive species presence	Cause a strong enough disturbance to ecosystem to transition into release phase. Limit the ecosystem of undesired resources/species and provide desired species/resources to build upon in follow phases.
Release	Lake with disease outbreak causing mass mortality	1) If invasive and(or) undesired species, nothing. If native and(or) desired species, restocking is required so that ecosystem structure and interactions rebuilds mirroring pre-collapse ecosystem state.
Reorganization	Lake in springtime following mass winter-kill event	1) If invasive and(or) undesired species, nothing. If native and(or) desired species, restocking is required so that ecosystem structure and interactions rebuilds mirroring pre-collapse ecosystem state.

1.12 Figures

(α) phase: resources release, ecosystem structure and interactions renew. Reorganization and recovery of the inland fishery if release us 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.

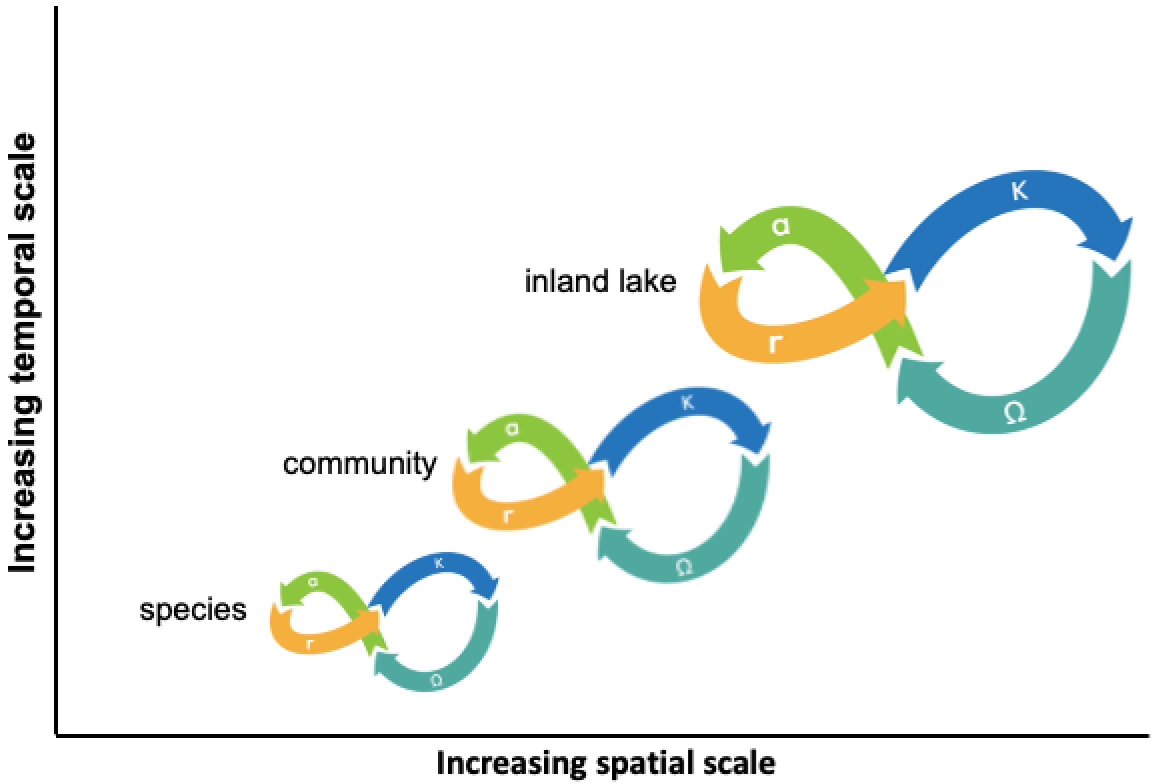


Figure 2. Species-, community-, and inland lake-level nested adaptive cycles comprising a panarchy for a north-temperate inland lake ecosystem.

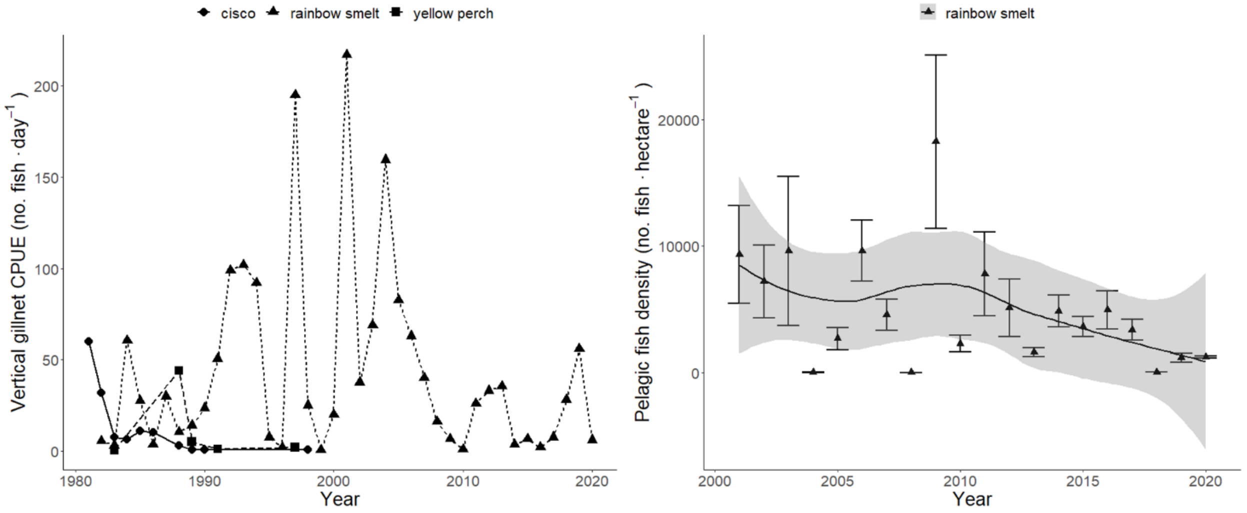


Figure 3. Long-term trends in cisco *Coregonus artedi*, rainbow smelt *Osmerus mordax*, and yellow perch *Perca flavescens* vertical gillnet catch per unit effort (no. fish · day^{-1}; left) and rainbow smelt mean ± SE pelagic density (no. fish · hectare^{-1}; right) for Sparkling Lake (Vilas County, Wisconsin) during 1980 – 2020 and 2001 – 2020, respectively. Grey shading for pelagic fish density corresponds to 95% confidence interval. Zeros have been removed for clarity.

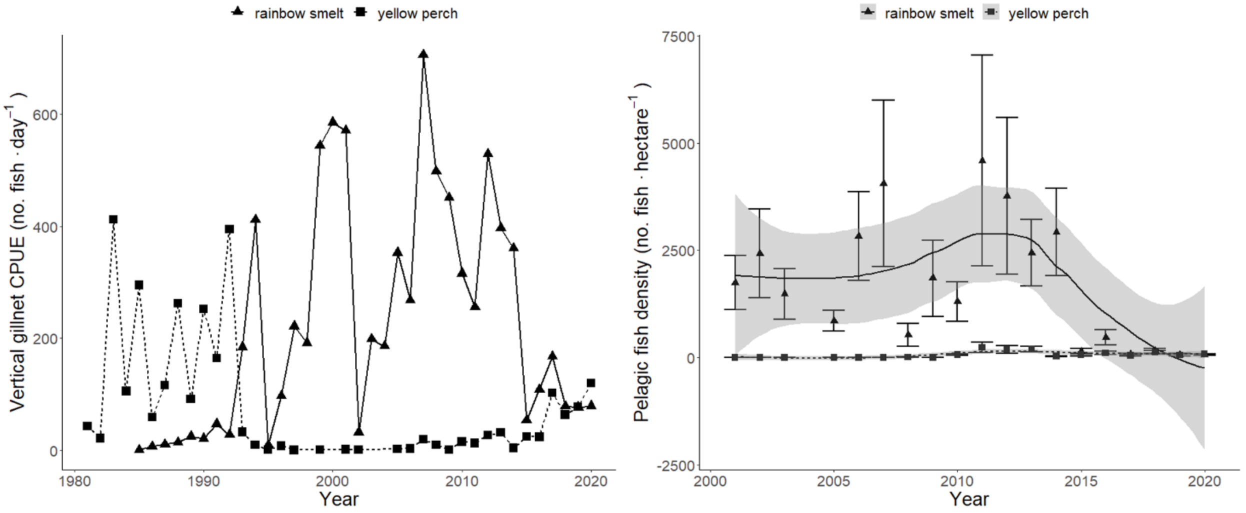


Figure 4. Long-term trends in rainbow smelt *Osmerus mordax* and yellow perch *Perca flavescens* vertical gillnet catch per unit effort (no. fish · day^{-1}; left) and mean ± SE pelagic fish density (no. fish · hectare^{-1}; right) for Crystal Lake (Vilas County, Wisconsin) during 1980 – 2020 and 2001 – 2020, respectively. Grey shading for pelagic fish density corresponds to 95% confidence intervals. Zeros have been removed for clarity.

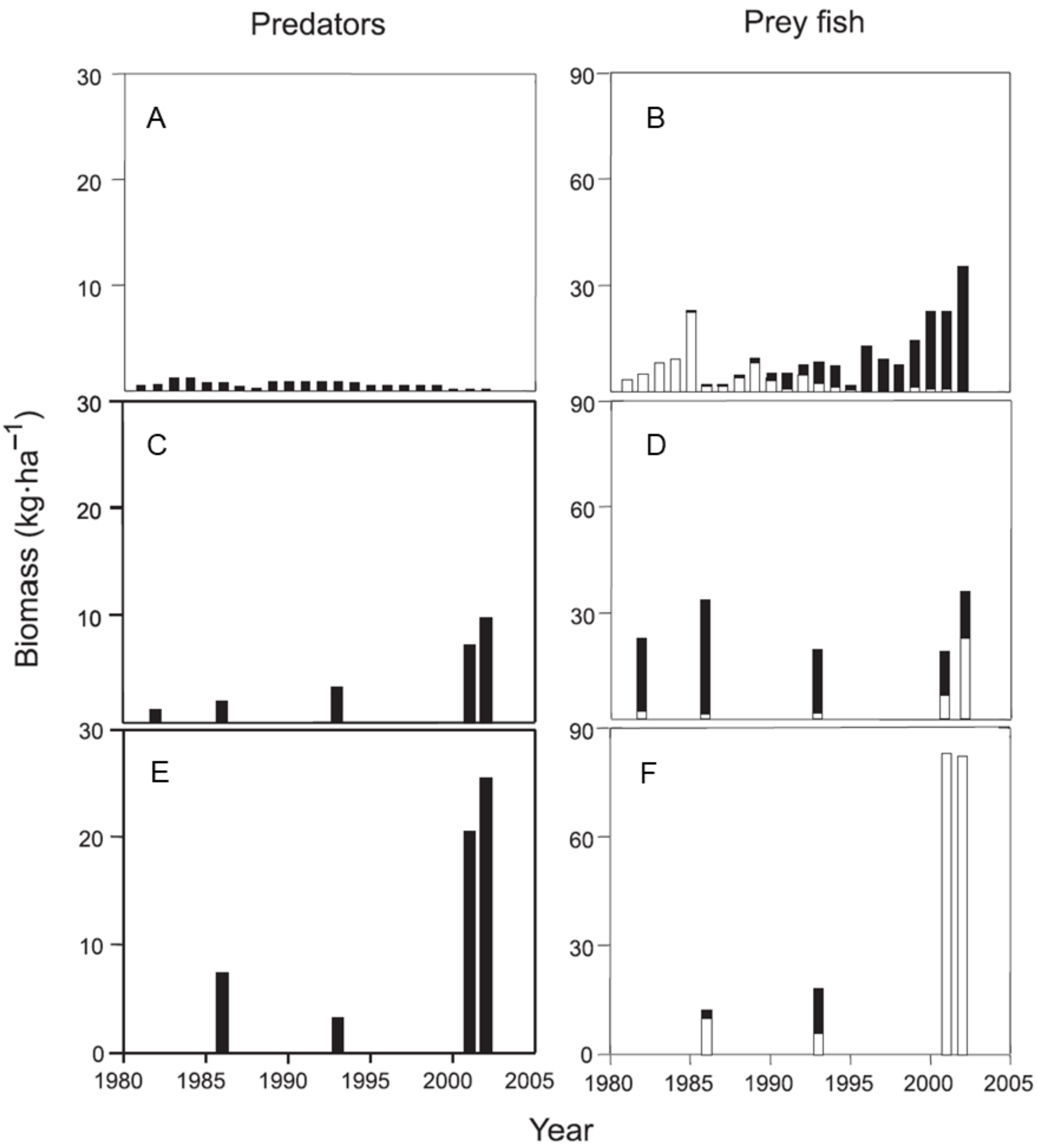


Figure 5. The estimated biomass of predator and prey species in each study lake from 1982 to 2002. (A) The biomass of predatory fish in Crystal Lake represented as a combined estimate of lake trout (*Salvelinus namaycush*) and walleye (*Stizostedion vitreum*). (B) The biomass of rainbow smelt (*Osmerus mordax*; solid bars) and native [yellow] perch (*Perca flavescens*; open bars) in Crystal Lake. (C) The biomass of walleye in Fence Lake. (D) The biomass of rainbow smelt (solid bars) and native cisco (*Coregonus artedi*; open bars) in Fence Lake. (E) Walleye biomass through time in Crawling Stone Lake. (F) The biomass of rainbow smelt (solid bars) and native cisco (open bars) in Crawling Stone Lake. Note the difference in scale for the y axis between predator and prey species (Krueger & Hrabik 2005). Reprinted with permission from D.M. Krueger and T.R. Hrabik.

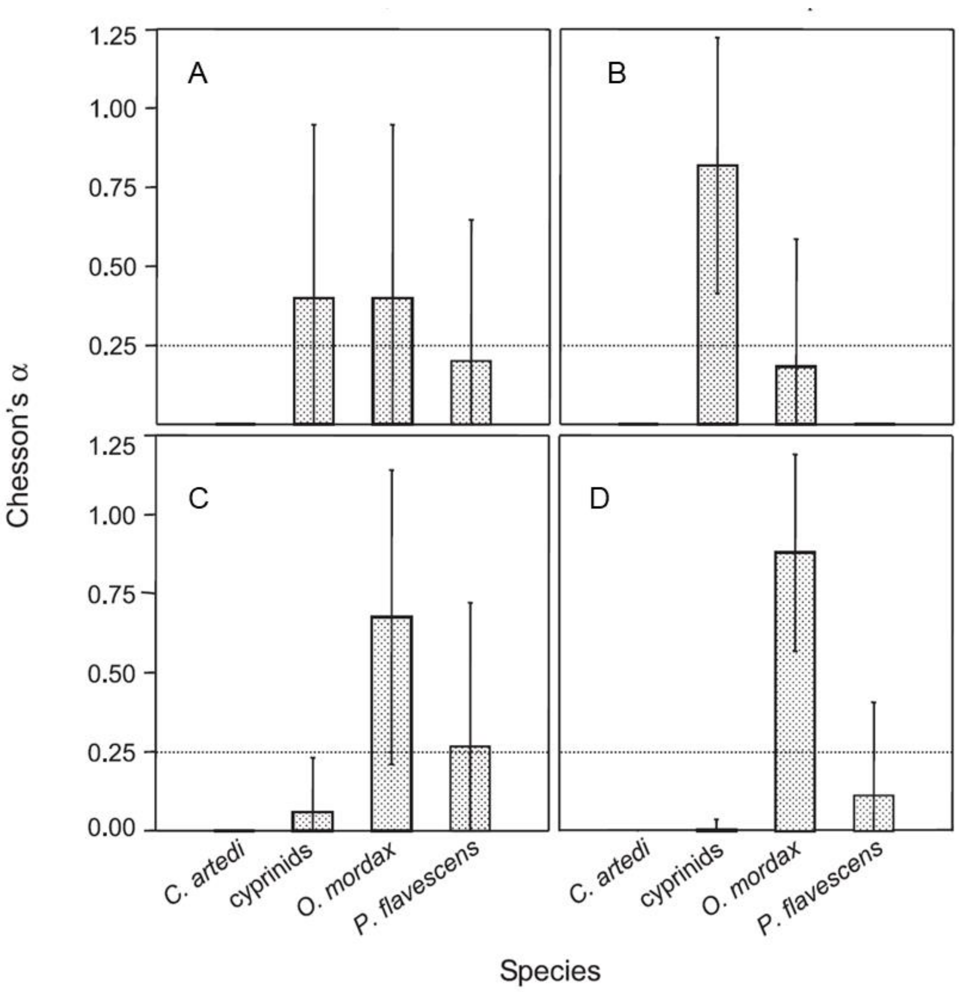


Figure 6. Chesson's index of prey selection for walleye (*Stizostedion vitreum*) caught in Fence Lake in (A) May, (B) June, (C) July, and (D) August of 2002. Error bars indicate 95% confidence intervals; the dotted horizontal line in each box represents neutral selection (Krueger & Hrabik 2005). Reprinted with permission from D.M. Krueger and T.R. Hrabik.

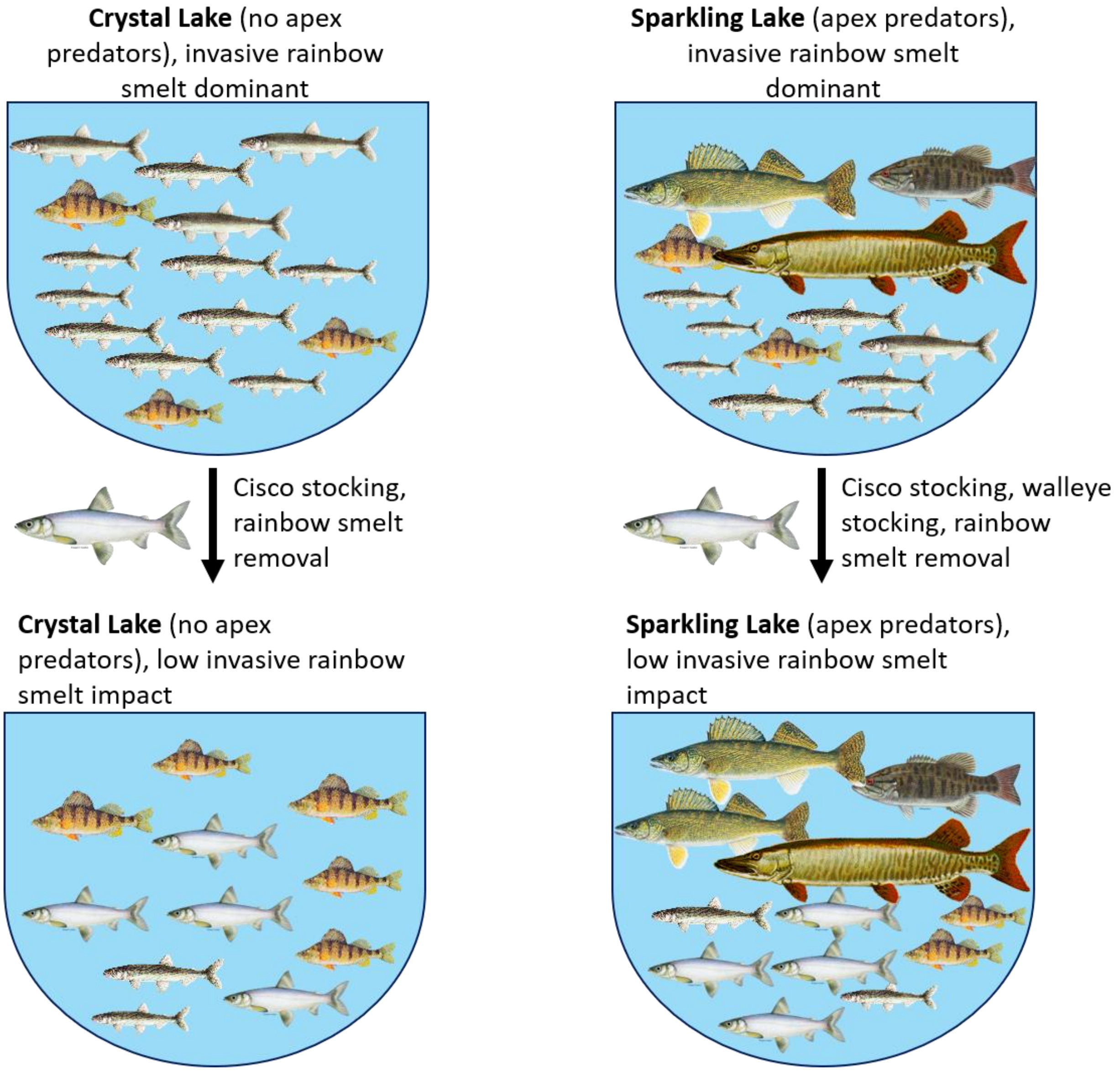


Figure 7. Experimental reintroduction of native cisco *Coregonus artedi* and control of invasive rainbow smelt *Osmerus mordax* in Crystal and Sparkling Lakes (Vilas County, Wisconsin) by leveraging panarchy theory. Crystal Lake contains no apex predators and a native planktivore in the form of yellow perch *Perca flavescens*. Sparkling Lake also contains yellow perch as well as apex predators in the form of walleye *Stizostedion vitreum*, muskellunge *Esox masquinongy*, and smallmouth bass *Micropterus dolomieu*. Sparkling Lake will continue to be stocked with walleye.

Chapter 2: Invasive Control and Native Restoration: Directing Ecosystem Transformation Through Purposeful Food Web Manipulations

Submitted on 23, February 2024 as: Mrnak, J.T., M.V. Wilkinson, L.W. Sikora, L.M. Feucht, A.M. Mrnak, M.J. Vander Zanden, and G.G. Sass. Invasive Control and Native Restoration: Directing Ecosystem Transformation Through Purposeful Food Web Manipulations (*In review*), Ecological Applications.

Abstract

Ecosystems are abruptly changing due to invasive species and global climate change. In lakes, invasive rainbow smelt *Osmerus mordax* (Mitchill, 1814) can cause negative ecosystem effects through competitive and predatory interactions with native species leading to food webs shifts away from native species dominance, altered zooplankton communities, and the decline or extirpation of native cool- and cold-water fishes. We conducted two whole-lake removals of invasive *O. mordax* and stockings of native cisco *Coregonus artedi* (Lesueur, 1818). Between two experimental lakes, 12,311 adult *O. mordax* were removed and 4,594 adult *C. artedi* were stocked over four years. The experimental lake food webs were purposefully reconfigured to native species dominance following experimental manipulation. On average and across species and gears, native species relative abundance and density significantly increased following invasive *O. mordax* removals and *C. artedi* stockings. *O. mordax* are currently 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. Given that global change is transforming ecological environments at an alarming rate, shifting food web dynamics and ecosystem structures present new challenges to natural resource management that typically *resist*s or *accepts* ecological change. We used a holistic management framework based on theoretical panarchy and guided by RAD strategies 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 *O. mordax* driven negative effects.

Key words: *ecosystem-based fisheries management, fisheries, invasive species, natural resource management, whole-lake experiment, panarchy, resist-accept-direct*

2.1 Introduction

Ecosystems around the globe are abruptly changing (Turner et al. 2020, Weiskopf et al. 2020). Aquatic ecosystems can undergo abrupt change due to invasive species and global climate change (Rahel and Olden 2008, Carpenter et al. 2011, 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 (Folke et al. 2004, Carpenter et al. 2011, Embke et al. 2022). 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, Thompson et al. 2021, Mrnak et al. 2023). 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 (Lynch et al. 2016, Embke et al. 2022, Feiner et al. 2022). Invasive species (Perales et al. 2021, Bethke et al. 2023, Martin et al. 2023) and habitat loss (Christensen et al. 1996, Marburg et al. 2006, Sass et al. 2017) in combination with other stressors (e.g., overexploitation, pollution) reduces or weakens the potential for freshwater ecosystems to support sustainable fisheries (Post 2013, Hilborn et al. 2015, Walsh et al. 2016, Mrnak et al. 2018, Embke et al. 2019).

Invasive species are drivers of ecological change (Vander Zanden et al. 2010). Rainbow smelt *Osmerus mordax* (Mitchill, 1814), native to the North Atlantic coast, have invaded many north-temperate inland lakes (Evans and Loftus 1987, Hrabik et al. 1998, Mercado-Silva et al. 2007). *O. mordax* can cause significant negative ecosystem effects via competition and(or) predation due to their rapid population growth, early spawning phenology, omnivorous diet, and eurythermal life history (Evans and Loftus 1987, Sass et al. 2010, Sheppard et al. 2012, Grosholz et al. 2021). Thus, *O. mordax* interacts (directly or indirectly) with a wide range of native biota at multiple trophic levels. The most well documented negative effects of *O. mordax* on native aquatic ecosystems include shifting food webs, altering zooplankton communities, and the decline or extirpation of native cool- and cold-water fishes (e.g., yellow perch *Perca flavescens* (Mitchill, 1814), walleye *Sander vitreus* (Mitchill, 1818), cisco *Coregonus artedi* (Lesueur, 1818), lake whitefish *Coregonus clupeaformis* (Mitchill, 1818); Evans and Loftus 1987, Hrabik et al. 2001, Lepak et al. 2023). A thorough review on the invasion history, biology, and ecology of *O. mordax* in North America are presented in Mrnak et al. (2023).

Removing *O. mordax* from a north-temperate ecosystem may reduce competition and(or) predation pressure on native fishes, potentially alleviating critical population bottlenecks (Krueger and Hrabik 2005, Lawson et al. 2015, Gaeta et al. 2015, Mrnak et al. 2023). Management to control or eradicate *O. mordax* 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 *O. mordax* abundance (Lawson et al. 2015, Gaeta 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 *O. mordax* may exhibit, these invaders may reach high densities and dominate the fish community again if left unchecked (Mrnak et al. 2023). Invasive *O. mordax* control and native species recovery was documented for two lakes in Northern Wisconsin (Krueger and Hrabik 2005). In response to declining native *C. artedi*, Krueger and Hrabik (2005) increased *S. vitreus* predation rates through stocking and regulatory protection. Due to selective predation by *S. vitreus* on *O. mordax*, a competitive and(or) predatory release was lifted off the dwindling remnant *C. artedi* population, allowing for their recovery (Krueger and Hrabik 2005). Mrnak et al. (2023) concluded that *O. mordax* control and(or) eradication success depends on whether: 1) enough *O. mordax* were removed to devoid their niche space; and 2) devoid niche space became filled with desired native species.

Two whole-lake experimental removals of invasive *O. mordax* and stockings of native *C. artedi* were conducted 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 *O. mordax* through intensive removals and native *C. artedi* introductions; and (2) test for changes in the relative abundance and density of the native fish community.

2.2 Methods

Study area

Experimental (Crystal Lake, 46.000878, -89.612474; Sparkling Lake, 46.007317, -89.700080) and reference (Trout Lake, 46.033541, -89.673653; Anderson Lake, 46.170762, -89.344326) lakes are located in Vilas County, Wisconsin, USA (Figure 1) and have similar lake characteristics but different fish communities (Shay et al. 2024). At the beginning of our experiment in 2020, Crystal Lake contained invasive *O. mordax*, no native *C. artedi*, and no top predators, while Sparkling Lake contained invasive *O. mordax*, native top predators in *S. vitreus*, muskellunge *Esox masquinongy* (Mitchill, 1824), and smallmouth bass *Micropterus dolomieu* (Lacepede, 1802), and no remaining native *C. artedi*. Trout Lake's fish community is dominated by native *C. artedi* and contains no invasive *O. mordax*, while the Anderson Lake fish community is dominated by invasive *O. mordax* with no native *C. artedi* present (Parks and Rypel 2018, Mrnak et al. 2023). Crystal Lake experienced marked declines in the *P. flavescens* population following *O. mordax* invasion in 1985 (Hrabik et al. 1998, 2001, Lawson et al. 2015, Mrnak et al. 2023). Following *O. mordax* invasion in Sparkling Lake in 1982, *C. artedi* were extirpated from the system (Hrabik et al. 1998; Mrnak et al. 2023) and *S. vitreus* recruitment (i.e., relative abundance of non-stocked age-0 *S. vitreus* collected in fall electrofishing surveys) declined (Gaeta et al. 2015). Similar to other imperiled *S. vitreus* populations across the Midwest USA, Sparkling Lake has been stocked with extended growth fingerling *S. vitreus* (~150-220mm total length; TL) during the fall of odd years since 1997 (see Elwer et al. 2023)

Experimental manipulation

Native species introduction efforts

Native *C. artedi* introductions into the experimental lakes occurred in November of 2020 and 2021. Before *C. artedi* could be moved across the landscape, the donor lake (White Sand

Lake; Vilas County, Wisconsin, USA; 46.083402, -89.587942; Figure 1) *C. artedi* population needed to test negative for viral hemorrhagic septicemia and whirling disease by Wisconsin Department of Natural Resources Fish Veterinarians (Figure 2a; negative results acquired on November 2nd of 2020). Donor *C. artedi* were captured from White Sand Lake during peak spawn via AC boat electrofishing when water temperatures were 4 – 6°C (November 4 – November 13th; Figure 2b). All captured *C. artedi* were enumerated and a subset (n = 50) were measured for total length (TL) and sexed to estimate the male:female ratio (Figure 2c). Captured *C. artedi* were moved from the electrofisher live well to an insulated hatchery truck containing oxygenated water from the recipient lake (i.e., Crystal or Sparkling lake; mitigate invasive species spread; Figure 2d; Figure 2e). Based on a summer 2020 population estimate and conversations with the local fishery biologist, the 2020 *C. artedi* introduction goal was 14.8 adult *C. artedi*/ha into Crystal and Sparkling lakes. These densities equated to 587 and 962 adult *C. artedi* being stocked into Crystal and Sparkling lakes respectively in November of 2020. After an additional *C. artedi* population estimate on White Sand Lake in summer of 2021, introduction efforts were doubled in fall of 2021. The 2021 *C. artedi* introduction goal was 29.6 adult *C. artedi*/ha into Crystal and Sparkling lakes. These densities equated to 962 and 1,887 adult *C. artedi* being stocked into Crystal and Sparkling lakes respectively in 2021. There were no observed *C. artedi* mortalities on the night of the transfer or on the following day after circumnavigating each lake's shoreline.

Invasive species removal efforts

To better understand the status of the *O. mordax* population in Crystal Lake following the mixing experiment (i.e., Lawson et al. 2015) and to set the stage for our manipulation, 1,520 (22.5 kg) and 779 (16.4 kg) *O. mordax* were removed from Crystal Lake using mini fyke netting

(0.6 × 1.2 m, 0.65 cm bar mesh) in the springs of 2018 and 2019, respectively. Intensive *O. mordax* removal efforts started in spring of 2021 in the experimental lakes using mini-fyke nets and continued through 2023 (Figure 3a). About two weeks before ice-out (April 1st – April 26th), a chainsaw and(or) spud bar was used to break ice perpendicular to shore for mini fyke net deployment (~3 × 10m rectangle; Figure 3b; Figure 3c). 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 *O. mordax* spawn (shortly after ice-out). Mini fyke net locations were chosen based on observed *O. mordax* spawning habitat (gravel, cobble) and previous research (Lischka and 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 3d). Invasive *O. mordax* were separated and donated to an animal rehabilitation facility, while all other fish were returned to the lake (Figure 3d). In addition to our intensive *O. mordax* removal method (pre-ice-out mini fyke nets during *O. mordax* spawn), *O. mordax* were also removed from the experimental lakes when captured in our summer vertical gillnet monitoring surveys (see below).

Fish sampling

Standardized surveys

During 2020 – 2023, standardized monthly vertical gillnet sampling and bimonthly hydroacoustic surveys were conducted post-stratification (mean date during study among lakes was June 15th) 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 and -70 dB for target strength data with a transmitted pulse duration of 0.4 ms. Hydroacoustic surveys were conducted at least 30 min beyond nautical twilight to mitigate the likelihood of backscattering via fish schooling behavior and followed standardized and replicable whole-lake transects at a mean vessel speed of ~9 km/hr. 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 was 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 nearly followed the Great Lakes Standard Operating Procedure for acoustic data (Parker-Stetter et al. 2009, Mrnak et al. 2021); 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 hr vertical gillnet surveys to apportion species-specific hydroacoustic estimates using gillnet count and fish length data. We followed standardized North Temperate Lakes Long-Tern Ecological Research protocols (Feucht et al. 2023, Magnuson et al. 2024) and deployed seven monofilament gillnets in the deep basin of each lake from surface to bottom. After 24 hr, vertical gillnets were picked and all fish were identified to species, enumerated, measured (TL; nearest mm), and weighed (nearest g). Gillnets were 3 x 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 gillnet catches. Two individuals of the same species needed to be captured in the gillnets for that species to be represented in the hydroacoustic data. We used single target analyses to estimate sigma values (excluding targets > -55 dB), which were then applied to S_v data 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 (Heald et al. 2017; 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 gillnet sampling provided relative abundance estimates (catch-per-unit-effort, CPUE; number fish · net night^{-1}), while active hydroacoustic surveys provided whole-lake density estimates (number fish · ha^{-1}). 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 *O. mordax* removed from the experimental lakes was estimated by extrapolating lengths and weights to unmeasured fish based on the measured sample. A subset of measured *O. mordax* (daily maximum = 30 *O. mordax*/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 *O. mordax* 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 *O. mordax* had an assigned weight, *O. mordax* 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 *O. mordax* removed from experimental lakes in 2020 came from standardized vertical gillnet monitoring surveys and not intensive removals.

Testing for fish community changes focused on summer of 2020 (baseline, pre-manipulation) and 2023 (post-manipulation) vertical gillnet (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 *C. artedi*, *O. mordax*, and *P. flavescens* as age-1+ (adult) or age-0 (young-of-year; Hrabik et al. 2001; Mrnak et al. 2021). Only adult *S. vitreus* were present in vertical gillnet and hydroacoustic surveys. Only adult (i.e., ≥75mm) fish were used in CPUE and density analyses. A Shapiro-Wilk test indicated that CPUE and density data were non-normally 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 *C. artedi, O. mordax, P. flavescens,* and *S. vitreus* before (2020) and after the experiment (2023), a one-way ANOVA was used. Hypothesis tests were considered significant at $\alpha \leq 0.5$.

2.3 Results

Experimental manipulation

12,311 adult invasive *O. mordax* were removed from Crystal and Sparkling lakes during 2021 – 2023 (Figure 4). Over 99.9% of all removed *O. mordax* came from spring mini fyke net surveys, with only 107 individuals being removed via vertical gillnets in 2020. 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. In total, 381.3 and 1.6 kg of invasive *O. mordax* were removed from Crystal and Sparkling lakes, respectively.

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

Fish community responses

After two *C. artedi* stocking events and three intensive *O. mordax* removals, the Crystal and Sparkling lake fish communities shifted from invasive to native species dominance (Table 1; Figure 4). Invasive *O. mordax* vertical gillnet CPUE (number fish · net night^{-1}) and hydroacoustic density estimates (number fish · ha^{-1}) significantly declined in both experimental lakes (all $p < 0.001$; Table 1). *O. mordax* CPUE and density declined by 88.2% and 96.4% in Crystal Lake during 2020 - 2023 (Figure 5). Native *P. flavescens* exhibited a significant positive response, where CPUE increased by 555.7% and density increased by 142.9% (all $p \leq 0.01$; Table 1; Figure 5).

O. mordax CPUE declined by 87.5% in Sparkling Lake during 2020 - 2023 and *O. mordax* did not show up in the 2023 hydroacoustic density estimates due to inadequate sample sizes in vertical gillnet surveys (Figure 6). There was no change in CPUE of *S. vitreus* after the experimental manipulation ($p = 0.51$; Table 1). *S. vitreus* were present in the 2022 and 2023 hydroacoustic surveys after not being observed during 2020 – 2021 estimates (Figure 6).

C. artedi 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, *C. artedi* were present in all 2023 vertical gillnet and hydroacoustic surveys (Table 1; Figure 5; Figure 6).

Reference populations

Trout Lake's reference *C. artedi* population density was similar before and after the experiment ($p = 0.09$; Table 1; Figure 7). *C. artedi* vertical gillnet CPUE for Trout Lake increased by 131.9% during 2020 - 2023 ($p = 0.03$; Table 1; Figure 7). Anderson Lake's reference *O. mordax* population density increased by 121.1% during the experiment ($p < 0.01$; Table 1; Figure 8), while vertical gillnet CPUE did not change ($p = 0.09$; Table 1; Figure 8).

2.4 Discussion

Whole-lake manipulations to direct an ecosystem

The food webs of Crystal and Sparkling lakes were purposefully and successfully reconfigured to native species dominance (Figure 4). Intensive and directed removal efforts targeted at the adult spawning stock of the *O. mordax* populations resulted in ecosystem-wide declines in relative abundance and density of this invader. Adult *C. artedi w*ere successfully reintroduced into the experimental lakes and appeared to have colonized the recently devoid *O. mordax* niche space, as observed by consistent *C. artedi* presence in standardized surveys. Removing adult invasives and introducing adult natives should undermine the reproductive potential of *O. mordax*, while increasing the probability of successful *C. artedi* reproduction (Myers et al. 1999, Maunder and Punt 2013, Thorson 2020). Though a more long-term lens is needed to adequately assess ecosystem transition, resilience, and persistence (Carpenter et al. 1995, Holling 2001, Trisos et al. 2020, Mrnak et al. 2023), short-term biotic responses indicated that a predatory and(or) competitive hold has been lifted off *P. flavescens* in Crystal Lake, as observed by a significant increase in their relative abundance, density, and biomass following the experimental manipulation. We also observed a more consistent presence of *S. vitreus* in the pelagic zone of Sparkling Lake beginning in 2022. This may be indicative of a cost-benefit species-interaction change where *S. vitreus* may be shifting from littoral resource(s) to select for the novel native pelagic resource provided by *C. artedi* reintroduction (Krueger and Hrabik 2005; Martin and Vander Zanden 2023). Additional diet and isotopic analyses will be needed to support or fail to support this hypothesis.

Diminished abundances of *O. mordax* in Crystal and Sparkling lakes should lead to reduced or mitigated negative effects on the native food webs of the lakes (Evans and 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 *O. mordax* ecosystem effect strength will be mitigated (Hrabik et al. 1998, 2001, Krueger and Hrabik 2005, Mercado-Silva et al. 2007, Lawson et al. 2015, Gaeta et al. 2015, Mrnak et al. 2023). We hypothesize that the presence of top predators (e.g., *S. vitreus, E. masquinongy, M. dolomieu*) will mediate the interactions between native *C. artedi* and *P. flavescens* and invasive *O. mordax* (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 (> 10yr), we hypothesize that there will be greater *C. artedi* reintroduction success (i.e., relative increase in population growth rate and equilibrium population size) and invasive *O. mordax* 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 sub-adult *O. mordax* not vulnerable to removal gears. 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.

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 *C. artedi* or *O. mordax*, 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). *O. mordax* 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 and Hrabik 2005). Trout Lake *C. artedi* relative abundance and density increased during 2020 – 2022 and then declined in 2023. This was not surprising as inland *C. artedi* population dynamics are highly variable (Parks and Rypel 2018, Martin et al. 2023) and largely driven by predator-prey interactions with the native lake trout *Salvelinus namaycush* (Walbaum, 1972) population in Trout Lake (Martin and Vander Zanden 2023). We do not believe the reduction in Trout Lake *C. artedi* relative abundance in 2023 was attributed to regional factors, but rather represents natural population fluctuation. Regardless of causal mechanisms, invasive *O. mordax* biomass decreased in both experimental lakes and increased in Anderson Lake, while native *C. artedi* biomass increased in both experimental lakes and decreased in Trout Lake (Figure 4). 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 to understand ecosystem shifts in response to perturbation or management intervention (Sikora et al. 2021, 2022, Embke et al. 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. 1995, 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. 1995, 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 *O. mordax* summer pelagic densities during 2020 - 2021. This response occurred following minimal summer vertical gillnet monitoring removals in 2020 (n = 24 *O. mordax* removed) and directed spring mini fyke net removals in 2021 (n = 4 *O. mordax* removed). We believe this drastic reduction in estimated *O. mordax* density following minor removals can be attributed to a hyperabundant population of minnows (i.e., Cyprinidae) throughout Sparkling Lake, most notably emerald shiner (*Notropis atherinoides*). Irrespective of nearshore or offshore location in 2020, *N. atherinoides* were visually present throughout the lake. This more than likely caused backscattered returns to the hydroacoustic unit and thus inflated density estimates (Dillon et al. 2020, DuFour et al. 2021a, 2021b). Despite this, the passive sampling approach of vertical gillnets indicated that *O. mordax* relative abundance has been in decline since 2020. Beginning in 2021, *C. artedi* 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 (Thompson et al. 2021, Rahel 2022, Schuurman et al. 2022). 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). The most common RAD strategy has been to *resist* undesired ecological change through fish stocking and harvest regulation, often with little success (Embke et al. 2022, Feiner et al. 2022, Lynch et al. 2022). *Accept* strategies are less common and include the cessation of stocking species disfavored by current ecosystem dynamics and promoting ones that are favored (e.g., centrarchids; Lynch et al. 2022). The final RAD pathway of *directing* the ecosystem 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)

Panarchy theory provided a framework of nature's rules that accounts for complex ecosystem dynamics such as stability and change (Holling 1973, 2001, Gunderson and 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; conservation, release, reorganization, and growth (Mrnak et al. 2023). Our whole-lake experiments applied panarchy theory to invasive species management (Mrnak et al. 2023). *O. mordax* 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., Lawson et al. 2015; Gaeta 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 *O. mordax* were physically removed from both lakes while adult *C. artedi* 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 *O. mordax* removals and *C. artedi* additions. Given our management action to purposefully push these ecosystems to reorganize (*O. mordax* removals, *C. artedi* stocking) and the likelihood to self-organize around desirable resources and interactions (continued *O. mordax* removals and *C. artedi* stocking), we predict the ensuant growth phase will contain desirable resources and interactions leading to an ecosystem transition that differs from the former *O. mordax* dominant regime (Vander Zanden et al. 1999, Mrnak et al. 2023). In this context, panarchy theory created an ecologically-grounded pathway to *direct* these ecosystem transformations. Our results also suggest that inducing a release phase (*O. mordax* removals) prior to management intervention (*C. artedi* reintroduction) 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 represents a holistic pathway towards 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 oriented rather than based in an ecosystem or food web context (Kitchell et al. 2000, Pikitch et al. 2004, Hilborn 2011, Mrnak et al. 2023, Radinger et al. 2023). Across the globe, there is a critical need for 'food web thinking' (Vander Zanden et al. 1999; Mrnak et al. 2023, Radinger et al. 2023). 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.

2.5 ***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 represents an underutilized novel approach to 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 that allow for the greatest ecosystem service provision potential – a species assemblage 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).

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Author Contributions

J.T. Mrnak, M.J. Vander Zanden, and G.G. Sass conceptualized the experiment; J.T. Mrnak, L.W. Sikora, M.V. Wilkinson, L.M. Feucht, A.M. Mrnak, and G.G. Sass conducted the experimental manipulation and collected data; J.T. Mrnak conducted the analyses and wrote the manuscript. All authors participated in reviewing and editing the manuscript. Multiple funding strings were secured by J.T. Mrnak, M.J. Vander Zanden, and G.G. Sass.

Conflict of Interest Statement

We declare no conflict of interest in this article.

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2.8 Tables

Table 1. Species-survey-specific relative abundance (vertical gillnet CPUE; number fish · net night^{-1}) and density (hydroacoustic estimates; number fish · ha^{-1}) for the experimental (Crystal Lake, Sparkling Lake) and reference (Trout Lake, Anderson Lake) lakes before (2020) and after (2023) rainbow smelt *Osmerus mordax* removals and cisco *Coregonus artedi* introductions. Blank spaces 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	65.0	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		1.9			
	Yellow Perch	VGN	84.0	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	8.0	1.0	-87.5	$F_{1,4} = 126.4$	Yes
		Hydro	1312.32				
	Cisco	VGN		8.67			
		Hydro		54.4			
	Walleye	VGN	1.33	1.67	25.6	$F_{1,4} = 0.5$	No
		Hydro		14.14			
Trout (cisco reference)	Cisco	VGN	173.0	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	10.5	80.33	665.0	$F_{1,3} = 5.8$	No
		Hydro	208.82	461.62	121.1	$F_{1,7} = 21.9$	Yes

2.9 Figure captions

Figure 1. Map of Vilas County, Wisconsin, USA showing experimental (Crystal Lake, Sparkling Lake), reference (Anderson Lake, Trout Lake), and cisco *Coregonus artedi* donor (White Sand Lake) systems.

Figure 2. Photographs of the cisco *Coregonus artedi* stocking efforts for the experimental manipulation. Wisconsin Department of Natural Resources Senior Aquatic Veterinarian preparing *C. artedi* samples for viral hemorrhagic septicemia and whirling's disease testing (a); researchers capturing *C. artedi* via boat electrofishing on the donor lake (White Sand Lake; Vilas County, Wisconsin USA; b); researchers processing captured *C. artedi* for demographic information prior to transfer into the stocking truck (c); stocking truck being filled with recipient lake water (Crystal or Sparking lakes; Vilas County, Wisconsin USA; d); and researcher netting *C. artedi* out of the stocking truck to be stocked into the recipient lake (e). Photograph credit; Joe Mrnak (a and e) and Amber Mrnak (b, c, and d).

Figure 3. Photographs of the invasive rainbow smelt *Osmerus mordax* removal efforts for the experimental manipulation. Crystal Lake (Vilas County, Wisconsin USA) at the beginning of the *O. mordax* removal efforts in 2022 (a); researcher stepping over a set mini fyke net after clearing a 3m x 10m area of >30cm thick ice on *O. mordax* preferred spawning habitat (rock, gravel; b); researcher maintaining ice around a mini fyke net (c); and researcher processing removed *O. mordax* for demographic information prior to transport to a local animal rehabilitation facility (d). Photograph credit; Joe Mrnak (a, b, c, and d).

Figure 4. Whole-lake fish biomass estimates derived from vertical gillnet and hydroacoustics 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 *Osmerus mordax* are shown in red. Native cisco *Coregonus artedi*, yellow perch *Perca flavescens*, and walleye *Sander vitreus* are shown in blue, gold, and black, respectively.

Figure 5. Trends in vertical gillnet catch per unit effort (no. fish · net night^{-1}) and mean ± SE pelagic density estimates (n. fish · hectare^{-1}) from hydroacoustics for cisco *Coregonus artedi*, rainbow smelt *Osmerus mordax*, and yellow perch *Perca flavescens* 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 6. Trends in vertical gillnet catch per unit effort (no. fish · net night^{-1}) and mean ± SE pelagic density estimates (n. fish · hectare^{-1}) from hydroacoustics for cisco *Coregonus artedi*, rainbow smelt *Osmerus mordax*, and walleye *Sander vitreus* in the Sparkling 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 gillnet catch per unit effort (no. fish · net night^{-1}) and mean ± SE pelagic density estimates (n. fish · hectare^{-1}) from hydroacoustics for cisco *Coregonus artedi* in

Trout Lake (*C. artedi* reference), 2020 – 2023. Vertical dashed line indicates the beginning of the experimental manipulation on Crystal and Sparkling lakes.

Figure 8. Trends in vertical gillnet catch per unit effort (no. fish · net night^{-1}) and mean ± SE pelagic density estimates (n. fish · hectare^{-1}) from hydroacoustics for rainbow smelt *Osmerus mordax* in Anderson Lake (*O. mordax* reference), 2020 – 2023. Vertical dashed line indicates the beginning of the experimental manipulation on Crystal and Sparkling lakes.

2.10 Figures

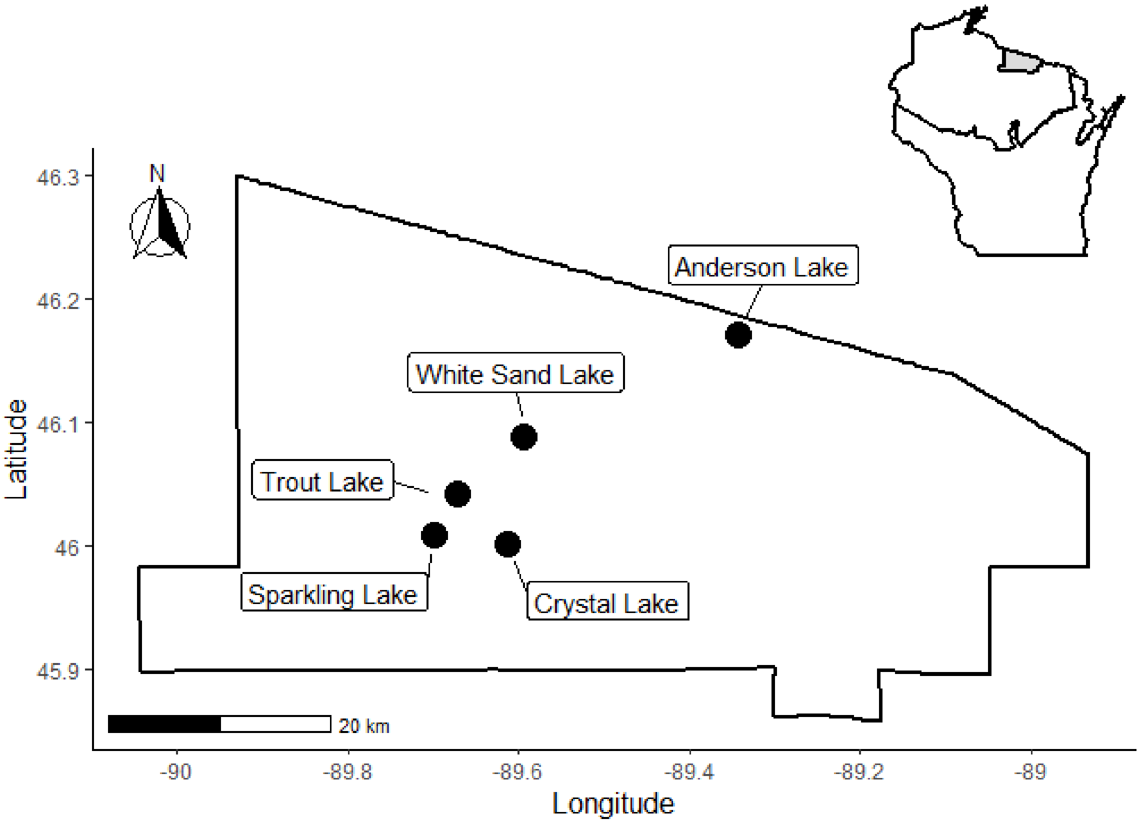


Figure 1.

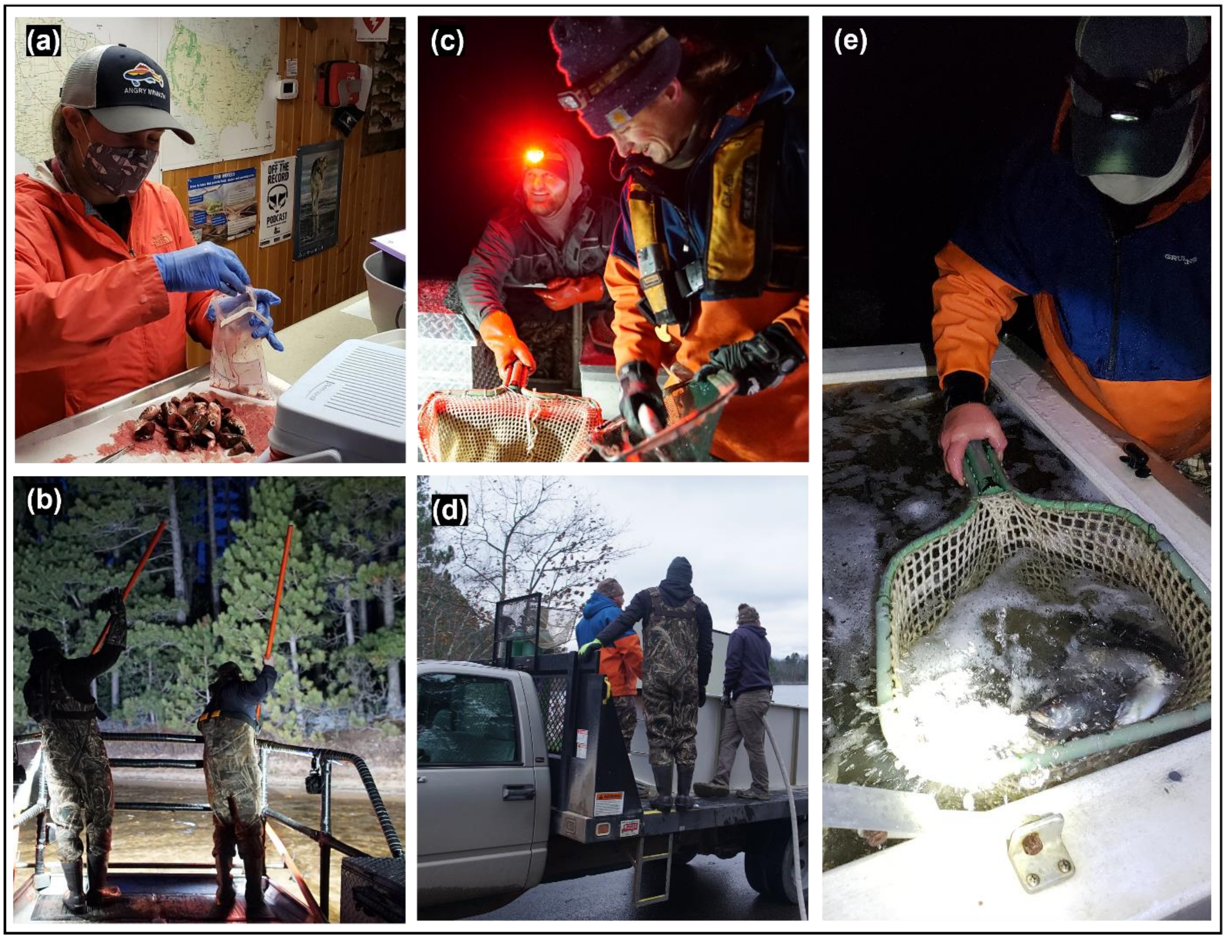
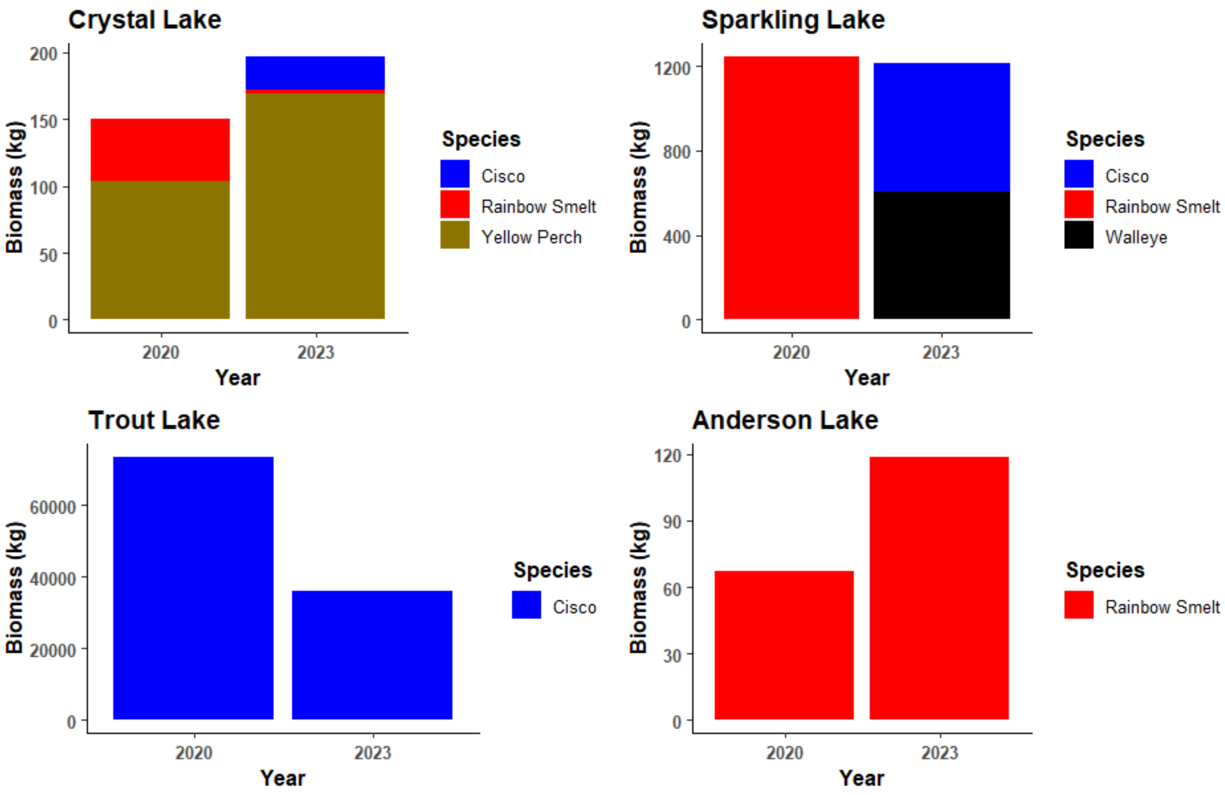


Figure 2.

Figure 3.


Crystal Lake

Sparkling Lake

Trout Lake

Anderson Lake

Figure 4.

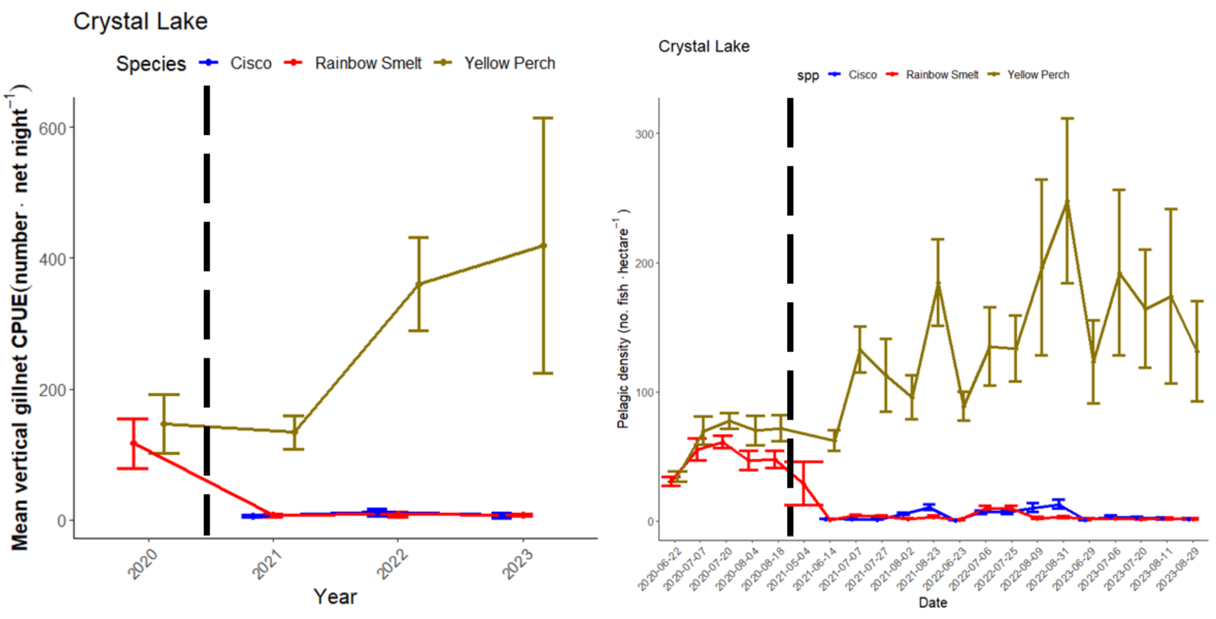

Crystal Lake
Species
Cisco
Rainbow Smelt
Yellow Perch
Mean vertical gillnet CPUE(number · net night^{-1})
600
400
200
0
2020
2021
2022
2023
Year
Crystal Lake
spp
Cisco
Rainbow Smelt
Yellow Perch
Pelagic density (no. fish · hectare^{-1})
300
200
100
0
2020-06-22
2020-07-07
2020-07-20
2020-08-04
2020-08-18
2021-05-04
2021-06-14
2021-07-07
2021-07-27
2021-08-02
2021-08-23
2022-06-23
2022-07-06
2022-07-25
2022-08-09
2022-08-31
2023-06-29
2023-07-06
2023-07-20
2023-08-11
2023-08-29
Date

Figure 5.

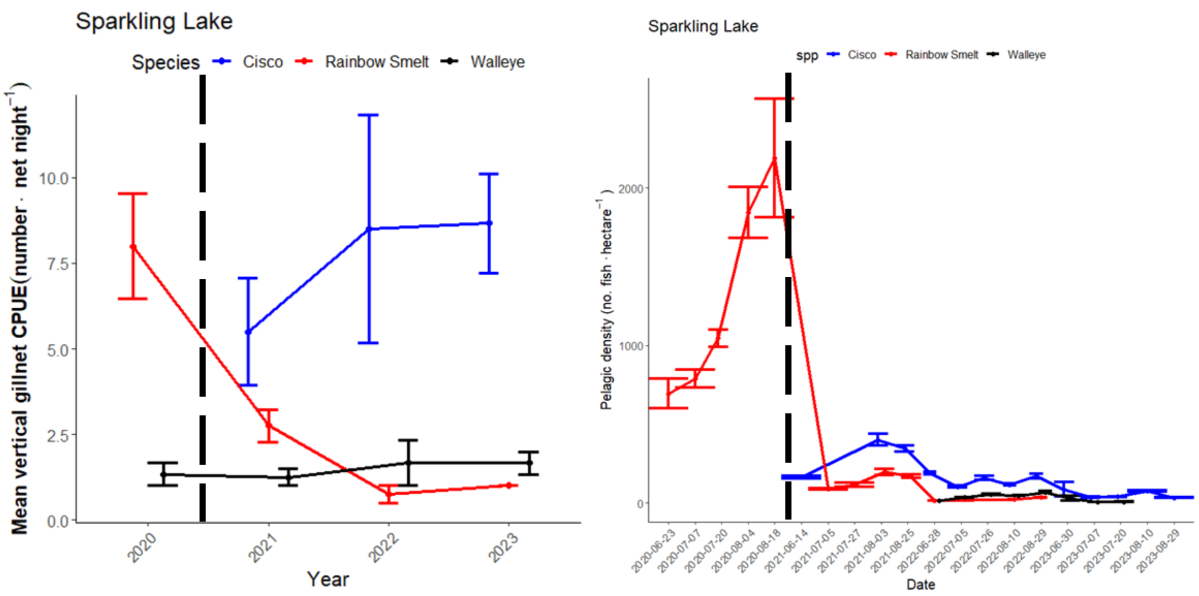
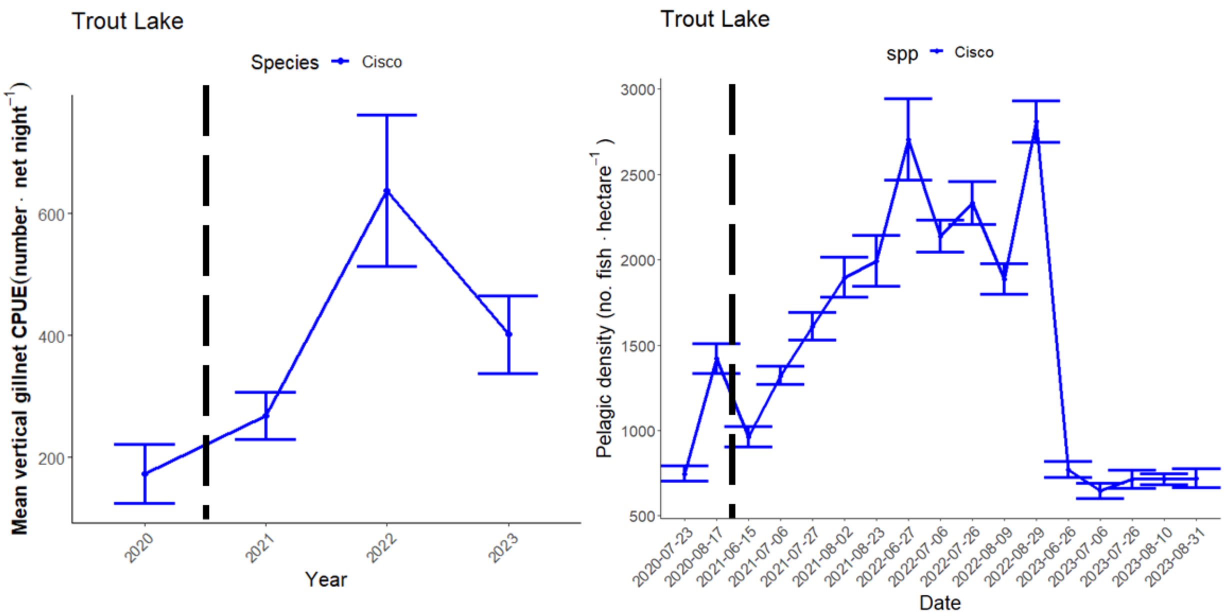

Sparkling Lake
Species
Cisco
Rainbow Smelt
Walleye
Mean vertical gillnet CPUE(number · net night^{-1})
10.0
7.5
5.0
2.5
0.0
2020
2021
2022
2023
Year
Sparkling Lake
spp
Cisco
Rainbow Smelt
Walleye
Pelagic density (no. fish · hectare^{-1})
2000
1000
0
2020-06-23
2020-07-07
2020-07-20
2020-08-04
2020-08-18
2021-06-14
2021-07-05
2021-07-27
2021-08-03
2021-08-25
2022-06-28
2022-07-05
2022-07-26
2022-08-10
2022-08-29
2023-06-30
2023-07-07
2023-07-20
2023-08-10
2023-08-29
Date

Figure 6.


Trout Lake
Species
Cisco
Mean vertical gillnet CPUE(number · net night^{-1})
600
400
200
2020
2021
2022
2023
Year
Trout Lake
spp
Cisco
Pelagic density (no. fish · hectare^{-1})
3000
2500
2000
1500
1000
500
2020-07-23
2020-08-17
2021-06-15
2021-07-06
2021-07-27
2021-08-02
2021-08-23
2022-06-27
2022-07-06
2022-07-26
2022-08-09
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2023-07-26
2023-08-10
2023-08-31
Date

Figure 7.

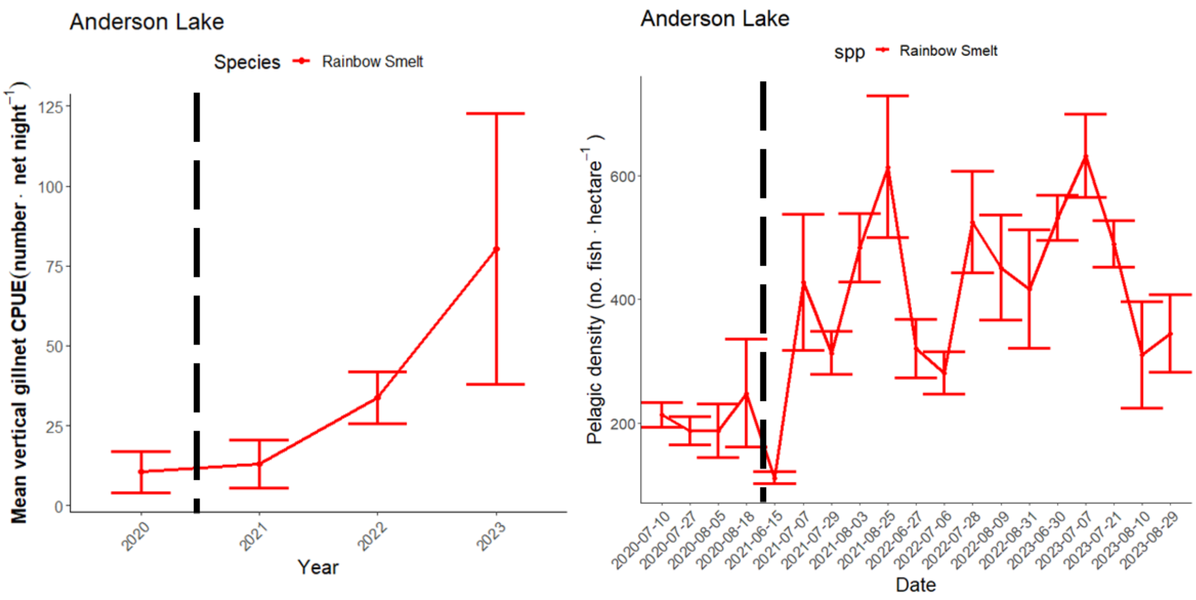
Anderson Lake
Species
Rainbow Smelt
Mean vertical gillnet CPUE(number · net night^{-1})
0
25
50
75
100
125
2020
2021
2022
2023
Year
Anderson Lake
spp
Rainbow Smelt
Pelagic density (no. fish · hectare^{-1})
200
400
600
2020-07-10
2020-07-27
2020-08-05
2020-08-18
2021-06-15
2021-07-07
2021-07-29
2021-08-03
2021-08-25
2022-06-27
2022-07-06
2022-07-28
2022-08-09
2022-08-31
2023-06-30
2023-07-07
2023-07-21
2023-08-10
2023-08-29
Date

Figure 8.

Chapter 3: Diminishing productivity and hyperstable harvest in northern Wisconsin walleye fisheries

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Abstract

Managing fisheries in a changing socio-ecological environment may require holistic approaches for identifying and adapting to novel ecosystem dynamics. Using 32 years of Ceded Territory of Wisconsin (CTWI) walleye (*Sander vitreus*) data, we estimated production (*P*), biomass (*B*), population turnover (*P/B*), yield (*Y*), and yield over production (*Y/P*) and tested for hyperstability in walleye yield. Most CTWI walleye populations showed low *P*, and *B*, and *Y/P* < 1. Yet, production overharvest (*Y/P* > 1) was prevalent among Wisconsin walleye recruitment-based management approaches (natural recruitment [NR], stocking-only, combination). Production, *B*, and *P/B* have declined in NR populations, while *Y* and *Y/P* have remained constant. Walleye *Y* was hyperstable along a production gradient among all management approaches and fishery types (i.e., angling only, angling/tribal harvest combined). Diminishing productivity and hyperstable yield may be jointly contributing to observed walleye declines. We classified lakes into management groups of low, medium, or high vulnerability to harvest based on *Y/P* and *P/B* dynamics and recommend that exploitation may need to decline to maintain or increase the adaptive capacity of CTWI walleye.

Key words: *yield, production, stability, ecosystem-based fisheries management, adaptive capacity*

3.1 Introduction

The ability of fisheries to provision ecosystem services is being threatened by global environmental change (Carpenter et al. 2011; Lynch et al. 2016). Freshwater fisheries are rapidly changing in response to aquatic invasive species (Walsh et al. 2016; Bernery et al. 2022), climate and habitat changes (Myers et al. 2017; Tingley et al. 2019), and overexploitation (Embke et al. 2019; Cooke et al. 2023). These interactions and potential novel ecosystem dynamics may create a match-mismatch between existing management frameworks and the current ecosystem regime (Mrnak et al. 2023). Given the complex and often interconnected nature of these drivers, there is a critical need for more holistic ecosystem-based approaches to achieve sustainable fisheries management (Hilborn 2005, 2011; Paukert et al. 2016; Carpenter et al. 2017; Radinger et al. 2023).

Walleye (*Sander vitreus*) populations are being negatively influenced by environmental change across their native midwestern USA range (Boehm et al. 2022; Feiner et al. 2022b; Hansen et al. 2022; Krabbenhoft et al. 2023). In northern Wisconsin, adult walleye population abundances have declined by ~36% over the past 20 years (Hansen et al. 2015a, 2018; Rypel et al. 2018; Embke et al. 2019). Natural recruitment declines and failures have been identified as the critical bottleneck leading to observed declines in adult abundance, along with persistent exploitation in these harvest-oriented fisheries (Gaeta et al. 2013; Embke et al. 2019; Gostiaux et al. 2022; Krabbenhoft et al. 2023). Ecological stressors leading to natural recruitment declines include invasive species (Mercado-Silva et al. 2007; Bethke et al. 2023; Mrnak et al. 2023), fish species community changes (i.e., increases in centrarchid abundance, bullheads *Ameiurus* spp.; Hansen et al. 2015b, 2017; Kelling et al. 2016; Sullivan et al. 2020; Sikora et al. 2021; Broda et al. 2022; Dassow et al. 2023), and shifting food web interactions leading to increased competition and(or) predation (Hansen et al. 2015c, 2018; Kelling et al. 2016). Abiotic factors associated with walleye natural recruitment declines include climate driven change leading to reductions in walleye thermal-optical habitat (Hansen et al. 2017, 2019; Zebro et al. 2022; Mahlum et al. 2023), phenological variability (Brandt et al. 2022; Feiner et al. 2022a), and physical habitat degradation (Christensen et al. 1996; Sass et al. 2017; Raabe et al. 2020). These abiotic drivers generally pose unique challenges to managers and stakeholders as they are beyond managerial and regional control (Carpenter et al. 2017; Dassow et al. 2022; Embke et al. 2022). Empirical evidence for depensatory recruitment dynamics (i.e., reduced juvenile survival at low adult stock sizes) has also been documented for Ceded Territories of Wisconsin (~northern 1/3 of state; CTWI; Figure 1) walleye populations, likely related to altered predator-prey interactions and environmental change (Sass et al. 2021; Dassow et al. 2023).

The CTWI walleye decline is of critical concern to managers, anglers, and Ojibwe tribes given the cultural, recreational, ecological, and economic importance of walleye in the region (Nesper 2002; Embke et al. 2020; Krabbenhoft et al. 2023). Management actions targeted at resisting walleye decline and(or) restoring natural recruitment have largely focused on stocking extended growth fingerlings to supplement juvenile populations that later on, might increase adult abundance (Jennings et al. 2005; Raabe et al. 2020; Feiner et al. 2022b; Lawson et al. 2022). However, the efficacy of this stocking program remains largely debated (Sass et al. 2022a; Elwer et al. 2023). Instituting conservative harvest regulations for walleye to reduce adult exploitation (i.e., reduced bag limit, increased minimum length limits, protected no-harvest slot length limits) and liberalized regulations to incentivize harvest of other species (e.g., no minimum length limit, increased bag limit for largemouth bass *Micropterus salmoides*) are management actions frequently used to combat walleye decline (Krueger and Hrabik 2005;

Hansen et al. 2015c; Sullivan et al. 2020; Krogman et al. 2022). Whole-lake species removals of direct/indirect predators and(or) competitors is a sporadically used management tool in attempts to restore walleye populations (i.e., centrarchids, Embke et al. 2022; Bullheads *Ameiurus* spp., Sikora et al. 2021, 2022; rainbow smelt *Osmerus Mordax,* Gaeta et al. 2015; Mrnak et al. 2023). Despite management interventions, system stressors are independently and(or) jointly driving Wisconsin walleye populations away from being self-sustaining (i.e., declines in recruitment, recruitment failures; Rypel et al. 2018; Krabbenhoft et al. 2023).

Loss of population sustainability may be attributable to the large role that humans play in the social-ecological systems in which walleye exist (Post et al. 2002; Ostrom 2009; Golden et al. 2022). For example, production overharvest (Embke et al. 2019; Sass et al. 2022b) and angler/tribal (hereafter 'fisher') behavior have been linked to observed walleye declines (Gaeta et al. 2013; Mrnak et al. 2018; Sass and Shaw 2020). A critical assumption of recreational fisheries as social-ecological systems is the potential to self-regulate and maintain a desired regime for the long-term without allowing for instability and population collapse (Post et al. 2002; Ostrom 2009). Walleye recreational and subsistence fisheries were believed to self-regulate in a sustainable feedback loop where fisher effort responds proportionally to population declines and(or) increases (Post et al. 2002; Golden et al. 2022). However, non-linear relationships between fishery dynamics and fisher behavior are prevalent and often create challenges for sustainable fisheries management (Carpenter et al. 1994; Erisman et al. 2011; Johnston et al. 2018; Mrnak et al. 2018; Feiner et al. 2020; Mosley et al. 2022).

Non-linear relationships may occur when fishers maintain catch or yield rates across wide ranges in fish abundance or production, resulting in a curvilinear or asymptotic relationship. These relationships demonstrate hyperstability (i.e., catch rate is maintained during declining abundance, but rapidly declines once a critical, low abundance threshold is reached) or hyperdepletion (i.e., catch rates increase exponentially with abundance; Ward et al. 2013; Golden et al. 2022). Hyperstable relationships may mask population collapse (Harley et al. 2001; Post et al. 2002; Maggs et al. 2016). Many Wisconsin fisheries have demonstrated hyperstability of catch and harvest (Dassow et al. 2020; Feiner et al. 2020; Mosley et al. 2022), including the joint CTWI walleye fishery (e.g., angling catch rates and tribal spearfishing harvest rates; Hansen et al. 2005; Mrnak et al. 2018).

Fish production estimates integrate population vital rates such as abundance, recruitment, growth, and mortality (Waters 1977; Downing 1984; Kwak and Waters 1997) and are specifically suited to study exploited fish populations (Ricker 1946; Waters 1992; Rypel et al. 2015, 2018; Embke et al. 2019). Thus, variables incorporated into fish production estimates are powerful indicators of socio-ecological change (Waters 1992; Valentine-Rose et al. 2007; Benke 2010; Rypel and David 2017; Myers et al. 2018; Rypel et al. 2018) and therefore represent an ecosystem-based approach to fisheries management and assessment (Mrnak et al. 2023; Radinger et al. 2023). Our objectives were to: 1) extend research on CTWI walleye production dynamics (Rypel et al. 2018) by updating previously developed models with 10-y of new data to reevaluate production (*P*; annual rate of new biomass accumulation), biomass (*B*; empirically estimated standing stock biomass), and biomass turnover (*P/B*) rates and relationships among walleye populations supported by different recruitment-based management approaches (i.e., sustained by natural recruitment only [NR]; sustained by a combination of natural recruitment and stocking [C]; sustained only by stocking [ST]; see Cichosz 2022 for more details); 2) evaluate the spatiotemporal dynamics of walleye yield (*Y*; empirical annual biomass harvest estimates) and yield in relation to production (*Y/P*; Embke et al. 2019); 3) assess the relationship between *Y* and

P, and test for hyperstability in walleye *Y* for each recruitment-based management approach and fishery type (i.e., recreational angling only, angling/tribal harvest combined); and 4) classify lakes into management groups of low, medium, or high vulnerability to harvest based upon yield and production metrics. These findings can be used by managers to identify vulnerable fisheries and better inform sustainable management practices, particularly if fishery production is in decline and fisher exploitation is consistent (or increasing).

3.2 Methods

Walleye datasets and fisheries

We used walleye population data sets and angler/tribal member creel surveys conducted by the Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) during 1990-2022 to address our objectives. Information collected as part of these standardized surveys include mark-recapture population estimates for a wide variety of walleye lakes in the CTWI, walleye demographic information (total length, weight, sex, age estimates), and records of catch and harvest for a subset of lakes (see Beard et al. 1997; Mrnak et al. 2018).

Adult mark-recapture walleye population estimates are completed every year on a subset of lakes (stratified random process) in the CTWI (Mrnak et al. 2018; Cichosz 2022). These population estimates are used to establish a 35% adult walleye exploitation limit reference point for the following years harvest season, which results in a less than 1 in 40 chance of exceeding the limit reference exploitation level (35%; Hansen et al. 1991). For WIDNR surveys, large-frame fyke nets are placed in littoral spawning habitat of selected lakes following ice-out and all captured walleye are marked with a year-specific fin clip. Fyke netting continues until about

10% of the adult walleye population is captured and marked based on previous population estimates. Fish were recaptured using an AC boom-electroshocking recapture run during peak walleye spawning. The Great Lakes Indian Fish and Wildlife Commission uses a two-night pulsed-DC electroshocking survey to generate walleye population estimates. Walleye are captured and marked on the first night and then recaptured on the second night. Walleye population abundance was estimated via Chapman's modification of the Petersen mark-recapture estimator (Ricker 1975). Only walleye population estimates with a coefficient of variation ≤ 0.4 were used for analyses (Beard et al. 1997).

All WIDNR and GLIFWC surveys measured all walleye for total length and weight, which we used to develop lake-year-specific length-weight regressions (Embke et al. 2019). Sex was recorded for mature individuals expressing gametes. An age structure (scale or dorsal fin spine) was collected for a subset of walleye based on lake-specific sex and available 13mm total length bins. Walleye age structures were then examined in the laboratory to produce an age estimate and lake-specific age-length key (Embke et al. 2019).

Lake-specific walleye yield was based on reported tribal harvest from GLIFWC and angler creel surveys conducted by the WDNR. Spring tribal spearfishing harvest most often occurs during peak walleye spawning. During spring tribal harvest, nightly permits are issued by tribal agents, where an individual tribal member may obtain more than one permit until the tribal harvest quota is fulfilled for a given lake. Regulations on tribal spearfishing allow for the harvest of any length walleye with only two fish per permit being ≥ 508mm. Lakes that are going to be spearfished are declared daily by the representative tribal agency, and a tribal creel clerk is present at the declared lake the night the lake will be spearfished. The tribal creel clerk issues individual permits to tribal members and records the numbers of hours spent fishing under each permit. Harvested walleye are examined by the tribal creel clerk with total length, weight, and sex being recorded.

Angler creel surveys in the CTWI are conducted by the WDNR based on a stratified roving access design (Hansen et al. 2000). Surveys can only be conducted on a subset of lakes each year. Lakes that have an adult walleye population abundance estimate are prioritized to have a creel survey in the same year (Beard et al. 1997; Hansen et al. 2000; Cichosz 2022). Angler creel surveys begin the first Saturday in May, concurrent with the start of the recreational angler walleye harvest season and end the first Sunday in March of the following year, when the recreational angler walleye harvest season closes. Creel clerks make instantaneous counts of the number of fishers on a lake and conduct interviews on a subset of fishers. During the interview, the creel clerk records hours fished, total catch by species, harvest, species targeted, and demographic information from harvested fish (i.e., total length, weight; Hansen et al. 2000). From this information, walleye angler effort, catch rates, and harvest can be calculated. The standard CTWI recreational angling walleye regulation is a three fish per day bag limit, with a 381mm minimum length limit, a protected 508 – 610mm no harvest slot length limit, with only one fish ≥601mm allowed. Various other harvest regulations are used on specific water bodies based on walleye abundance, individual growth rates, population size-structure, and(or) recruitment status, some of which are summarized in Mrnak et al. (2018).

Production (P), biomass (B), biomass turnover (P/B), yield (Y), and yield over production (Y/P) calculations

Production (*P*), biomass (*B*), biomass turnover (*P/B*), and yield (*Y*) were calculated for each lake-year combination (n=399) following methods established in Embke et al. (2019).

Production was estimated for each lake and year combination with available data by applying the instantaneous growth method to fish from all age-classes from age 5 to a_{max} (maximum age):

$$P_y = \sum_{a=5}^{a_{max}} G_{a,y} \bar{B}_{a,y}, \qquad \text{(eqn. 1)}$$

where a refers to an age class, P_y is total walleye production for year y ($kg \cdot ha^{-1} \cdot y^{-1}$), $G_{a,y}$ is the instantaneous growth rate of cohort aged a in year y. Given we lacked measurements of cohorts in repeated years, we estimated growth rate from consecutive cohorts in the same year (i.e., $\log_e(\frac{\text{mean weight at age a+1,y}}{\text{mean weight at age a,y}})$, $\bar{B}_{a,y}$ is the mean biomass ($kg \cdot ha^{-1}$) classes of cohort during the year, also estimated by substituting age-classes for time. For all analyses, individuals <5 years old were excluded, as immature walleye of these sizes are not reliably vulnerable to capture by fyke nets (Hansen et al. 1991).

To estimate loss of biomass due to fishing, we estimated age-specific yield (harvested biomass; kg) for each lake-year with available data (n=399). For tribal yield, the total number of fish harvested is known, but for angling harvest, the total number of fish harvested is projected by WDNR based on creel data. For both harvest types, a subsample of individual lengths of harvested fish was collected. To estimate yield, we randomly sampled with replacement from the available subset of length data for that lake-year combination and then assigned those values as lengths to the unmeasured fish from that same lake-year combination. Once all harvested fish had a corresponding length, we assigned ages and weights to all fish using the age-length keys and length-weight regressions developed through earlier calculations. From this information, we calculated the number of fish harvested for each age class (H_a) as well as mean weight-at-age of harvested fish ($W_{ha,a}$; kg), which we used to calculate age-specific tribal and angler biomass harvest ($Y_{t,a}$ and $Y_{f,a}$; kg):

$$Y_{t,a} \; or \; Y_{f,a} = H_a * W_{ha,a}, \qquad \text{(eqn. 2)}$$

Total annual biomass harvest (Y_y; kg · ha^{-1}) was calculated by summing $Y_{t,a,y}$ and $Y_{f,a,y}$ for each lake. All biomass harvest estimates were divided by lake-specific surface area (kg · ha^{-1}). We evaluated production harvest as biomass harvested relative to production (i.e., Y/P). See Embke et al. (2019) for detailed methods and open-source calculation code available on GitHub (https://github.com/hembke/Production-and-Biomass-Calculation).

Statistical analyses

Following methods and criteria from Rypel et al. (2018), we grouped lakes into three recruitment-based management approaches to test for differences in our response variables of interest: natural recruitment (NR; lakes with natural recruitment only), combination (C; lakes with some natural recruitment supplemented with stocking), and stocked-only (ST; lakes with no natural recruitment that are solely maintained via stocking). Lake-specific walleye recruitment status was designated based on previous age-0 electrofishing surveys and a GLIFWC flowchart that accounts for each lake-specific recruitment history and the most recent fall age-0 walleye survey (Cichosz 2022; Lawson et al. 2022; Elwer et al. 2023). Further information on CTWI recruitment categories can be found in Cichosz (2022) and Rypel et al. (2018). These recruitment-based designations represent a powerful tool within the joint CTWI walleye co-management framework as managers use them to track trends in a given lake’s walleye recruitment potential. They are also used for setting safe harvest levels based on a lake area v. population estimate regression mixed model (Hansen et al. 2015b; Cichosz 2022). Thus, linking these recruitment designations (i.e., management approach) to various walleye dynamics (e.g., production, yield) may be useful to managers applying policy and regulation across the landscape.

Given that the CTWI walleye fishery is a joint fishery (i.e., recreational angling and subsistence tribal harvest; Mrnak et al. 2018), we grouped lakes into two fishery type categories: angling only and angling/tribal harvest combined. Due to the small number of lakes that experienced tribal harvest and not angling (n = 8), we did not conduct an analysis on tribal harvest only lakes. These distinct fisheries are managed differently where the angling fishery is open access with limited regulation of effort, whereas the tribal spear fishery is based on lake-specific harvest quotas (Mrnak et al. 2018).

P, B, P/B, Y, and Y/P

We created relative frequency histograms for *P, B, P/B,* and *Y/P* by recruitment designation. We used a Shapiro-Wilk test to test for normality in data distributions. We used a mixed effects model with Tukey's post-hoc test to test for statistical differences in mean *P, B, P/B*, and *Y/P* among recruitment categories, where *P, B, P/B,* or *Y/P* were the response variables, recruitment category was the explanatory variable, and lake and year were random effects.

We tested for statistically significant changes over time in *P, B, P/B, Y*, and *Y/P* among recruitment categories using mixed effects regression models where *P, B, P/B, Y,* or *Y/P* was the response variable, year was the explanatory variable, and lake was a random effect. If data were non-normally distributed, values were $\log_{10}$-transformed to achieve normality prior to analysis. Analyses were considered statistically significant at $\alpha < 0.05$.

Hyperstability

We tested for hyperstability (i.e., relationship between fisher yield and adult walleye production) for each recruitment category (i.e., NR, C, ST) and fishery type (i.e., angling only, angling/tribal harvest combined) using the power function:

$$Y = qP^b, \qquad \text{(eqn. 3)}$$

where Y is the respective yield estimate, P is the annual rate of new biomass accumulation, q is a proportionality parameter, and b represents the curvature of the relationship. Hyperstability is evident when $b < 1$, $b = 1$ indicates a proportional relationship, and $b > 1$ indicates hyperdepletion (Feiner et al. 2020; Golden et al. 2022). We tested whether b was significantly < 1 for each recruitment category and fishery type using a one-tailed t-test. Analyses were considered statistically significant at $\alpha < 0.05$.

Lake classification

We classified lakes into management groups of low, medium, or high vulnerability to harvest based on yield over production (*Y/P*) and biomass turnover (*P/B*) dynamics. Vulnerability to harvest should be low when *Y/P* is low (<1) and biomass turnover is relatively quick. Conversely, systems with high *Y/P* (>1) and slow biomass turnover will likely be more vulnerable to sustained or increased harvest.

3.3 Results

P, B, P/B, Y, and Y/P

Production, *B*, and *Y/P* estimates were uniformly non-normal in their distribution among recruitment categories with a right-skew, peaks at low values, and long tails (all Shapiro-Wilk test $P < 0.001$; Figure 2). Production overharvest ($Y/P > 1$) occurred in about 20% (35 out of

179), 41% (76 out of 186) and 30% (10 out of 33) of the lake-years for NR, C, and ST lakes, respectively (Figure 2). Biomass turnover (*P/B*) values were normally distributed in NR (Shapiro-Wilk test $P = 0.34$) and C lakes (Shapiro-Wilk test $P = 0.65$) but were non-normally distributed for ST lakes (Shapiro-Wilk test $P = 0.001$; Figure 2). Across all years, *P/B* had modal peaks at 0.25, 0.20, and 0.15 for NR, C, and ST recruitment categories, respectively (Figure 2). Therefore, walleye *B* is replaced every 4.0, 5.0, and 6.7 years in NR, C, and ST lakes.

Mean walleye *P*, *B*, and *P/B* estimates were significantly greater in NR lakes compared to C and ST lakes (all mixed effects models, Tukey's $P < 0.001$; Figure 3). There were no differences in mean walleye *P*, *B*, or *P/B* values between C and ST lakes (Figure 3). Mean *P* (±SE) in NR, C, and ST lakes was 1.64 (0.08), 1.06 (0.06), and 0.81 (0.11) $kg \cdot ha^{-1} \cdot y^{-1}$. Mean *B* (±SE) in NR, C, and ST lakes was 7.64 (0.35), 6.02 (0.27), and 4.78 (0.51) $kg \cdot ha^{-1}$. Mean *P/B* (±SE) in NR, C, and ST lakes was 0.21 (0.005), 0.17 (0.005), and 0.16 (0.01) y^{-1}. There was no difference in mean walleye *Y/P* between NR and ST, and C and ST lakes. Mean walleye *Y/P* was statistically different between NR and C lakes (Tukey's $P = 0.007$; Figure 3). Mean *Y/P* (±SE) in NR, C, and ST lakes was 0.66 (0.05), 1.03 (0.05), and 0.72 (0.10).

Natural recruitment lakes exhibited significant decline in walleye *P* and *B* over time (mixed effect model $P < 0.001$ and $P = 0.01$, respectively) as did C lakes (both $P < 0.001$; Table 1; Figure 4). The slope for *P* and *B* over time in ST lakes was not different than zero (Table 1; Figure 4). Biomass turnover rate only significantly declined over time in NR lakes ($P = 0.02$) and was not different than zero in C or ST lakes (Table 1; Figure 4). Yield did not change over time in NR and ST lakes. In C lakes, *Y* significantly declined over time ($P = 0.03$; Table 1;

Figure 4). Across all recruitment categories, there was no change in *Y/P* over time (Table 1; Figure 4).

Hyperstability

Hyperstability in walleye yield rates across a gradient of walleye population productivities were observed across all recruitment categories and fishery types (e.g., angling only or angling/tribal harvest combined; all one-tailed t-test $P < 0.05$; Table 2; Figure 5; Figure 6). Hyperstability in the relationship between *Y* and *P* was similar for NR and C lakes ($b = 0.20$ and $b = 0.21$, respectively) and was most pronounced in ST lakes ($b = 0.17$; Table 2; Figure 5). Hyperstability was greater for angling only fisheries ($b = 0.17$) than in joint angling and tribal harvest fisheries ($b = 0.23$; Table 2; Figure 6).

Lake classification

Lakes were classified into management groups of low, medium, or high vulnerability to harvest based on $Y/P = 1$ (production overharvest) and $P/B = 0.19$ (median biomass turnover rate for dataset; Figure 7). The upper right quadrant represents productive fisheries with high levels of harvest while the lower right quadrant represents productive fisheries with low levels of harvest (Figure 7). Low vulnerability to harvest likely occurs when $Y/P < 1$ and $P/B > 0.19$ and was documented for 58%, 28%, and 22% of lake-years for NR, C, and ST recruitment categories, respectively (Figure 7). High vulnerability to harvest occurs when $Y/P > 1$ and $P/B < 0.19$ and was observed for 11%, 29%, and 24% of lake-years for NR, C, and ST recruitment categories, respectively (Figure 7). Medium vulnerability to harvest may occur when $Y/P > 1$ and $P/B > 0.19$ (less frequent) or when $Y/P < 1$ and $P/B < 0.19$ (more frequent; Figure 7).

3.4 Discussion

P, B, P/B, Y, and Y/P

As expected, Ceded Territory of Wisconsin walleye productivity was greatest in lakes with a natural reproduction (NR), recruitment-based management approach. Production and *B* values were significantly greater in walleye populations solely supported by NR compared to populations supported by a combination of natural reproduction and stocking (C) or stocking only (ST). Further, NR lakes had the shortest population turnover time (mean 4.7 y) and least frequent production overharvest (i.e., $Y/P > 1$). Given the decline in NR walleye *P, B,* and *P/B* over time (Figure 4) and the fact that the proportion of NR lakes is declining (i.e., more lakes transitioning to C or ST; Rypel et al. 2018; Raabe et al. 2020), this is of great management and tribal subsistence concern as formerly more robust walleye populations are now declining.

Including 10-y of new data revealed some novel insights between our research and Rypel et al. (2018), but also reaffirmed an ongoing, similar trajectory of decline in productivity of northern Wisconsin walleye populations. Walleye productivity remained highest in lakes solely supported by NR and was right-skewed across all recruitment-based management approaches, indicating that low *P* and *B* populations still dominate the landscape (Rypel et al. 2018; Embke et al. 2019). Although Rypel et al. (2018) did not find a significant change in NR *P* or *B* over time, the non-significant negative slopes (i.e., Table 3 in Rypel et al. (2018)) were similar to the significant negative slopes reported here (Table 1). One critical difference between our study and Rypel et al. (2018) was in *P/B* change over time in naturally reproducing populations. Rypel et al. (2018) reported a significant positive increase in *P/B* over time, indicating that NR population turnover was expected to occur more rapidly in the future (mean NR $P/B = 0.23$, 4.3-y population turnover, positive trend). In our study with 10-y of new data, we found a significant negative slope for *P/B* over time in NR lakes, indicating that population turnover is likely to take more time in the future (mean NR *P/B* = 0.21, 4.7-y population turnover, negative trend). This may suggest that habitats and systems that have historically supported greater walleye production and natural recruitment are losing their capacity to do so (Rypel et al. 2018; Embke et al. 2019). Multiple mechanisms and(or) theories have been postulated to explain walleye productivity and natural recruitment declines including invasive species, climate and habitat changes leading to species interaction shifts, production overharvest, and(or) anthropogenic stressors (Vander Zanden and Olden 2008; Hansen et al. 2015a, 2015c, 2017; Kelling et al. 2016; Sass et al. 2017, 2021; Rypel et al. 2018; Embke et al. 2019).

Production overharvest (*Y/P* > 1) occurred most often in lakes supported by a combination of natural reproduction and stocking (41% of lake-years) followed by ST lakes (30% of lake-years), with NR lakes having the least frequent production overharvest (20% of lake-years). Production overharvest in lakes solely supported by stocking was expected as stocking is conducted to provide opportunities for harvest rather than to reestablish natural recruitment. These results corroborate those in Embke et al. (2019) which reported *Y/P* > 1 for ~40% of all NR and C (combined) walleye lakes in the CTWI. Regardless of the frequency of occurrence, production overharvest is occurring in CTWI walleye populations and may be problematic as sustained *Y/P* > 1 in NR or C lakes may lead to a biomass depletion rate that is insurmountable to overcome with existing management frameworks (i.e., management plans not adjusted for exploitation based on population productivity; Waters 1992; Embke et al. 2019; Elwer et al. 2023). Importantly, *Y* did not change over time in NR and ST lakes, with a slight decline in *Y* in C lakes over time (Figure 4), pointing to changes in biomass harvest as a nonsingular driver of production overharvest in CTWI walleye fisheries (Embke et al. 2019). Rather, the joint effects of declining standing stock biomass and decreasing biomass turnover rates are resulting in larger proportions of remaining biomass being harvested (removed) at similar effort levels (i.e., catchability (q) is increasing; Mrnak et al. 2018; Embke et al. 2019).

There is a critical and challenging management concern with declining walleye productivity and natural recruitment across the CTWI. In lakes supported by a combination of natural reproduction and stocking, mean walleye P has decreased by about 58% from 1.34 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ in 1990 to 0.56 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ in 2021 and P/B decreased from about 0.22 y^{-1} (4.5 y population turnover) in 1990 to 0.09 y^{-1} in 2021 (11.1 y population turnover). Therefore, it currently takes over 6.5 more years to replace C systems walleye biomass now than in 1990, further demonstrating the declining productivity of CTWI walleye populations (Rypel et al. 2018; Embke et al. 2019). Given the decline in lakes categorized as NR and increase in lakes categorized as C (Rypel et al. 2018; Raabe et al. 2020), these CTWI trends are likely linked to regional walleye recruitment declines (Hansen et al. 2017; Zebro et al. 2022; Krabbenhoft et al. 2023). This issue is known (Hansen et al. 2015a; Hansen et al. 2017; Embke et al. 2019), yet a mechanistic understanding for the decline is lacking. Many management actions exist to potentially increase the productive capacity of these walleye fisheries including key habitat restorations (Sass et al. 2017, 2019, 2023; Raabe et al. 2020; Krabbenhoft et al. 2023), food web manipulations reducing competitive and(or) predatory pressures on walleye (Sikora et al. 2021; Embke et al. 2022; Mrnak et al. 2023; Dassow et al. 2023), and(or) reductions or restrictions placed on fisher harvest, particularly as yield approaches production (i.e., management plan adjusts exploitation based on population productivity ; Rypel et al. 2018; Embke et al. 2019; Radinger et al. 2023). A novel approach may be needed as declining biomass turnover is indicative of natural recruitment declines and the erosion of the productive capacity of these fisheries. The safe-operating space concept (i.e., using actions within managerial control to offset drivers outside of managerial control; Carpenter et al. 2017; Hansen et al. 2019) and the Resist-Accept-Direct climate adaptation framework (Dassow et al. 2022; Feiner et al. 2022) provide two promising ecosystem-based fisheries management approaches that may aid in the conservation of walleye populations. Current CTWI walleye co-management may also consider adjusting exploitation based on individual walleye population productivities as the ability to withstand harvest (*P/B*) is variable across lakes and recruitment-based management approaches (Figure 7). Additionally, for the very low *Y/P* lakes (underexploited), management could aim to increase exploitation in an attempt to take pressure off lakes where *Y/P* > 1.

Hyperstability

The CTWI walleye fishery was repeatedly hyperstable in yield rates across a gradient of population productivities for all recruitment-based management approaches and fishery types (i.e., angling only, angling/tribal harvest combined). Unlike previous research that reported greater hyperstability in recreational angler walleye catch than tribal walleye harvest along an adult walleye density gradient (Mrnak et al. 2018), hyperstability in walleye yield was greatest in angling only fisheries than ones with both angling and tribal harvest, indicating that anglers may be more efficient at harvesting walleye at low production values. Regardless, CTWI walleye fisheries do not exist in a sustainable feedback loop where fisher yield rates proportionally respond to increases or decreases in walleye production. These hyperstable relationships between walleye yield and production may occur due to fish aggregating behavior (i.e., spawning, optimal habitat; Rose and Kulka 1999; Dassow et al. 2020), angler/tribal harvester behavior, experience, technology, movement (Post et al. 2002; van Poorten et al. 2016; Tidd et al. 2017), and(or) recruitment variability and depensatory population dynamics (Post 2013; Ward et al. 2013; Golden et al. 2022), which are known to exist for CTWI walleye (Sass et al. 2021;

Dassow et al. 2023; Krabbenhoft et al. 2023). Due to spawning behavior (Mrnak et al. 2018) and Percidae patch dynamics (Mrnak et al. 2021), walleye often aggregate which may make them more vulnerable to harvest (yield), even at low densities (production values; Ellis and Giles 1965; Mrnak et al. 2018). The large number of available walleye lakes in the CTWI provides ample harvest opportunities for fishers (Gaeta et al. 2013; Rypel et al. 2019; Embke et al. 2020). This allows for fishers to seek out lakes that provide acceptable harvest rates and avoid lakes where harvest rates are unacceptable, thus alleviating an ecological pressure from that fishery (i.e., fisher harvest). However, this behavior may ultimately homogenize the CTWI fishery landscape and result in systems being driven towards the point of invisible collapse (i.e., by the time yield rates respond to reduced production, fishery may be too far gone for recovery; Post et al. 2002; Ward et al. 2013; Mrnak et al. 2018; Feiner et al. 2020; Golden et al. 2022). The vast number of CTWI walleye lakes likely buffers against an invisible collapse by providing ample local opportunities compared to Alberta Lakes (Post et al. 2002). Importantly, this buffering mechanism would only occur if fishers self-regulate and thus respond to changes in their yield rates (Ward et al. 2013; Mrnak et al. 2018).

Hyperstability leads to unpredictable responses by fishers to changes in the fish population and creates a management challenge when facing this uncertainty (Fulton et al. 2011; Ward et al. 2013). Based on our findings, hyperstability in catch and harvest rates across abundance gradients, and yield across a production gradient based, appear common for many Wisconsin fisheries (Hansen et al. 2005; Mrnak et al. 2018; Dassow et al. 2020; Feiner et al. 2020; Mosley et al. 2022). Moreover, hyperstable relationships may mask the probability of overfishing (production overharvest) and limit the ability of management intervention to prevent or slow overexploitation when fish population status is evaluated solely on fisheries-dependent data (Carpenter et al. 1994; Fulton et al. 2011; Johnston et al. 2013; Feiner et al. 2020). Observed hyperstability in fisher harvest rates are indicative of consistent exploitation and directed walleye effort across a range of walleye population productivities, despite ample fishing opportunities. Therefore, the hyperstable relationships we identified suggest that fisher behavior may not respond to common management interventions in open access recreational and quota-based subsistence fisheries that do not significantly affect fisher yield rates. Fishers will likely not self-regulate harvest until production significantly declines (if at all), drastically reducing management options for fishery conservation (Allen et al. 2013; Maggs et al. 2016; Feiner et al. 2020). Our results highlight the importance of quantifying relationships between fisher harvest dynamics and walleye production for effective sustainable fisheries management (Beardmore et al. 2011; Post 2013; Mrnak et al. 2018; Feiner et al. 2020; Golden et al. 2022). A better understanding of walleye harvest dynamics is critically needed given that the safe operating space (i.e., Carpenter et al. 2017) of walleye may be compromised by interacting ecological changes resulting in sustained long-term recruitment declines (Hansen et al. 2015b, 2015a) and continual exploitation (Embke et al. 2020). Based on our findings and using the safe operating space concept, exploitation could be adjusted based on population productivity to offset current challenges faced by walleye that are out of managerial control.

3.5 *Management Implications*

Lakes in the CTWI solely supported by natural recruitment appear to be the most resilient fisheries and the least vulnerable to harvest. Indeed, walleye lakes with $Y/P < 1$ and $P/B > 0.19$ currently represent sustainable fisheries (Figure 7). Yet, all fisheries with $Y/P < 1$ are by definition sustainable. Therefore, walleye lakes with $Y/P < 1$ and $P/B < 0.19$ do represent successful sustainable fisheries, but with a lower potential to absorb increases in harvest. Given that the ‘low vulnerability to harvest’ space is dominated by NR populations, it appears that the current walleye co-management system is almost entirely reliant on consistent natural recruitment (Figure 7). When natural recruitment is inconsistent, which has been the case in the CTWI for the last several decades (Krabbenhoft et al. 2023), the current management system has been relatively inflexible to changes in walleye productivity and exploitation. That said, stocking of walleye fingerlings has been used to rehabilitate natural recruitment and to increase abundance (albeit with limited success) and in turn, recreational harvest regulations have been adjusted to reduce exploitation and protect longer and older female walleye. Our results show that the co-management system for CTWI walleye may be improved by adjusting exploitation based on walleye population productivity. Rypel et al. (2018) and Raabe et al. (2020) noted that more lakes are transitioning from NR to C or ST over time. Therefore, NR lakes with $Y/P < 1$ and $P/B > 0.19$ should have the most conservative fisher harvest regulations and greatest monitoring focus to ensure sustainable management where production overharvest remains low and population turnover remains high.

Northern Wisconsin walleye production is in decline and fisher yield (harvest) is not adjusting to this decline. This means that exploitation has remained consistent over time despite declining walleye productivity (i.e., fishers are harvesting the same size slice (yield) out of an ever-shrinking pie (productivity)). Our results suggest that exploitation needs to decline in both fisheries in order to maintain or increase the adaptive capacity of CTWI walleye (i.e., the ability of species to cope with or adjust to ecological change; Thurman et al. 2020). We also recommend that the open-access nature of the recreational angling fishery be evaluated as a more extreme conservation measure if needed. A limitation or reduction in angler effort could potentially reduce total exploitation, but due to hyperstable relationships, the reduction in effort likely needs to be substantial. Similar to Embke et al. (2019), we recommend a transition away from traditional population estimate based management regimes (e.g., Hansen et al. 1991; Beard et al. 1997; Chichosz 2022) to one based on holistic ecological principles, fisher dynamics, and empirical data known to be influenced by ecological change. This framework could use walleye production, biomass, and yield estimates to limit annual walleye yield relative to the production capacity of the walleye population (i.e., restrict $Y/P < 1$; Embke et al. 2019). Indeed, production, biomass, and yield are more sensitive to a walleye's ecological environment than simple population estimate-based approaches (Waters 1977; Downing 1984; Kwak and Waters 1997) and may therefore capture critical ecological processes, habitats, and(or) species interaction shifts influencing CTWI walleye.

Productivity metrics (i.e., P, B, P/B, Y, Y/P) are useful tools for assessing and managing fish populations given future environmental change predictions (i.e., Carpenter et al. 2011). Productivity metrics incorporate key population vital rates (e.g., abundance, recruitment, growth, mortality; Waters 1977; Downing 1984; Kwak and Waters 1997) that are known to be influenced by environmental change and fisher behaviors (Lynch et al. 2016; Hansen et al. 2022; Krabbenhoft et al. 2023), including exploitation (Ricker 1946; Waters 1992; Rypel et al. 2015, 2018; Embke et al. 2019). Our productivity approach that acknowledges the socio-ecological system of walleye fisheries and includes fisheries dependent and independent data may represent a more holistic pathway to sustainable fisheries management (Sass et al. 2017; Mrnak et al. 2023; Radinger et al. 2023). This approach is currently being tested in a 10-yr, whole-lake walleye production overharvest experiment on Escanaba Lake, Wisconsin that includes tribal and recreational harvest components (Sass et al. 2022b). Escanaba Lake is an experimental fisheries research lake with a compulsory angler creel census where we began testing the walleye population response to prolonged production overharvest (*Y/P* = 1.5; 150% of annual production) in 2022. Through this experiment, we will test whether consistent production overharvest negatively influences adult walleye abundance and age-0 recruitment and changes the fish community of the lake. Walleye population responses to the manipulation will also be compared to responses of other walleye populations with the same CTWI angler harvest regulation (i.e. 381mm minimum length limit, 508-610mm no harvest protected slot length limit, only one fish ≥ 610mm allowed, with a daily bag limit of three fish) using standardized long-term monitoring data. Adult abundance, age-0 recruitment, exploitation, and fisher behavioral responses will be compared among lakes to test for similarities and differences to inform CTWI walleye management. Understanding walleye population responses to consistent production overharvest is critical for managing the joint walleye fishery in the CTWI. Knowledge gained from the Escanaba Lake experiment could be used to inform the co-management system for walleye in the CTWI.

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3.8 Tables

Table 1. Mixed effects modeling results testing for change over time in walleye (*Sander vitreus*) $\log_{10}$-transformed production (*P;* kg·ha^{-1}·yr^{-1}), biomass (*B;* kg·ha^{-1}), biomass turnover (*P/B;* y^{-1}), yield (*Y;* kg·ha^{-1}), and yield over production (*Y/P;* y^{-1}) in Ceded Territory of Wisconsin lakes among recruitment-based management approaches (i.e., recruitment categories; NR = natural reproduction, C = combination, ST = stocked-only). Coefficient estimates (intercept, slope) and P-values from mixed effects models are reported. *Denotes statistical significance ($P < 0.05$).

Recruitment category	Intercept	Slope	P-Value
NR			
P	6.72	-0.003	<0.001*
B	6.98	-0.003	0.013*
P/B	0.82	-0.0003	0.024*
Y	1.48	-0.0006	0.64
Y/P	-1.54	0.0008	0.49
Combination			
P	6.57	-0.003	0.001*
B	11.45	-0.005	<0.001*
P/B	0.46	-0.0001	0.19
Y	5.76	-0.0027	0.031*
Y/P	2.14	-0.0009	0.56
Stocked-Only			
P	8.05	-0.003	0.13
B	9.67	-0.004	0.25
P/B	1.13	-0.0005	0.05
Y	-0.98	0.0005	0.77
Y/P	-2.91	0.001	0.52

Table 2. Non-linear modeling results testing for hyperstability in the relationship between adult walleye (*Sander vitreus*) yield ($kg \cdot ha^{-1}$) and adult walleye production ($kg \cdot ha^{-1} \cdot yr^{-1}$) for each recruitment-based management approach (i.e., recruitment category; NR = natural reproduction, C = combination, ST = stocked-only) and fishery type (recreational angling only, angling/tribal harvest combined). Coefficient estimates (± 1SE), degrees of freedom (df, residual df), and P-values from one-tailed t-test for β < 1 are reported. *Denotes statistical significance ($P < 0.05$).

Recruitment Category	Fishery Type	α (± 1SE)	β (± 1SE)	df, residual df	P-value
NR		0.51 (0.10)	0.20 (0.05)	1, 177	<0.001*
C		0.55 (0.07)	0.21 (0.05)	1, 185	<0.001*
ST		0.28 (0.08)	0.17 (0.07)	1, 31	0.03*
	Angling	0.42 (0.10)	0.17 (0.06)	1, 87	0.006*
	Angling/tribal harvest	0.54 (0.07)	0.23 (0.04)	1, 299	<0.001*

3.9 Figures

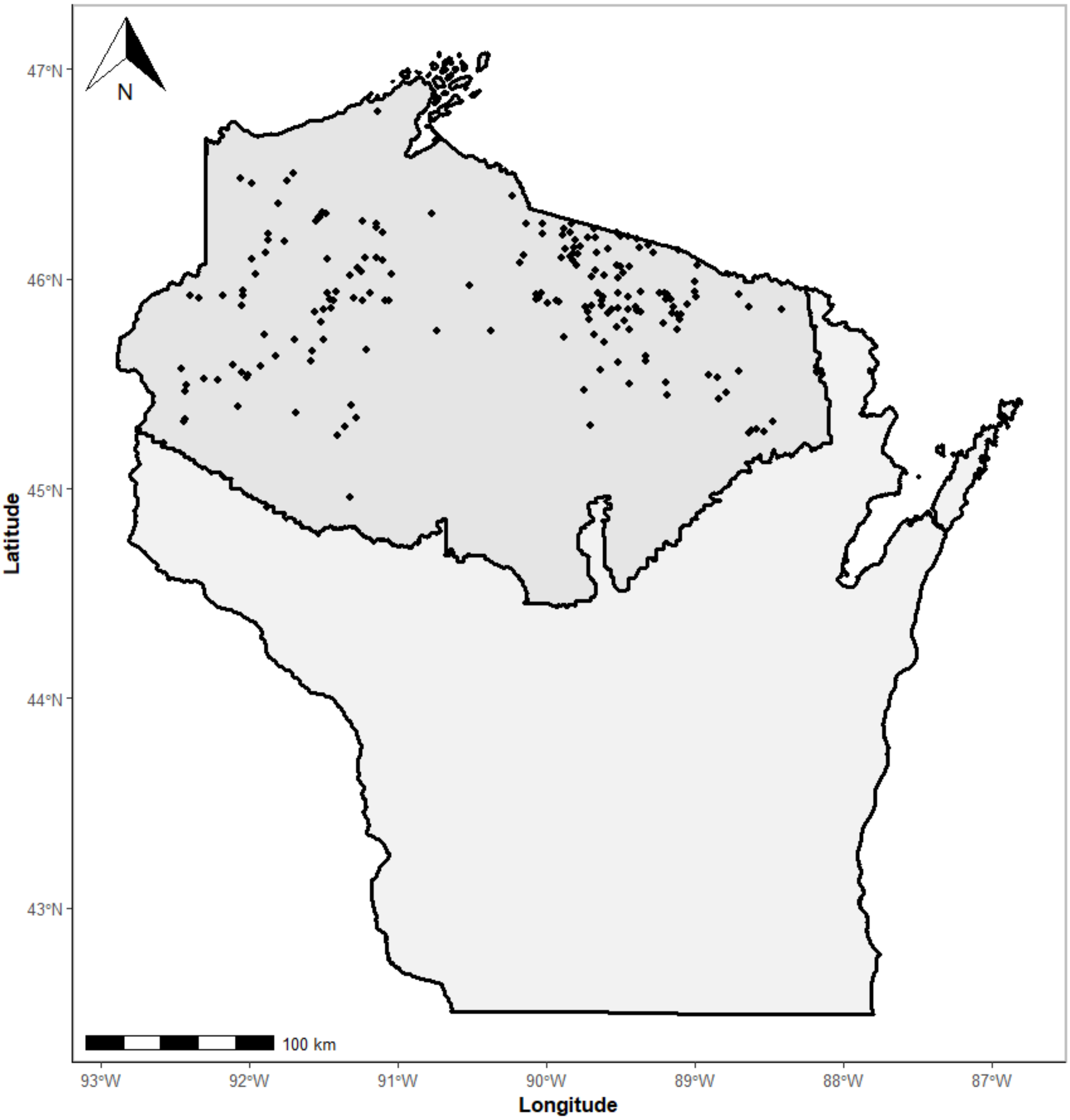

Figure 1. Map of Wisconsin with the Ceded Territories of Wisconsin highlighted in grey. All lakes used in this study are represented by a point on the map. Note that the same lake may be sampled in multiple years.

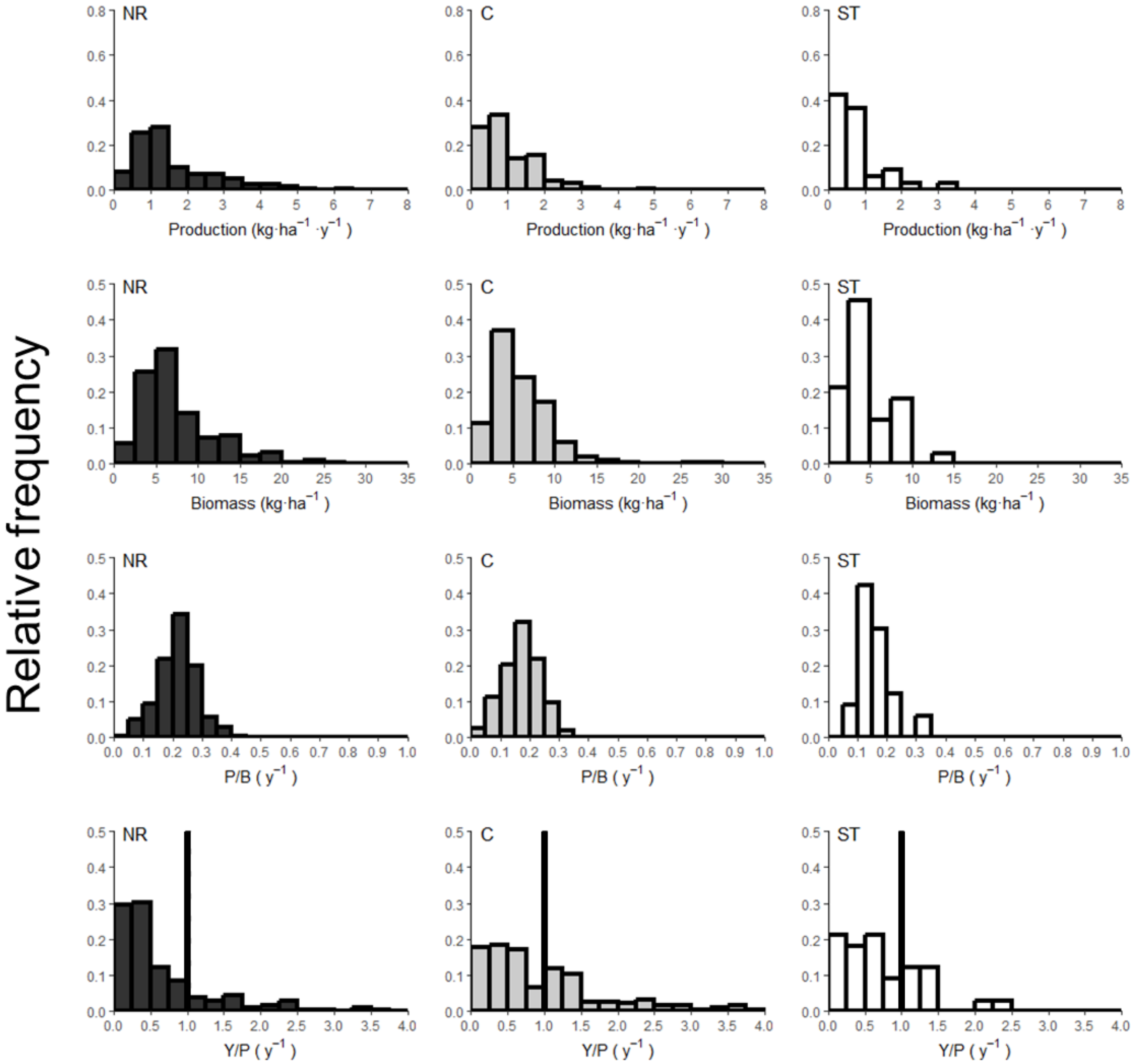

Figure 2. Relative frequency of walleye (*Sander vitreus*) population characteristics in the Ceded Territories of Wisconsin lakes. First row: production (*P;* kg·ha^{-1}·yr^{-1}). Second row: biomass (kg·ha^{-1}). Third row: biomass turnover (*P/B;* y^{-1}). Fourth row: yield over production (*Y/P;* y^{-1}). Recruitment-based management approaches include NR = natural reproduction, C = combination of natural reproduction and stocking, or ST = stocked-only during 1990 – 2022. Solid lines for the yield over production distributions (*Y/P* = 1) indicates the threshold at which biomass harvest exceeds annual production (production overharvest; *Y/P* > 1).

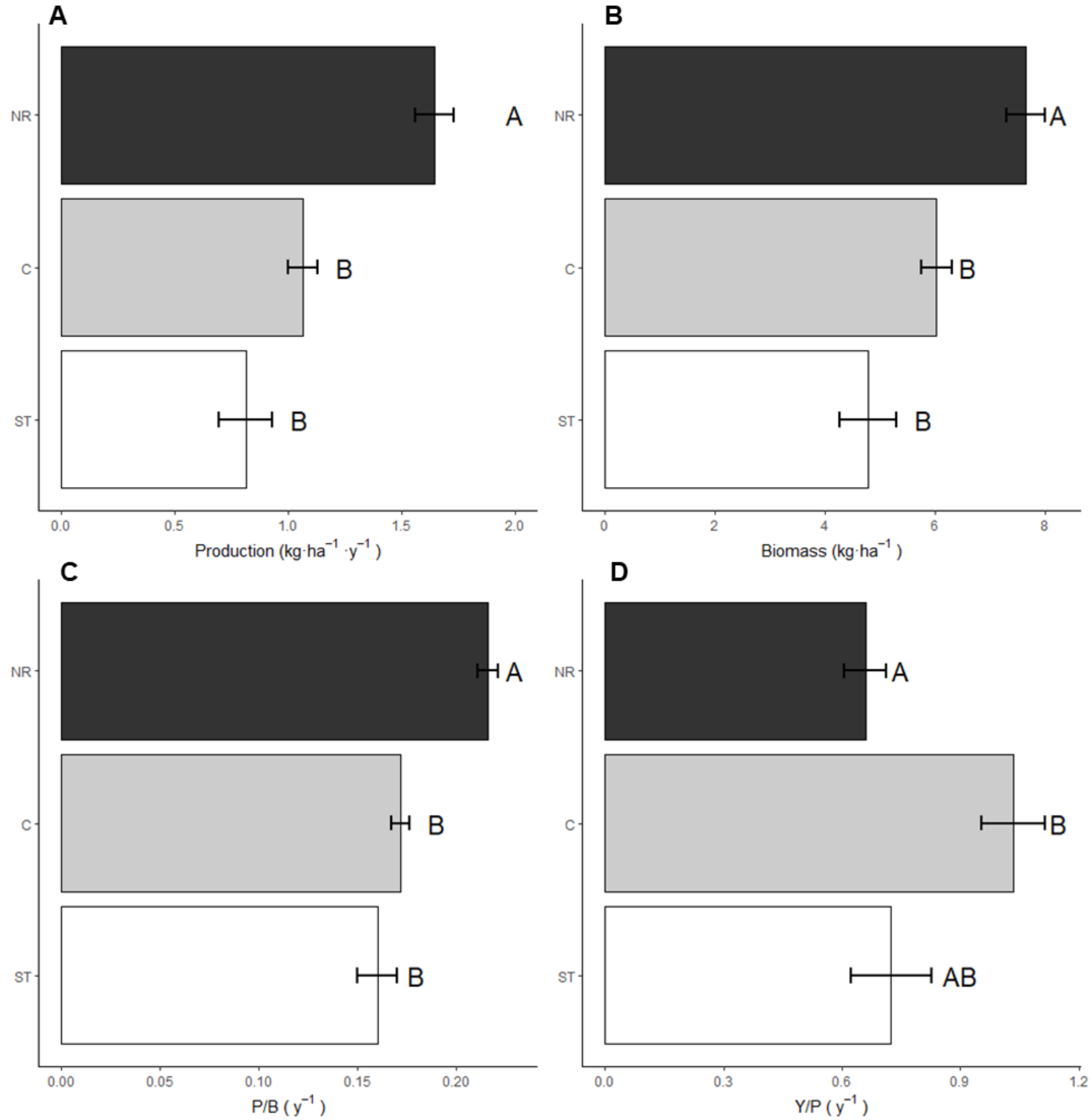

Figure 3. Mean (± 1SE) walleye (*Sander vitreus*) production (P; kg·ha^{-1}·yr^{-1}; panel A), biomass (b; kg·ha^{-1}; panel B), biomass turnover (P/B; y^{-1}; panel C), and yield over production (Y/P; y^{-1}; panel D) in the Ceded Territories of Wisconsin lakes among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = stocked-only) during 1990 – 2022. Different letters indicate means that are statistically different (mixed effect model Tukey's $P < 0.05$ on $\log_{10}$-transformed response variables).

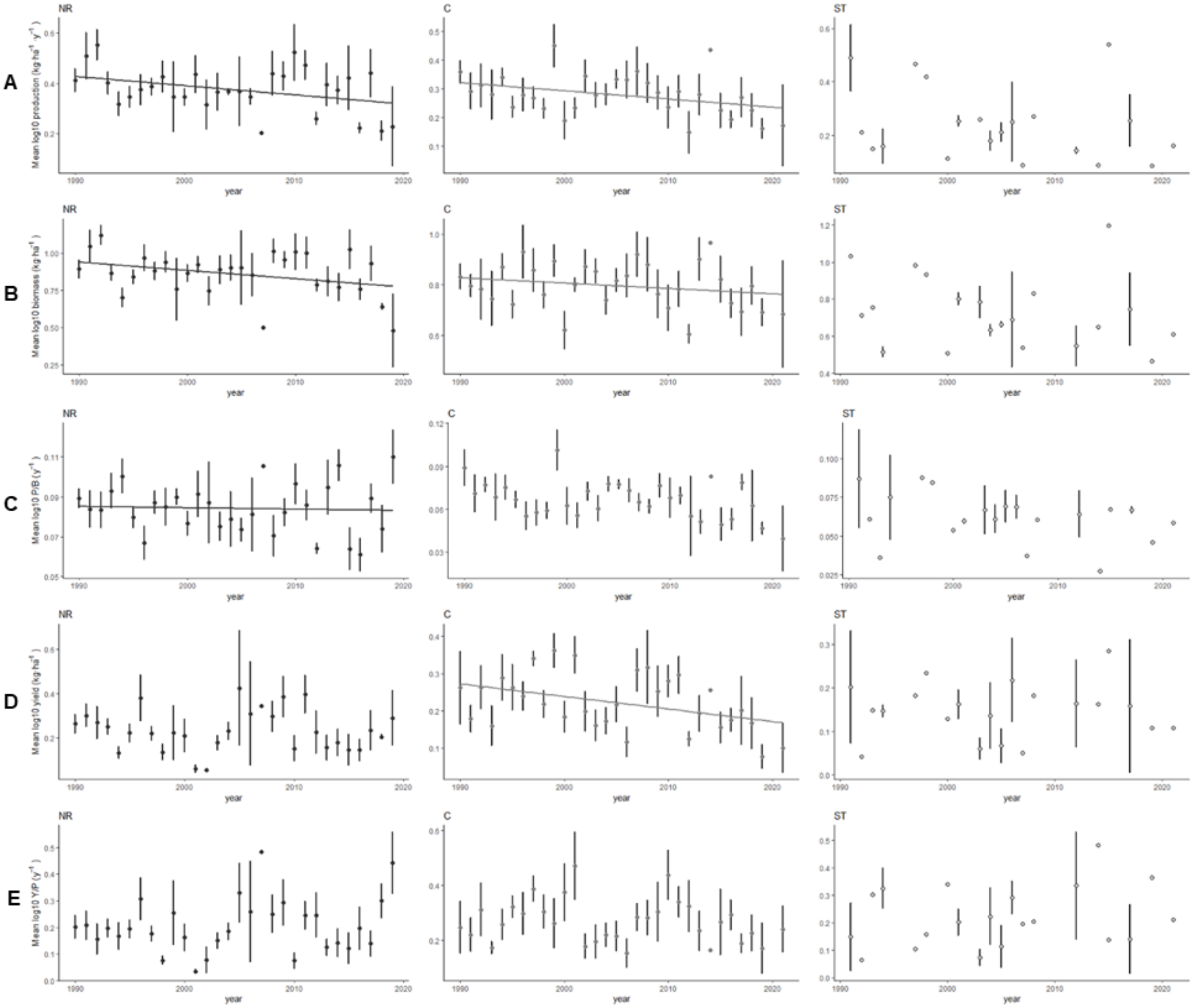

Figure 4. Annual mean (± 1SE) walleye (*Sander vitreus*) $\log_{10}$-transformed production (*P;* $kg \cdot ha^{-1} \cdot yr^{-1}$; row A), biomass (*b;* $kg \cdot ha^{-1}$; row B), biomass turnover (*P/B;* y^{-1}; row C), yield (*Y;* $kg \cdot ha^{-1}$; row D), and yield over production (*Y/P;* y^{-1}; row E) over time in the Ceded Territories of Wisconsin lakes among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = stocked-only) during 1990 – 2022. Best fit regression lines indicate a significant trend (i.e., slope ≠ 0; mixed effect $P < 0.05$)

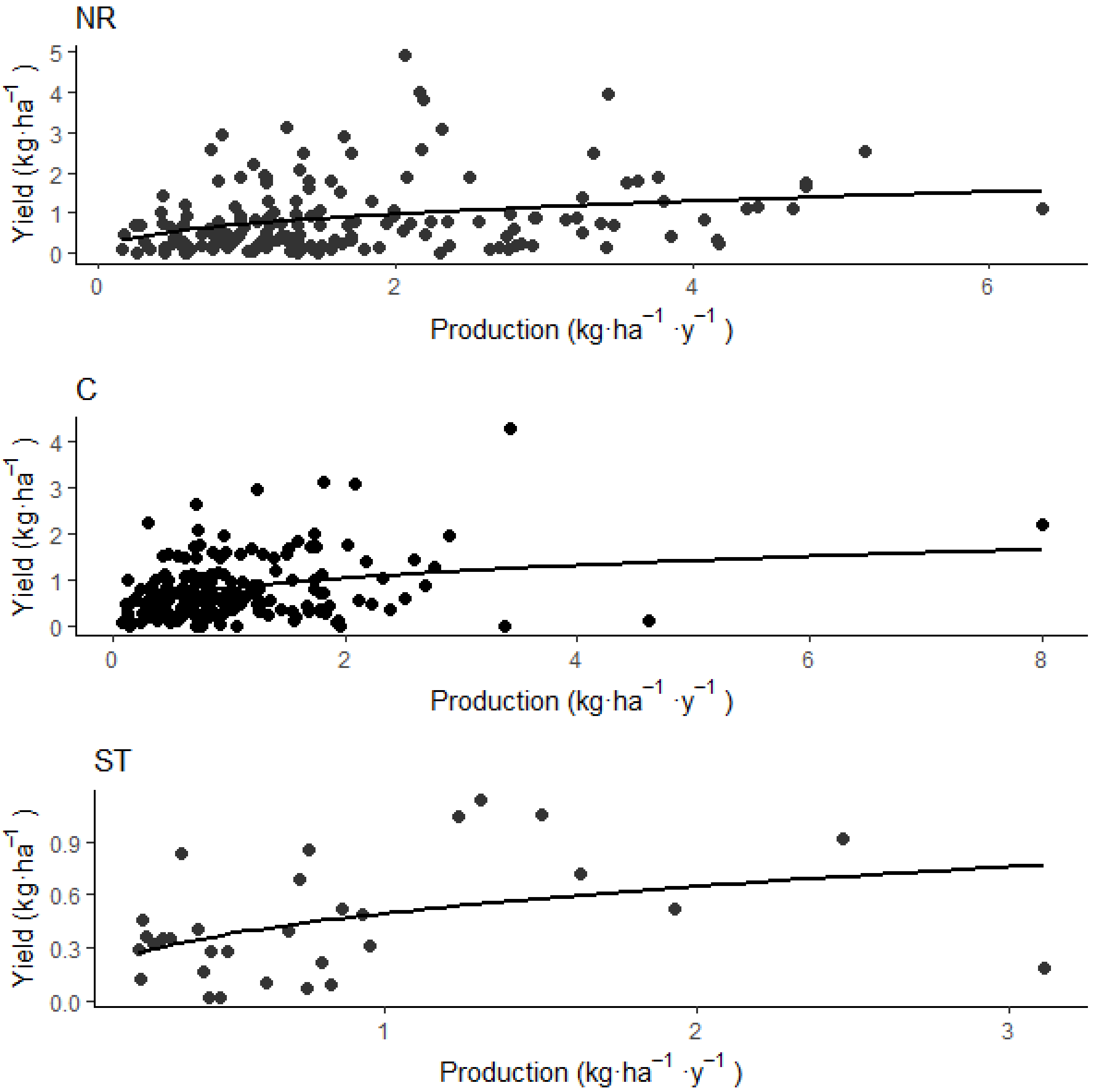

Figure 5. Hyperstable relationships between Ceded Territories of Wisconsin walleye (*Sander vitreus*) yield (Y; kg·ha^{-1}) and production (P; kg·ha^{-1}·yr^{-1}) among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = stocked-only) during 1990 – 2022. Each data point represents a single lake-year estimate.

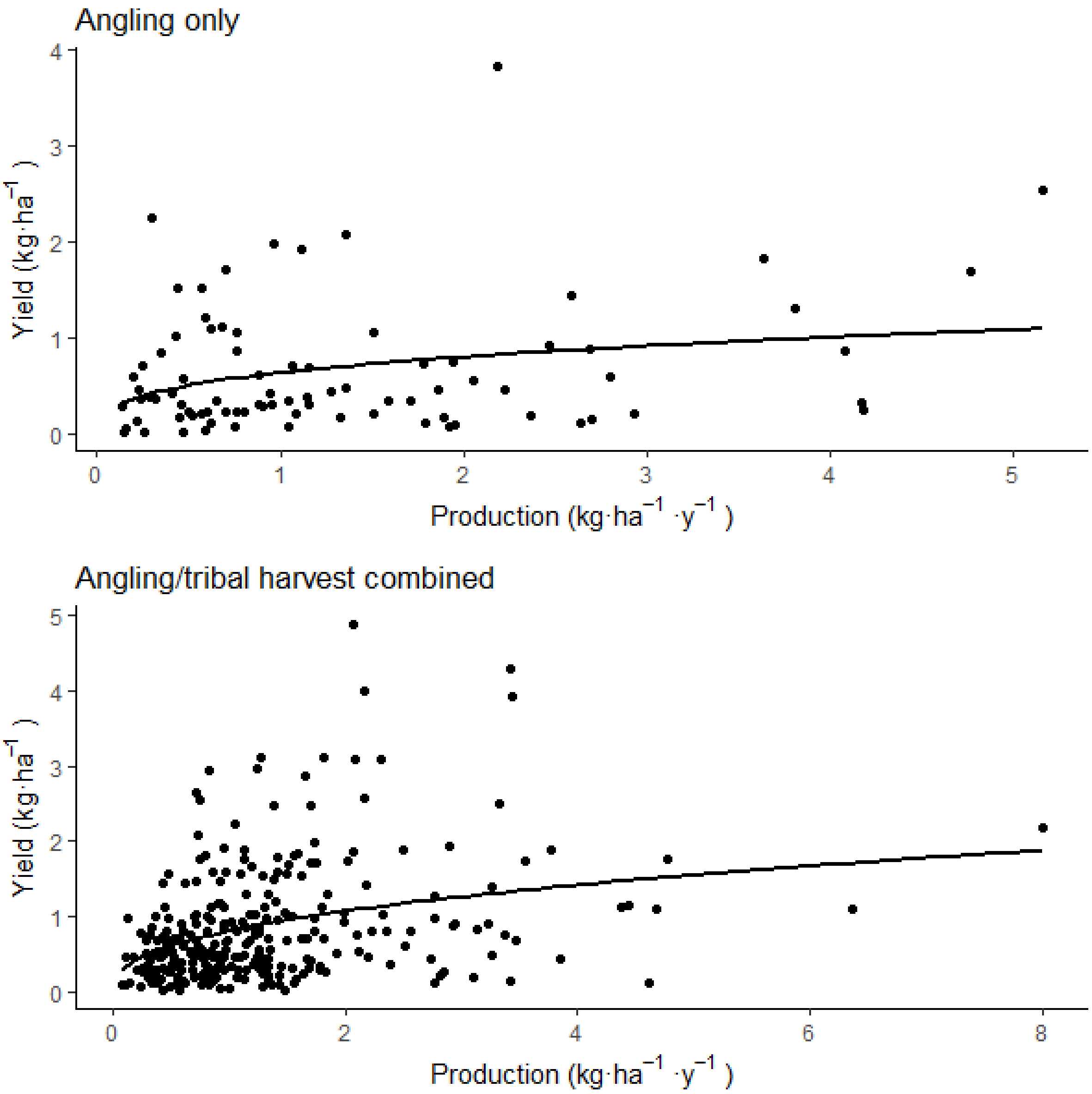

Figure 6. Hyperstable relationships between Ceded Territories of Wisconsin walleye (*Sander vitreus*) yield (Y; kg·ha^{-1}) and production (P; kg·ha^{-1}·yr^{-1}) between fishery type (i.e., recreational angling only or angling/tribal harvest combined) during 1990 – 2022. Each data point represents a single lake-year estimate.

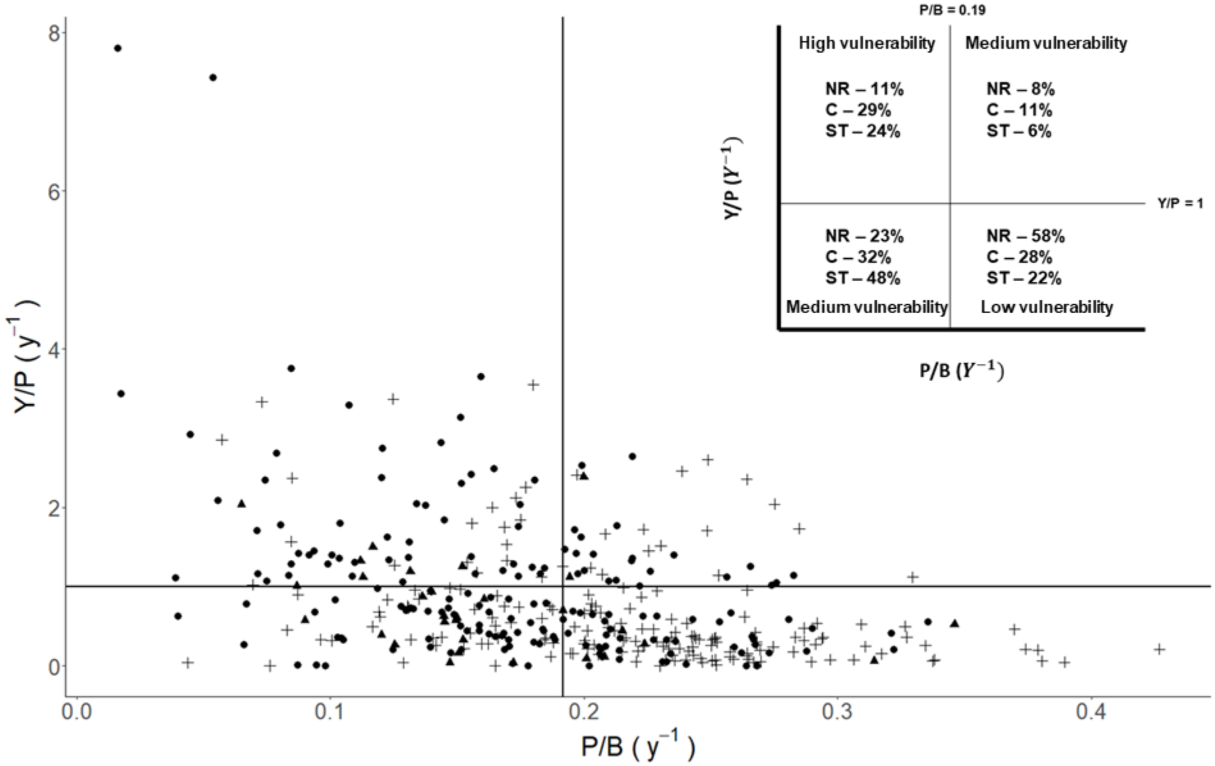

Figure 7. Walleye (*Sander vitreus*) yield over production (*Y/P;* y^{-1}) versus biomass turnover (*P/B;* y^{-1}) for the Ceded Territories of Wisconsin during 1990 – 2022. Each point represents one lake-year combination with the shape of the point corresponding to recruitment-based management approach (i.e., recruitment category; NR = natural reproduction (+), C = combination of natural reproduction and stocking (•), and ST = stocked-only (▲)). The horizontal solid line establishes the 1.0 harvest threshold where 100% of biomass produced is harvested. The vertical solid line shows the overall median biomass turnover rate for the time series (0.19 y^{-1}). The inset identifies vulnerability to harvest (low, medium, or high) and the proportional breakdown for each recruitment category as it relates to the *Y/P* and *P/B* thresholds.

Chapter 4: Hydroacoustic Surveys Underestimate Yellow Perch Population Abundance: The Importance of Considering Habitat Use

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Abstract

When estimating fish population abundance, it is important to recognize that differing habitat use may cause one gear type to be more effective and less biased than another. We generated and compared population abundance estimates (PE) for adult Yellow Perch in Crystal Lake, Wisconsin using a spring mini fyke net mark-recapture survey and summer hydroacoustic surveys. Mean PE from the spring mark-recapture survey was 11,051 adult Yellow Perch (95% CI = 9,878 – 12,541). This mean was 4 – 8.5x greater than the range of mean summer hydroacoustic estimates (mean ± 95% CI = 1,291 ± 312 and 2,912 ± 703). Due to Yellow Perch spawning behavior, we assumed that the spring mark-recapture survey sampled the entire adult population, while summer hydroacoustics sampled the post-spawn pelagic component. Using the mean of all hydroacoustic surveys (PE = 2,492, n = 5), we estimated that about 22% of adult Yellow Perch selected for pelagic habitats post-spawn. Our study emphasizes the importance of evaluating gear bias and has implications for future assessments, particularly when the target species may exhibit multiple habitat preferences within a lake.

Keywords: *habitat use; sampling gear bias; inland fisheries; fisheries management*

4.1 Introduction

Fisheries management relies on accurate estimates of fish population abundance. The accuracy of a population abundance estimate (PE) is a function of how well and how consistently actual fish abundances are approximated. Sampling accuracy for a variety of methods can be affected by habitat complexity (Rodgers et al. 1992; Kruse et al. 1998; Mullner et al. 1998), habitat size (Bayley and Dowling 1993; Kruse et al. 1998; Peterson et al. 2004), fish species and size (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003), fish density (Kruse et al. 1998; Rosenberger and Dunham 2005), sampling effort (Riley and Fausch 1992; Riley et al. 1993; Peterson et al. 2004), and fish behavior (Kubečka et al. 2012; DuFour et al. 2018). All methods have potential error, thus research testing for biases and limitations of specific gears is of high management relevance.

Hydroacoustic surveys are a commonly used method to provide pelagic fish abundance estimates used to inform management (Rudstam et al. 2009; Kubečka et al. 2009). Despite frequent and widespread use, hydroacoustic data can be subject to error and bias before, during, and after surveys. These factors have forced careful consideration before the use of this method and a push for wide-spread standardization (Dillon et al. 2019, 2020; DuFour et al. 2021). For example, survey design and echosounder settings are critical first considerations known to influence abundance estimates (Guillard and Verges 2007; Godlewska et al. 2011). During a survey, error can be incorporated into abundance estimates by including backscattered returns from non-target organisms (e.g., pelagic macroinvertebrates; Dillon et al. 2020), fish movement in and out of insonified zones (Lawson and Rose 1999; Neilson et al. 2003, DuFour et al. 2018), and vessel avoidance (Wheeland and Rose 2015, DuFour et al. 2017, 2018). After a survey, *post hoc* processing and analysis may introduce error depending on analytical decisions being made (e.g., target strength threshold, pulse length determination level, minimum and maximum normalized pulse lengths, maximum beam compensation, and minor- and major-axis angles; Parker-Stetter et al. 2009; Rudstam et al. 2009; Dillon et al. 2019). Though a common and powerful tool for estimating pelagic fish abundance, hydroacoustic surveys are not immune to error and bias, as with all sampling methods.

Yellow Perch *Perca flavescens* are an ecologically important fish that support harvest-oriented recreational fisheries across North America (Gaeta et al. 2013). Adult Yellow Perch can occupy either the littoral or pelagic zones of north-temperate lakes (Krieger et al. 1983; Whiteside et al. 1985; Radabaugh et al. 2010), which may complicate accurate stock assessment. Systems with abundant littoral habitat and prey are known to support robust populations of this popular sportfish (Fish and Savitz 1983; Lyons 1987; Fullhart et al. 2002). Nevertheless, Yellow Perch are often captured in high numbers during vertical gillnet surveys (Kraft and Johnson 1992; Madenjian and Ryan 2011; Yu et al. 2011; Doll et al. 2014), indicating strong pelagic habitat use (Mills and Forney 1988; Radabaugh et al. 2010). Regardless of habitat preferences, most mature Yellow Perch will be present in the littoral zone of lakes during the spawning period (7 – 11°C; Herman et al. 1959; Johnson 1971; Krieger et al. 1983). During the spawning period, male Yellow Perch fertilize egg ribbons released by mature females that are then deposited on coarse woody habitat, macrophytes, or other structures (Becker 1983). Post-spawn, adult Yellow Perch may then remain in the littoral zone or move to more pelagic habitats as both provide (different types and levels of) predation refuge, prey resources, and potentially reduced intra-specific competition (Whiteside et al. 1985; Radabaugh et al. 2010). Dichotomous habitat use by Yellow Perch requires managers to carefully consider what gears to use and when and where to use them in order to properly estimate population abundance.

Within-system, cross-habitat (i.e., littoral versus pelagic) PE studies are infrequent for Yellow Perch. Research on Yellow Perch sampling gears have addressed size selectivity

(Rudstam et al. 1984; Paradis et al. 2008; Doll et al. 2014), catch rates (Mangan et al. 2005; Rydell et al. 2010), and density or abundance differences of various gear types (Isermann et al. 2002; Paradis et al. 2008; Kocovsky et al. 2010; Dembkowski et al. 2012). However, these studies focused on one habitat type within a system (i.e., littoral or pelagic). Kraft and Johnson (1992) examined Yellow Perch between fyke-nets (littoral) and gillnets (pelagic) in Green Bay, Lake Michigan, but only explored size selectivity. To our knowledge, there is no comparative study examining PE differences between habitats on the same Yellow Perch population. Further, there are very few studies comparing fyke net and hydroacoustic surveys, and those that have were focused on riverine salmonids (Johnson et al. 1992; Ranson et al. 1996; Ploskey and Carlson 1999). In our review of the literature, no studies have summarized or quantified the proportion of a single Yellow Perch population representing either littoral or pelagic habitat use.

Differing habitat use by portions of a population may create issues by misrepresenting the “entire” adult population; PEs will be biased if a certain method or gear only targets one habitat for a species that uses multiple habitats. We hypothesized that PEs generated from a spring mark-recapture survey would best represent an adult Yellow Perch population due to their littoral spawning requirements. Conversely, summer hydroacoustic surveys would be biased towards the post-spawn pelagic component of the population. To address our hypotheses, we generated PEs for adult Yellow Perch using a spring fyke net mark-recapture survey and summer hydroacoustic surveys. Our objectives were to: 1) compare differences in PEs between surveys and 2) quantify the percentage of the adult Yellow Perch population representing a littoral or pelagic habitat preference.

4.2 Methods

Study site .—

Crystal Lake (46.001°N, 89.610°W) is an oligotrophic, 46 ha seepage lake in Vilas County, Wisconsin with a maximum depth of 20.5 m (Lawson et al. 2015; Figure 1). Crystal Lake exhibits exceptionally clear water with Secchi depths ranging historically from 6 to > 8 m; during summer 2020, mean Secchi depth was 6.25 m. Crystal Lake is circular with a littoral zone composed of a sandy substrate, few macrophytes, and little coarse woody habitat. Crystal Lake's fish assemblage is dominated by invasive Rainbow Smelt *Osmerus mordax* and Yellow Perch and supports no substantial recreational fishery.

Spring fyke netting .—

Immediately after ice-out on May 11, 2020, six mini fyke nets (0.6 x 1.2 m frame, 0.6 x 4.5 m lead, 6.35 mm stretched mesh) were set in Crystal Lake, nets were distributed around the littoral zone (Figure 1). Nets were never moved and were picked daily following a 24 h soak time. All adult Yellow Perch captured in the fyke nets were marked using a fin clip and total length (mm), weight (g), and sex were recorded. Yellow Perch were defined as an adult if they were ≥75mm since all individuals of that length expressed gametes. This length-at-maturity designation was held for the entire study. The marking and recapture period lasted until ≥ 10% of the population was recaptured, which occurred on May 28, 2020. A PE was then calculated for adult Yellow Perch using the Chapman-modified, continuous Schnabel procedure (Chapman 1951; Ricker 1975). Due to relatively large numbers of recaptures, we calculated 95% confidence intervals (CI) for 1/PE by using t-values from the normal distribution of recaptures. These limits were then inverted to give a 95% CI for the PE (Ricker 1975). Normally distributed catch in our fyke nets indicated that we effectively captured the spawning period (i.e., gradual increase in captures and recaptures, peak catch during mid-survey, gradual decrease in captures and recaptures towards end of survey). Further, adult Yellow Perch sex ratios were consistent and stable over time at ~1.5 females to 1 male suggesting a relatively equal probability of capture between sexes. Although this population estimation procedure assumes the use of multiple gears (e.g., fyke nets and an electrofishing run) to sample all available fish, we could not electrofish Crystal Lake due to low water conductivity (13 µS) that could not be overcome with our gear. Despite this, our mini fyke nets were capable of sampling all lengths of available adult Yellow Perch in Crystal Lake (due to mesh size), reducing the effect of violating this assumption.

Hydroacoustic surveys.—

Adult Yellow Perch (i.e., ≥ 75mm) pelagic abundance was estimated once in June and twice in both July and August of 2020 with hydroacoustic surveys. 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 below -100 dB for S_v data and -70 dB for target strength data. Transmitted pulse duration was set at 0.4 ms. Hydroacoustic surveys were conducted at least 30 minutes after nautical twilight following a standardized and replicable 2,778 m whole-lake transect (NTL-LTER; Magnuson et al. 2006) at a vessel speed of ~5.5 kts (10.2 km/h). Our whole-lake transect surveyed habitat >3 m in depth (Figure 1). We calibrated our system prior to the first survey using a tungsten carbide sphere (38.1 mm diameter) following Foote et al (1987). Observed target strength (-40.00 dB) fell within acceptable limits of the nominal target strength (-40.56 dB).

All acoustic data was analyzed using Echoview software (v5.4). We excluded the top 2 m of the water column from analysis, including the 1 m transducer depth and twice the transducer nearfield range (0.49 m). We applied a ~0.25 m bottom exclusion line to delineate returns from the benthic acoustic dead zone. Data criteria closely followed the recommendations of the Great Lakes Standard Operating Procedures (Parker-Stetter et al. 2009); -55 dB target strength threshold, 6 dB pulse length determination level, 0.5 minimum and 1.5 maximum normalized pulse length, 6 dB maximum beam compensation, and minor- and major-axis angles at 1°.

To inform species composition from the hydroacoustic surveys, we used 24 h vertical gillnet surveys to calibrate (apportion) species-specific estimates using count and length data. For each set, we followed standardized NTL-LTER protocols (Magnuson et al. 1994, 2006) and deployed seven monofilament nets in the deep hole of the lake from surface to bottom (~20.5 m; Figure 1). Vertical gillnets were 3 m x 30m with stretched mesh sizes of 19, 25, 32, 38, 51, 64, or 89 mm. Species-specific average length was then transformed into a target strength following the multi-species model developed by Love (1971). Species classes were assigned using average target strength and then assigned a proportion of total biomass (derived from gillnet catches). We then used single target analyses to estimate sigma values (excluding targets below -55 dB), which we then applied to S_v data to estimate adult Yellow Perch pelagic density for each 200 m segment along the whole-lake transect (n = 14). This segment length was chosen because correlation analyses have shown that 200 m segments are generally not spatially correlated (Holbrook 2011; Heald et al. 2017). We treated each 200 m segment as a replicate such that whole-lake density and associated 95% CI could be estimated. A PE was then calculated by multiplying the mean and 95% CI density estimates by total lake surface area. Since Crystal Lake has very little surface area <3 m deep (Figure 1), we did not correct our whole-lake estimate for the non-insonied waters <3 m.

A bootstrapped (n = 5,000 iterations) Kolmogorov-Smirnov test was used to test for differences in the length distributions of adult Yellow Perch collected between mini fyke nets and vertical gill nets. Our null hypothesis was no difference in the length distributions between gears with an $\alpha = 0.05$.

4.3 Results

Population characteristics and abundance estimates

During spring fyke netting, 886 Yellow Perch were measured for length and weight. Mean ± SD total length and weight were 156.8 ± 35.9 mm and 39.9 ± 29.9 g, respectively. For vertical gillnetting, 336 Yellow Perch were captured and measured during June, July, and August. Mean ± SD total length and weight was 161.4 ± 32.4 mm and 42.6 ± 26.3 g, respectively. Total length distributions of Yellow Perch sampled with mini fyke nets in May did not differ from those sampled during June, July, and August with vertical gillnets (Kolmogorov–Smirnov bootstrap *p-value* > 0.05, $D = 0.07$; Figure 2). The adult Yellow Perch PE derived from the spring fyke net mark-recapture survey was greater than all summer hydroacoustic PEs (Figure 3). The spring fyke net survey resulted in a 4 – 8.5x greater adult Yellow Perch PE compared to summer hydroacoustic surveys.

4.4 Discussion

Seasonal habitat use by adult Yellow Perch can interact with inherent biases of different sampling methods to affect PEs. Our adult Yellow Perch spring fyke net survey produced a substantially larger PE than did our summer hydroacoustic surveys. This corroborates the littoral spawning behavior of Yellow Perch (Becker 1983; Robillard and Marsden 2001) suggesting that mature individuals must be in the littoral zone for a successful spawning event to occur. Yellow Perch spawning requirements support our assumption that the spring fyke net survey targeted the entire available adult population within Crystal Lake unless some mature fish skipped spawning. Post-spawn, Yellow Perch populations may subdivide between littoral and pelagic environments as both habitats provide the species with adequate refuge and resources (Whiteside et al. 1985; Radabaugh et al. 2010). We conclude that our summer hydroacoustic surveys sampled the component of the adult Yellow Perch population that inhabited the pelagic zone. From this, it appears that of all adult Yellow Perch (i.e., ≥75 mm) in Crystal Lake (PE = 11,051), about 22% (PE = 2,492; average of all hydroacoustic estimates) exhibit pelagic habitat use during summer stratification. Inversely, of our estimated 11,051 adults, results suggest that about 78% (8,630) remained littoral (i.e., <3 m) post-spawn.

Although fish move and may go back and forth between habitats (Woolnough et al. 2009), limited deviation among hydroacoustic estimates implies a relatively static subpopulation with minimal immigration or emigration between littoral and pelagic habitats of Crystal Lake. This suggests a one-time movement of adult Yellow Perch from littoral to pelagic habitats post-spawn as opposed to a daily exchange of individuals between littoral and pelagic environments. We reason that our lowest hydroacoustic estimate from June 22, 2020 (PE = 1,291) likely captured the transition of this pelagic component divergence, as the thermocline was just beginning to establish (NTL-LTER *unpublished data*). Greater hydroacoustic survey frequency would provide more clarity on this behavioral transition (i.e., more sampling events between isothermic spring conditions and late summer stratification). A follow up summer (post-stratification) tagging study covering both habitat types would remove uncertainty around the assumption of site fidelity. Further, contemporaneous sampling between gears, habitats, and seasons may help explain our observed differences in adult Yellow Perch PEs.

Sampling gears used in fishery assessments have inherent biases that can lead to inaccurate quantification of population abundances (e.g., Bonar et al. 2009; Pine et al. 2012), which may result in inappropriate management decisions. The mark-recapture fyke net survey used in our study is only applicable to the adult Yellow Perch population during the spawning period. Outside of the spawning period, reduced littoral movement (and thus recapture rates) likely reduces the effectiveness and power of this survey. Given the amount of effort (time) needed to produce an informative mark-recapture PE (i.e., reach ≥10% recaptures), we recommend starting a survey following ice-out. Further, fyke nets can be biased by mesh size, net location, lead length, and frame dimensions (Hubert et al. 2012). These factors should all be considered with the survey objective prior to deployment. Nevertheless, when the species of interest is an obligate littoral spawner and cool-water fish (e.g., Yellow Perch, Walleye *Sander vitreus*, Muskellunge *Esox masquinongy*), a spring fyke net mark-recapture survey is recommended to estimate adult population abundance. This survey design is ideal for some littoral spawners (e.g., Yellow Perch) because the species will be most aggregated during the spawn (Treasure 1981; Fago 1998). Similarly, hydroacoustic surveys can become biased under a plethora of scenarios (Dillon et al. 2019, 2020; DuFour et al. 2017, 2018, 2021), even for an ideal study system like Crystal Lake (i.e., deep/clear, no pelagic macroinvertebrates, simple fish community). For many oligotrophic north-temperate lakes, bias likely occurs when the species of interest exhibits or has the potential to exhibit multiple habitat preferences (e.g., littoral versus pelagic), such as Yellow Perch. Here, the species is not restricted to the survey area at all times and may avoid detection. For example, 78% of the Yellow Perch that appeared to remain littoral post-spawn could have been in the non-insonified pelagic (i.e., top 2 m of water column, bottom 0.25 m of water column) or littoral (<3 m) zones of Crystal Lake. Moreover, vessel avoidance by Yellow Perch could have played a role in our observed PE differences. When the species of interest is an obligate cold- or deep-water fish, such as invasive Rainbow Smelt or native Cisco *Coregonus artedi*, habitat preferences (i.e., oxy-thermal requirements) could require the species to stay within the survey area, making detection avoidance less likely (i.e., Rainbow Smelt and Cisco rarely use epilimnion). Conversely, if the Crystal Lake water level were to decrease by 1 m, the vast majority of littoral coarse woody habitat would be above the water line (NTL-LTER *unpublished data*). This could potentially force the littoral component of the Yellow Perch population to more pelagic habitats and thus become more restricted within our survey arena. Overall, understanding the seasonal behavior and ecology of a target species is critical to accurate fisheries PEs and assessments.

4.5 Management implications

The status of Yellow Perch populations largely remains a "black box" for some state agencies (including the Wisconsin Department of Natural Resources) and researchers due to a lack of standardized sampling protocols, management focus, and limited resources. Outside of Yellow Perch relative abundance indices derived from creel surveys and electrofishing catch-per-unit-effort estimates from general fish surveys (Hansen et al. 1998; Beard et al. 2003; Rypel et al. 2016; Feiner et al. 2020), relatively little is known about Yellow Perch population dynamics and abundance in many north-temperate lakes. Yet, Yellow Perch can be a keystone species, whereby declines in population abundance may foreshadow or cause negative cascading effects on upper trophic level fish recruitment and production (Forney et al. 1974; Hansen et al. 1998; Beard et al. 2003; Sass et al. 2006; Gaeta et al. 2014). Our results suggest that post-spawn, adult Yellow Perch may exhibit variable habitat use within populations and ecosystems. In north-temperate lakes, we recommend that accurately quantifying Yellow Perch populations will require littoral (e.g., fyke netting) sampling gears used during the spring spawning period and the use of pelagic gears (e.g., vertical gill netting, hydroacoustics) to test whether a pelagic component exists. However, we caution the use of hydroacoustic surveys to represent the "entire" adult population when the species of interest can exhibit multiple habitat preferences or occupy non-insonified zones of a lake. Finally, it is worth noting that our objective during these surveys was to produce an informative PE. Thus, we dedicated substantial time and effort to meet that objective. For example, we conducted the spring mark-recapture survey for 17 days before reaching ≥ 10% recaptures. It is unlikely that a management agency with many lakes on their annual sampling rotation could expend this amount of effort. If effort expended in our spring mark-recapture survey is similar to what would be required or used by others, we suggest conducting the spring mark-recapture PE on a less frequent basis (e.g., every 3-5 years). During the non-spring PE years, hydroacoustic surveys could be conducted as they require much less effort (time). Hydroacoustic PEs could then be applied to estimate the littoral component of the adult Yellow Perch population.

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4.8 Figures

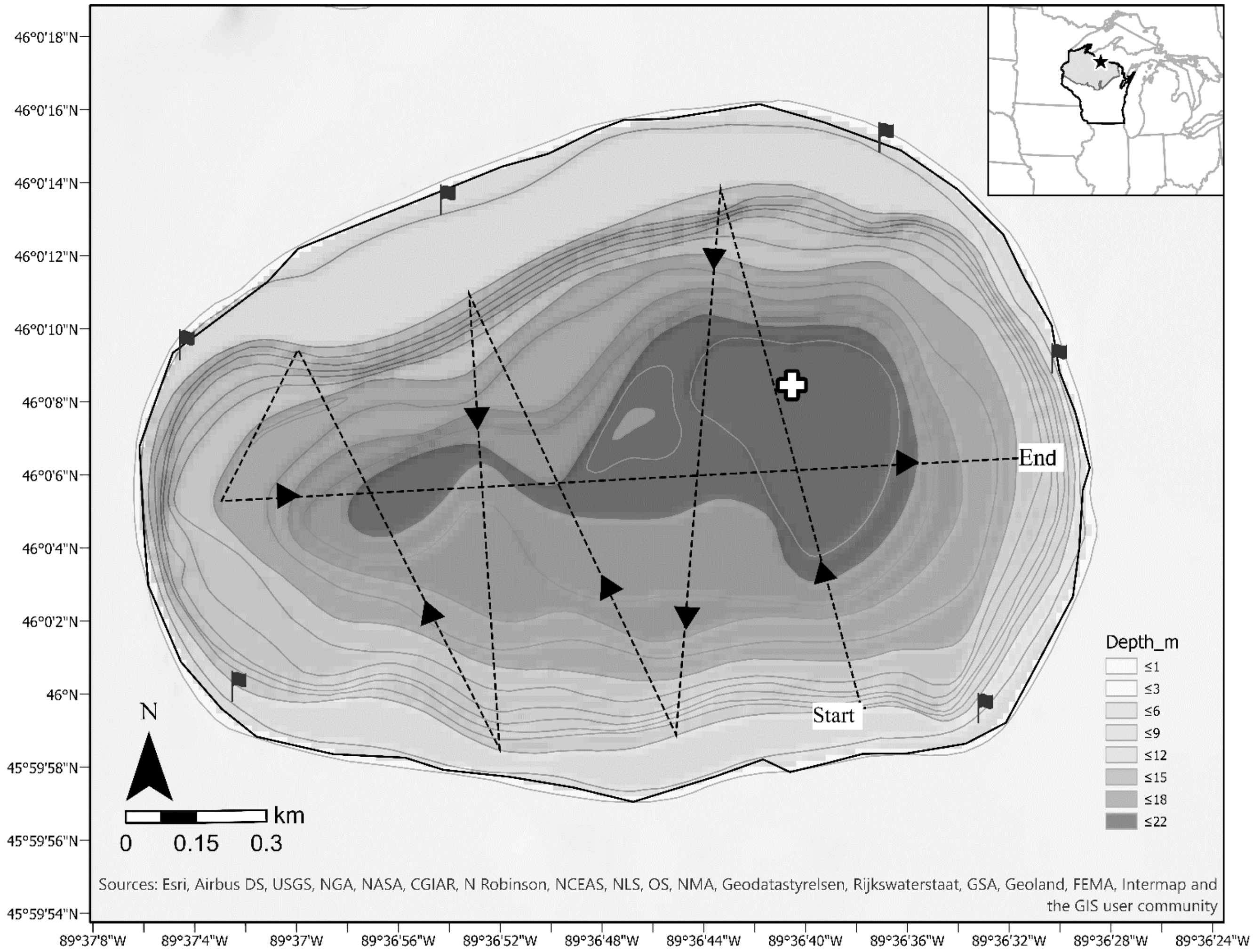

Figure 1. Map of Crystal Lake (Vilas County, WI, USA) with mini fyke net locations (black flag) used for the spring mark-recapture survey and vertical gillnet locations (white cross) and transects (dashed lines) used for summer hydroacoustic surveys to estimate adult Yellow Perch *Perca flavescens* population abundance in 2020.

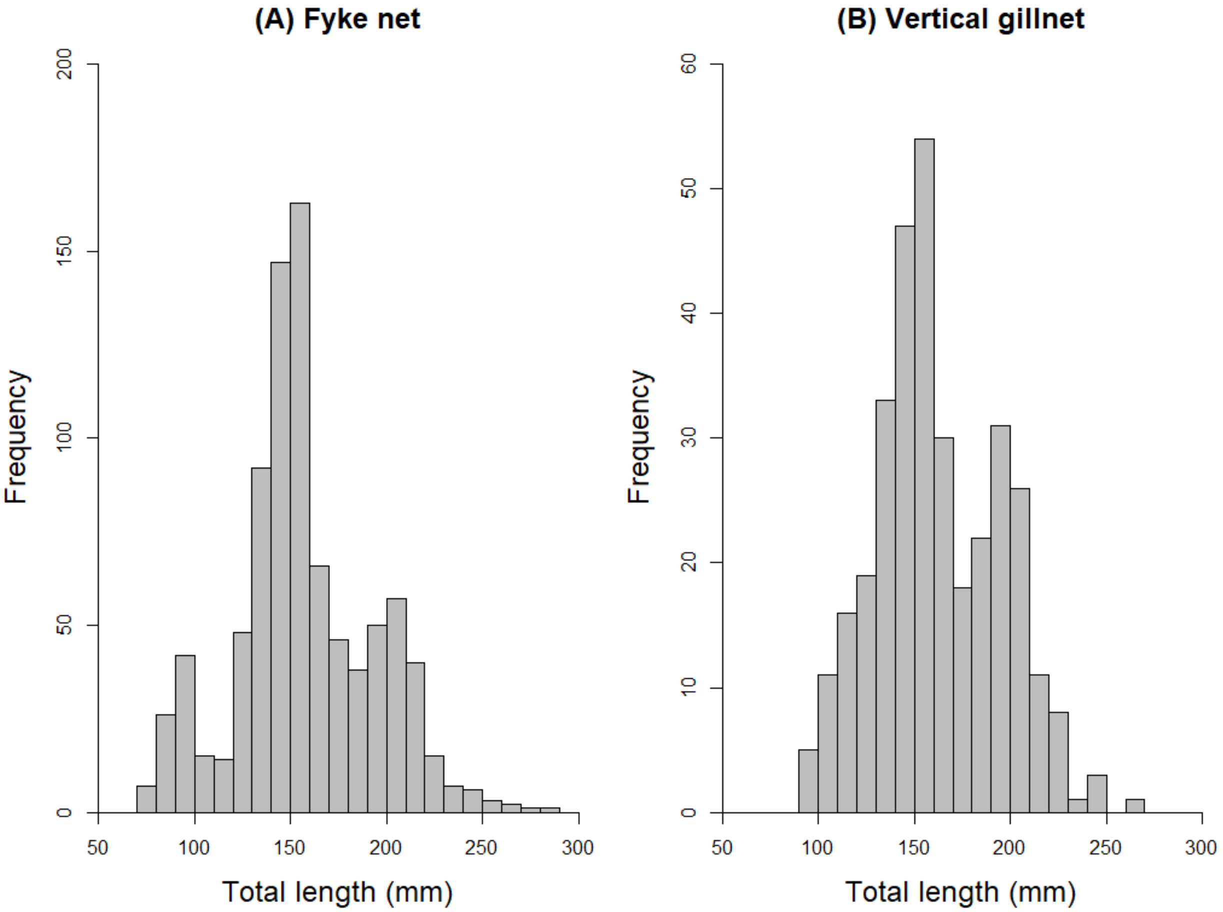

Figure 2. Total length (mm) frequency histograms for Yellow Perch *Perca flavescens* sampled from Crystal Lake (Vilas County, WI, USA) with mini fyke nets during May (A; left) and vertical gillnets during June, July, and August of 2020 (B; right).

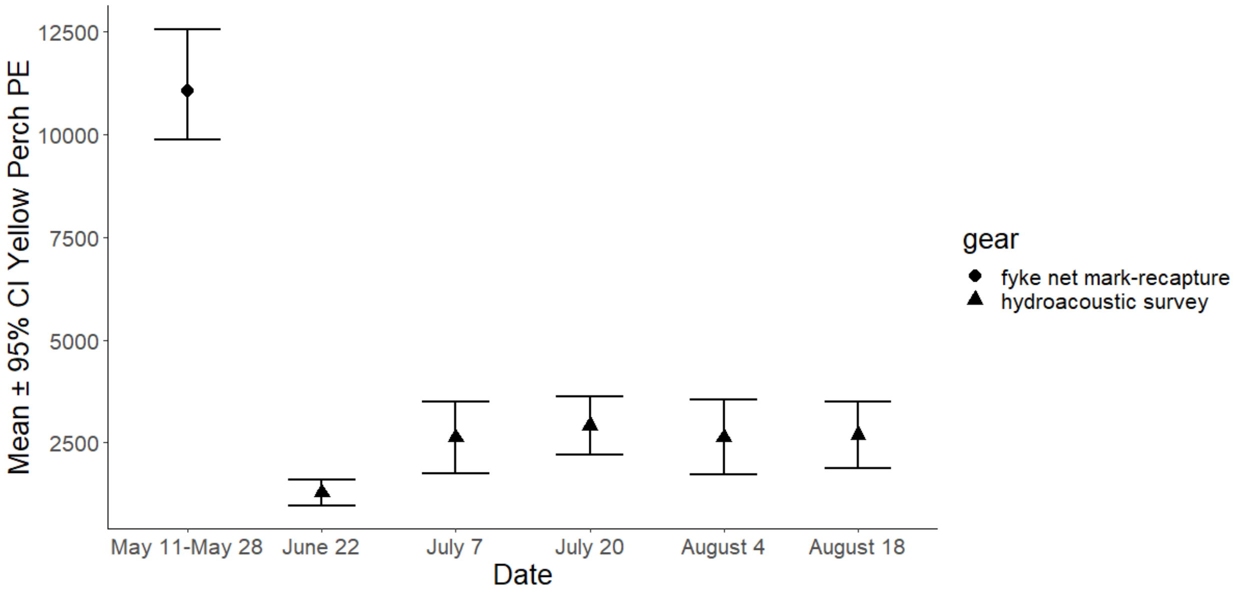

Figure 3. Mean ± 95% confidence interval (CI) for Yellow Perch *Perca flavescens* population estimates (PE) derived via a spring fyke net mark-recapture survey (diamond) and hydroacoustic surveys (triangles) in Crystal Lake (Vilas County, WI, USA) in 2020.

Conclusion

Freshwater ecosystems and the food webs they support are being increasingly altered by global environmental change, including invasive species expansion, loss of native species, climate change, habitat loss, and overexploitation. These shifting ecosystem dynamics present novel challenges for natural resource managers as current dynamics often do not align with current or historical management frameworks. Our ability to manage these highly dynamic resources can be improved through ecosystem-based approaches, such as "food web thinking". Here, consideration should be placed on key ecological processes, habitats, and species interactions rather than focusing on removing single stressors or supporting single species. In **chapter 1**, I reviewed and documented rainbow smelt (*Osmerus mordax*) invasion history, negative ecological effects, and management experiments aimed at control and(or) eradication. I then review and apply panarchy theory to discuss novel control and(or) restoration efforts in a food web context. Through this application of panarchy theory review, I concluded that the success of invasive rainbow smelt control and(or) eradication efforts depended on whether: 1) enough rainbow smelt were removed to devoid their niche space; and 2) devoid niche space was filled with desired native species from remnant populations or through stocking. I suggested that the probability of successful invasive species control and(or) native species restoration may be dependent on the four phases of the nested adaptive cycle (i.e., growth, conservation, release, and reorganization) through management intervention during the release phase and recommended the application of panarchy theory should be viewed as a conceptual extension of efforts to restore ecosystems and(or) manage fisheries using a food web and ecosystem context (i.e., "food web thinking", ecosystem-based fisheries management). In **chapter 2**, I applied the Resist-Accept-Direct (RAD) framework to identify an applicable ecological adaptation strategy and panarchy theory as an ecologically-grounded pathway to purposefully direct ecosystem transformation. I purposefully leveraged panarchy theory during two whole-lake biomanipulations by intentionally forcing a release in the adaptive cycle and directing resource and species availability going into reorganization via manual invasive removals and native reintroductions. In **chapter 3**, I took my applied research beyond historical single-species management frameworks and combined ecologically sensitive production dynamics with fisher harvest to examine walleye stability across the Ceded Territory of Wisconsin. Additionally, I created an ecosystem-based vulnerability to harvest index where Wisconsin walleye fisheries were classified based on yield over production and population turnover rate. This productivity approach that acknowledged the socio-ecological system of walleye fisheries and includes fisheries dependent and independent data represents a more holistic pathway to manage sustainability within these fisheries. In **chapter 4**, I tested whether yellow perch seasonal habitat use interacts with sampling gear biases to explore what managers are truly assessing during a survey. This study emphasized the importance that population estimates (critical for quota/harvest regulation, resource availability for gamefishes, mass-balance or bioenergetic modeling, and(or) long-term modeling) are influenced by the interaction between species movement and survey biases and limitations and that species interactions are temporally and spatially dynamic.

Relevant authored/coauthored manuscripts

I was engaged with many projects beyond the scope of my dissertation during my graduate studies (September 2019 – March 2024). Here, I provide information on other manuscripts I authored and(or) coauthored over this time. This research ranges in emphasis from within system studies and spatially extensive analyses to a diet and feeding book chapter. Overall, this research contributes to our understanding of fish ecology and our ability to manage fisheries in a changing world.

Effect of water velocity and temperature on energy use, behaviour, and mortality of pallid sturgeon *Scaphirhynchus albus* larvae

Mrnak, J.T., L.B. Heironimus, D.A. James, and S.R. Chipps, (2020) *Journal of Fish Biology*, 97(6): 1690 – 1700. https://doi.org/10.1111/jfb.14532

Abstract

Natural reproduction of pallid sturgeon *Scaphirhynchus albus* has been limited for decades and a recruitment bottleneck is hypothesized to occur during the larval stage of development. In this study, we evaluated the effects of water velocity and temperature on the swimming activity, energy use, settling behaviour and mortality of endogenously feeding larvae. The swimming activity of drifting sturgeon larvae (i.e., fish exhibiting negative rheotaxis) increased at low water velocity. In subsequent experiments, we observed greater energy depletion and resultant mortality of larvae in no-flow environments (0 cm s^{-1}) compared to tanks with water velocity ranging from 3.5 to 8.3 cm s^{-1}. The growth rate of drifting larvae was positively related to water temperature (18.7–23.3°C), but reduced growth rate at low water temperature (18.7°C) resulted in protracted development that extended average drift duration by ~4 days compared to larvae reared at 23.3°C. This study provides evidence that cooler summer water temperatures, characteristic of present-day conditions in the upper Missouri River, can reduce larval development and extend both the drift duration and distance requirements of *S. albus*. Moreover, if dispersed into low velocity environments, such as in reservoir headwaters, larvae may experience increased mortality owing to a mismatch between early life stage drift requirements and habitat conditions in the river. Manipulation of water releases to increase seasonal water temperature below dams may aid survival of *S. albus* larvae by shortening the time and distance spent drifting.

Spatial and temporal patterns in native and invasive crayfishes during a 19-year whole-lake invasive crayfish removal experiment

Perelas, K.M., G.J.A. Hansen, C.L. Hein, **J.T. Mrnak**, B.M. Roth, J.R. Walsh, and M.J. Vander Zanden, (2021) *Freshwater Biology*, 66(11): 2105 – 2117. https://doi.org/10.1111/fwb.13818.

Abstract

Understanding where, when, and how native species persist in the face of invasive species-driven ecosystem change is critical for invasive species management and native species conservation.

In some cases, ecological interactions among native and invasive species are spatially structured, and spatial segregation can be a key coexistence mechanism for ecologically similar taxa. We evaluated 19-years of spatially explicit crayfish community data from a long-term whole-lake experiment, which includes 8 years of invasive rusty crayfish (*Faxonius rusticus*) removal followed by 11 years of post-removal data collection. We quantified the within lake spatiotemporal patterns of virile crayfish (*F. virilis*) and rusty crayfish and relate their dynamics to site-level habitat conditions. In response to removal efforts, rusty crayfish catch rates declined by >95%, and native virile crayfish catch rates increased by more than 20-fold. Ten years after ceasing removals, rusty crayfish have stayed at this relatively low abundance, and the virile crayfish population has remained stable. During removal, rusty crayfish abundances decreased non-uniformly throughout the lake. Only after rusty crayfish populations were at their lowest levels did the native virile crayfish population begin to show signs of a recovery. Virile crayfish recovery was highly localized within the lake, and likely influenced by habitat and rusty crayfish abundance. Initially, virile crayfish made the most substantial resurgence in an area of the lake with rocky habitat conditions, but through time their distribution shifted into adjacent suboptimal macrophyte and muck habitats as rusty crayfish became more abundant in nearby areas. In general, when the two species overlapped in space, virile crayfish abundance stayed low, or the population shifted to adjacent areas with fewer competitively dominant rusty crayfish. Our results suggest that habitat heterogeneity allowed virile crayfish to maintain a foothold despite high rusty crayfish densities. Removal efforts led to the recovery of virile crayfish, and spatial segregation facilitated both species coexisting at comparable abundances for a decade. Our results highlight that invasive species control, even in the absence of complete eradication, can benefit native species and that spatially structured interactions can promote coexistence.

Demographic and life history characteristics of Black Bullhead Ameiurus melas in a north temperate USA lake

Sikora, L.W., **J.T. Mrnak**, R. Henningsen, J.A. VanDeHey, and G.G. Sass, (2022) *Fishes*, 7(1): 21. https://doi.org/10.3390/fishes7010021.

Abstract

Black bullheads *Ameiurus melas* are an environmentally tolerant omnivorous fish species that are found throughout much of North America and parts of Europe. Despite their prevalence, black bullheads are an infrequently studied species making their biology, ecology, and life history poorly understood. Although limited information has been published on black bullheads, evidence suggests that bullheads can dominate the fish biomass and have profound influences on the fish community in some north temperate USA lakes. The goal of our study was to provide additional information on black bullhead population demographics, growth rates, life history characteristics, and seasonal diet preferences in a northern Wisconsin lake. Using common fish collection gears (fyke netting, electrofishing), fish aging protocols, fecundity assessments, and diet indices, our results suggested that black bullheads exhibited relatively fast growth rates, early ages at maturity, moderate fecundity, and a diverse omnivorous diet. Due to these demographic and life history characteristics, black bullheads have the potential to dominate fish community biomass in their native and introduced range. Results from our study may inform the management of black bullhead as native and invasive species.

Black Crappie Influence on Walleye Natural Recruitment in Northern Wisconsin Lakes

Broda, S.P., Z.S. Feiner, **J.T. Mrnak**, S.L. Shaw, and G.G. Sass. 2022, *North American Journal of Fisheries Management,* 42(5): 1202 – 1214. https://doi.org/10.1002/nafm.10814.

Abstract

Walleye *Sander vitreus* natural recruitment has declined in northern Wisconsin lakes over time. Several factors have been implicated to explain Walleye natural recruitment declines in Wisconsin, including climate change, Largemouth Bass *Micropterus salmoides* interactions, less desirable fish communities, production overharvest, and depensatory effects on recruit survival. Previous research in other systems has suggested that White Crappie *Pomoxis annularis* negatively influence Walleye recruitment, but interactions between Walleye recruitment and Black Crappie *Pomoxis nigromaculatus* have not been examined. We evaluated trends between Black Crappie and age-0 Walleye relative abundance (catch per effort [CPE]) collected in northern Wisconsin during 1991–2017. Specifically, we tested for (1) trends in age-0 Walleye and Black Crappie CPE over time, (2) a relationship between age-0 Walleye and Black Crappie CPE, and (3) the influence of several abiotic and biotic covariates (including Black Crappie CPE) on age-0 Walleye recruitment. Age-0 Walleye CPE declined and Black Crappie CPE increased significantly during 1991–2017. Within lakes, the relationship between age-0 Walleye and Black Crappie CPE showed a threshold effect such that age-0 Walleye CPE was always low when Black Crappie CPE was high. Of the abiotic and biotic covariates tested to explain variability in the age-0 Walleye and Black Crappie CPE relationship, only Black Crappie CPE was significant. Our results suggest that Black Crappie may negatively influence Walleye natural recruitment; however, we caution that our findings only reveal a pattern and not a mechanistic explanation for negative interactions between the species. Additional research is needed to test for mechanistic interactions between Walleye and Black Crappie and to inform co-management of these species.

Density-dependent and environment influences on juvenile walleye *Sander vitreus* (Mitchill) survivorship in northern Wisconsin lakes

Zebro, L.R., **J.T. Mrnak**, S.L. Shaw, S.R. Chipps, and G.G. Sass. 2022, F*isheries Management and Ecology*, 29(6): 897 – 910. https://doi.org/10.1111/fme.12591.

Abstract

Walleye, *Sander vitreus* (Mitchill), natural recruitment has declined in northern Wisconsin lakes over time. Age-0 and age-1 walleye relative abundance (catch per unit effort; CPE) data from northern Wisconsin (1986–2019) were used to test for abiotic (i.e. lake characteristics and temperature variables) and biotic (age-0 and age-1 CPE) factors influencing age-0 to age-1 walleye mortality. Age-0 to age-1 walleye mortality was elevated at high age-0 CPE and variable at low age-0 CPE, which indicated strong density-dependence. Environmental factors such as spawning and ontogenetic phenology (climate change and ice-off dates), trophic mismatches, and metabolic and consumptive demand influenced age-0 to age-1 walleye mortality less strongly. Elevated age-0 to age-1 walleye mortality at low age-0 CPE supports previous findings of depensatory recruitment dynamics in northern Wisconsin walleye populations. Additional research is needed to address elevated juvenile walleye mortality at low adult stock sizes and/or with declining natural recruitment to inform management decisions.

Evaluating the potential role of predation by native fish regulating the abundance of invasive spiny water flea

Martin, B.E., **J.T. Mrnak**, and M.J. Vander Zanden. 2023, *Journal of Freshwater Ecology*, 38(1): 2187470. https://doi.org/10.1080/02705060.2023.2187470.

Abstract

Predation by native predators can hinder the success of an invasive species. *Bythotrephes*, an invasive zooplankton species, established in Trout Lake, Vilas County, Wisconsin, USA, in 2014. However, by 2020, *Bythotrephes* densities dropped to densities where they were barely detectable. Cisco (*Coregonus artedi*), a native zooplanktivore, is an abundant fish species in Trout Lake and has been shown to significantly prey on *Bythotrephes*. Given the decline in *Bythotrephes*, we asked whether Cisco predation could have played a role in the observed decline in *Bythotrephes* densities. We modeled Cisco consumption of *Bythotrephes* using bioenergetic modeling and *Bythotrephes* production from a production to biomass model. The model results suggested that Cisco consumption was lower than *Bythotrephes* production during the early years of the invasion, but since 2017 Cisco consumption exceeded *Bythotrephes* production and has likely played a role in the observed *Bythotrephes* density declines. Our study provides quantitative context for predation on *Bythotrephes*, and alongside other studies, suggests native predators can control *Bythotrephes* densities. Leveraging predation by native species could be an invasive species management tool, so it is important to synthesize and document cases in which predation may control or reduce impacts of invasive species.

Seasonal habitat use of yellow perch *Perca Flavescens* in a north-temperate lake

Feucht, L.M., L.W. Sikora, G.P. Shay, G.S. Sass, and **J.T. Mrnak**. 2023, *Aquaculture, Fish and Fisheries*, 3(4): 380 – 387. https://doi.org/10.1002/aff2.123.

Abstract

Knowledge of species-specific fish biology, ecology, and habitat use is critical for informing science-based management. Yellow perch *Perca flavescens* are an ecologically and recreationally important fish species. Yet, for many north-temperate systems (e.g., inland lakes of Wisconsin), little is known about yellow perch seasonal habitat use and ecology. We characterized yellow perch seasonal spatial distribution, size–structure, and condition between littoral and pelagic habitats in Crystal Lake (Vilas Co., WI) during the open water period of

2021. Seasonal spatial distribution and population size–structure were characterized by contemporaneous sampling in littoral and pelagic habitats using mini-fyke nets and vertical gill nets, respectively. Relative abundance estimates for yellow perch in the littoral zone were greatest during early spring and declined throughout the open water season. Yellow perch pelagic relative abundance estimates were lowest in spring, peaked at the onset of stratification, and then declined and remained relatively consistent throughout the open water season. In general, yellow perch population size–structure and condition were greatest in the pelagic zone. Our findings suggest that after spring spawning, larger yellow perch prefer/select pelagic habitats, while sub-adults and juveniles prefer/select littoral habitats, potentially resulting from increased predator refugia and(or) resource availability. Our results emphasize the importance of evaluating gear and fishery assessment bias, particularly when the target species may use a range of habitat types within a system.

Evaluation of survival and cost to harvestable age of stocked fall fingerling walleye (*Sander vitreus*) in Northern Wisconsin Lakes

Elwer, B.M., J.A. VanDeHey, S.L. Shaw, L.W. Sikora, **J.T. Mrnak**, and G.G. Sass. 2023, *Fisheries Research*, (266): 106758. https://doi.org/10.1016/j.fishres.2023.106758.

Abstract

Walleye *Sander vitreus* are culturally and recreationally important in Wisconsin, USA and have experienced population declines in some lakes due to reduced natural recruitment. In 2013, the Wisconsin legislature implemented the Wisconsin Walleye Stocking Initiative, a statewide rehabilitation effort to help declining walleye populations through increased stockings of fall fingerling walleye (150–250 mm). Our objectives were to: (1) test for differences in natural mortality (*M*) of stocked walleye among stocking densities (12.4, 24.7, 37.1 fish/ha), lake recruitment status (some natural recruitment or no natural recruitment), and lake conductivity (surrogate for lake productivity); (2) estimate cost to harvestable age (i.e., age-4); and (3) compare predicted adult walleye abundance among lakes across various stocking densities in relation to Wisconsin walleye adult abundance standards (i.e., naturally reproducing population ≥7.4 adults/ha, "fishable" population ≥ 3.7 adults/ha). Fall fingerling stocked walleye M was lowest in lakes with some natural recruitment, with medium-low and high conductivities, and stocked at 24.7 and 37.1 fish/ha, respectively. Using a mixed-effects model, fall fingerling M was negatively related to stocking density but not lake recruitment status or conductivity. No conditions resulted in the naturally reproducing population density standard to be met after multiple stockings. Two to four stocking events were required to achieve the "fishable" population standard, depending on lake conditions. When estimating cost to harvestable age, lakes stocked at 24.7 fish/ha generally had the best survival resulting in the lowest cost to age-4 ($17.70 - $35.41/fish). Lakes stocked at 12.4 fish/ha had the highest cost to age-4 ($91.17 - $182.34/fish). Juvenile walleye survival from age-0 to age-1 was dependent on lake conductivity and recruitment status, with lakes stocked at 24.7 fish/ha providing the lowest cost to age-4. Our results may inform science-based decision making and best-case scenario stocking rates to increase the probability of reestablishing walleye natural recruitment.

Response of Yellow Perch to Water Level Fluctuations in Oligotrophic, North-Temperate Inland Lakes

Shay, G.P., G.G. Sass, and **J.T. Mrnak**. 2023, *Aquaculture, Fish and Fisheries*, 4(1): 1 – 10. https://doi.org/10.1002/aff2.148.

Abstract

Information on yellow perch *Perca flavescens* population dynamics and responses to various abiotic and biotic factors in oligotrophic, north-temperate inland lakes is limited. Water level fluctuations are known to influence available habitat and biological communities within the littoral zones of lakes, yet research is lacking for yellow perch in Wisconsin. The goal of our study was to characterize yellow perch population-level responses to natural water level fluctuations in four northern Wisconsin lakes using a 39-year time series. On average, increasing water level periods correlated with lower mean fyke net and gill net relative abundances (catch-per-unit-effort), though generally not statistically significant. Yellow perch mean relative weight varied among lakes and was significantly greater during increasing water level periods for all lakes except one. The lack of statistically significant findings potentially suggests a buffering mechanism of north-temperate oligotrophic lakes due to their small surface area to volume ratios, relative lack of nutrients, and(or) littoral structural habitat compared to other systems (e.g., shallow eutrophic lakes). Our results suggest that natural water level fluctuations may not be an environmental concern for yellow perch populations in some north-temperate oligotrophic inland lakes.

Stable isotopes reveal trophic ontogeny in Cisco (*Coregonus artedi*)

Martin, B.E., and **J.T. Mrnak**. *In review, Journal of Fish Biology.*

Abstract

Cisco (*Coregonus artedi*) are a widespread, coldwater, zooplanktivore native to North America. While Cisco are generally referred to as an “obligate zooplanktivore”, there is some evidence that the species exhibits considerable variability in trophic niche. Here, we assessed how Cisco body size relates to trophic position i.e., trophic ontogeny. We analyzed ^{13}C and ^{15}N isotopes from Cisco ranging from 127-271mm in body length (n = 66) from Trout Lake, Vilas County, Wisconsin, USA. ^{15}N isotopes showed smaller Cisco had a trophic position of ~3, and trophic position steadily increased to ~3.5 for larger Cisco. Further, ^{13}C isotope signatures showed Cisco transitioned to be more pelagically reliant (lower ^{13}C signatures). Using gill net catch data, we found that larger Cisco were using deeper habitats than smaller Cisco. Our results support Cisco have significant variability in trophic niche even though they are traditionally thought of as an obligate planktivore. Overall, we emphasize that researchers should be cautious

when generalizing Cisco trophic function, particularly when considering the broader food web.

Healing ogaa (walleye *Sander vitreus*) waters: lessons and future directions for inland fisheries rehabilitation

Embke, H.S., Z.S. Feiner, G.J.A. Hansen, **J.T. Mrnak**, C.I. Rounds, G.G. Sass, S.L. Shaw, and A.D. Schultz. *In review, Reviews in Fisheries Science and Aquaculture.*

Abstract

Inland fisheries provide important ecosystem services, however many face new challenges on top of chronic disturbances. In the Upper Midwestern United States, declines in cool- and coldwater fisheries have been observed, including ogaa/walleye *Sander vitreus* fisheries. In response to population declines, management agencies have implemented rehabilitation efforts; however, the frequency and intensiveness of efforts has increased recently given population declines. Evaluating intervention outcomes is critical for institutional learning and to understand strategy effectiveness. This review documents walleye rehabilitation efforts in the Upper Midwestern U.S. to discuss: 1) approaches used to rehabilitate populations; 2) similarities and differences in metrics of success; 3) factors leading to success versus failure; 4) common ecological and social themes influencing outcomes; and 5) recommendations that may increase future successful rehabilitation. Strategies included harvest regulation changes, stocking, food web manipulations, habitat enhancement and evaluation, and partner discussions. Overall, most rehabilitation plans failed to evaluate the role of environmental, habitat, and fish community factors in causing walleye population declines prior to implementing strategies. We propose an increased focus on ecosystem-based fisheries management principles and cultivating ecological conditions that favor walleye as a potential path for future rehabilitation plans. Lessons drawn from walleye rehabilitation plans are applicable to global inland fisheries to inform the conservation of declining fish populations given global change.

Estimating age, growth, and mortality of Cisco *Coregonus artedi* in north-temperate, oligotrophic inland lakes

Wilkinson, M.V., L.W. Sikora, L.M. Feucht, G.G. Sass, and **J.T. Mrnak**. *In review, Northeaster Naturalist.*

Abstract

Inland cisco *Coregonus artedi* are an energy-dense forage fish native to some Wisconsin north-temperate oligotrophic lakes. Cisco play a critical role within their native food webs as they are a common prey item for important gamefishes (e.g., lake trout *Salvelinus namaycush*, walleye *Sander vitreus*, and muskellunge *Esox masquinongy*) and can couple benthic-pelagic energy flow. Yet, relatively little information for this species within inland lakes exists. With future climate warming and species invasions predicted to drive population declines and, in some instances, extirpations (most notably at the southern extent of their range), there is a critical need

to increase our knowledge of this species to improve on our management capabilities. Thus, our objectives in this study were to characterize age, growth, and mortality parameter estimates for inland cisco from two northern Wisconsin lakes (Trout Lake and White Sand Lake, Vilas Co., WI). For Wisconsin inland cisco, we estimated a maximum age of 14-yr with the most common ages being 2- and 6-yr. Our von Bertalanffy parameter estimates indicate that inland cisco have a greater estimated mean asymptotic length (367 mm) and higher body growth coefficient (K = 0.126) compared to what has been observed in the Laurentian Great Lakes (313 mm and K = 0.111, respectively). Annual mortality was greater than expected (39.5%) and indicates population turnover every 2.5-yrs. This relatively high rate of mortality may be driven by density-dependence as White Sand and Trout lakes have greater cisco densities than surrounding inland lakes or the Laurentian Great Lakes. Updated age, growth, and mortality estimates for inland cisco will improve our management capabilities of this important species. Further, if monitored for the long-term, changes in these parameter estimates may be indicative of food web changes that may precede a negative population-level response. Thus, continual monitoring and assessment of age, growth, and mortality parameters are critical in moving towards a more holistic fishery management approach.

Assessment of Diets and Feeding Patterns

Chipps, S.R., J.E. Garvey, and **J.T. Mrnak**, 2024. *Assessment of Diets and Feeding Patterns*. Pages xxx – xxx *in* C.S. Guy, T.O. Brenden, and B.J. Irwin, editors. *Analysis and Interpretation of Freshwater Fisheries Data,* 2nd edition, American Fisheries Society, Bethesda, Maryland.

Structured Abstract

Aim – Our rationale for the development of this book was simple but twofold. First, there are numerous statistics reference texts available for biostatistical analyses. Our intent was not to repeat those efforts but to take a more functional approach. Rather than supply another test-oriented book (e.g., analysis of variance or multiple regression) with fisheries examples, the major fisheries data types dictated the development and presentation of statistical approaches. Secondarily, this book provides the profession with a frame of reference to encourage appropriate sample design, analysis, and interpretation of freshwater fisheries data. We narrowed the scope of the book to freshwater data types because we believed by including marine analytical methods the book would become excessively cumbersome. Although there is much overlap in freshwater and marine analytical methods, there are inherent differences with regard to research problems and data collection.

Main concepts/methods covered – We highlight the fundamentals of fish diet and feeding assessments, then go on to fill in additional knowledge gaps and detail advances made since the 1st edition release in 2007. This includes but is not limited to; designing appropriate sampling designs (field and experimental studies), estimating energy density using dry:wet weights, testing hypotheses using AIC analysis, use of zero-inflated discrete models to evaluate factors affecting consumption, and tracking every flow with stable isotope analysis.

Supplementary Materials (SM): Fisheries Management 101: Spring Mark-Recapture Surveys on Two Northern Wisconsin Lakes

Overview

We conducted spring mark-recapture surveys to estimate the population size of native fishes before, during, and after experimental manipulation on Crystal and Sparkling lakes, 2020 – 2023 (see Chapters 1 and 2). Using a variety of gears and the and the Chapman-modified, continuous Schnabel procedure (Chapman 1951; Ricker 1975), we estimated the population size of yellow perch (*Perca flavescens*) in Crystal Lake and walleye (*Sander vitreus*), muskellunge (*Esox masquinongy*), and smallmouth bass (*Micropterus dolomeiu*) in Sparkling Lake. In addition to population size estimates for the aforementioned species, we collected length data and reported relative abundance estimates (catch-per-unit effort; CPUE) for frequently observed species (e.g., bluegill *Lepomis macrochirus*, largemouth bass *Micropterus salmoides*, and rock bass *Ambloplites rupestris*).

SM.1 Introduction

Pelagic forage fishes play an important functional role in north temperate lakes whereby they structure zooplankton communities, serve as prey for piscivorous fishes, and are a vital link in the transfer of energy in lake food webs (Rudstam et al. 1993, 1994; Vander Zanden & Vadeboncoeur 2002; Kaufman et al. 2009). In chapter 1 and 2 of my dissertation, I focus on three pelagic forage fish species, cisco (*Coregonus artedi*), yellow perch (*Perca flavescens*), and invasive rainbow smelt (*Osmerus mordax*). Cisco are a native cold-water pelagic forage fish common to deep glacial lakes of the midwestern United States and Canada and are emblematic of cold-water fishes facing threats (i.e., species invasions, climate change, land use change;

Rudstam et al. 1993; Honsey et al. 2016; Renik et al. 2020; Mrnak et al. 2023). Indeed, climate models predict 25 – 70% of cisco populations will be extirpated by 2100 due to loss of deep water oxythermal habitat (Sharma et al. 2011). Climate driven and land use change extirpations have already been observed in the southern portion of their range (Honsey et al. 2016), including about a third of the lakes where cisco were historically present in Wisconsin (Renik et al. 2020). Cisco have been extirpated from Sparkling Lake (Vilas County, WI) with rainbow smelt predation on young-of-year and juvenile cisco being implicated as the mechanism (Hrabik et al. 1998). Yellow perch, a native cool-water forage fish, are not as vulnerable as cisco to the threats imposed by climate change. However, yellow perch have been facing localized declines and, in some cases, functional extirpations due to exotic species invasions and critical habitat loss (Sass et al. 2006; Gaeta et al. 2014). In Sparkling Lake, pelagic yellow perch disappeared from vertical gillnet catches following invasive rainbow smelt establishment (Magnuson et al. 2022). In Crystal Lake (Vilas County, WI), the yellow perch population declined to near undetectable levels following invasive rainbow smelt establishment (Magnuson et al. 2022; Mrnak et al. 2023). In contrast to cisco-rainbow smelt interactions in Sparkling Lake, the Crystal Lake yellow perch were too large to be consumed by rainbow smelt. Despite no direct interactions, thermal overlap and similar prey resources resulted in reduced yellow perch feeding success and condition (Hrabik et al. 1998) resulting in large-scale population decline. Invasive rainbow smelt clearly present a challenge for native pelagic forage fishes (Evans & Loftus 1987; Rooney & Paterson 2009; Mrnak et al. 2023). Rainbow smelt are native to the north Atlantic coast and have invaded many lakes in the Upper Midwest and Canada and are expected to continue to spread (Evans & Loftus 1987; Hrabik & Magnuson 1999; Mercado-Silva et al. 2007). Rainbow smelt are eurythermal and omnivorous, thus they interact extensively throughout the food web via direct and indirect interactions (Evans & Loftus 1987; Hrabik et al. 1998; Mrnak et al. 2023).

Whole-lake biomanipulations and ecological theory provide mechanisms to manage and restore aquatic ecosystems containing an invasive population (Krueger & Hrabik 2005; Mrnak et al. 2023). Overexploitation via deliberate overfishing and(or) predation by native piscivores represent two control mechanisms for invasive prey fishes, such as rainbow smelt. Here, I conducted two whole-lake biomanipulations to test the role of apex predators (piscivorous fishes; e.g., walleye *Sander vitreus*, muskellunge *Esox masquinongy*, smallmouth bass *Micropterus dolomieu*) in mediating the interaction between cisco, yellow perch, and rainbow smelt in a species reintroduction context (see Chapter 1 and 2). Apex predators can regulate community structure and have profound ecological effects that extend to the base of the food web (Pace et al. 1999; Terborgh & Estes 2010). This can include mediating interactions among its prey species (Abrams 1987a, 1987b), and this effect has been reported for cisco-rainbow smelt interactions (Krueger & Hrabik 2005). For example, extensive stocking of walleye into two different lakes reduced the abundance of rainbow smelt via selective predation, which shifted the species dominance from rainbow smelt to cisco and allowed the native cisco populations to recover (Krueger & Hrabik 2005). This concept that interactions between native and invasive forage fishes is mediated by the presence and(or) abundance of predators is the foundation of this research.

Estimating the size of a population is at the core of fisheries management. Indeed, a key component of many fisheries assessments is the determination of how many fish are in a population. Fishery assessments are critical for collecting demographic (e.g., size- and age-structure, sex ratio) and dynamic (e.g., mortality, growth, recruitment) population data, which are combined with the estimated population size to inform and guide management. In the context of Chapter 1 and 2, these population estimates will be used to test the predator mediation effect on invasive rainbow smelt control and native cisco introduction success. Specifically, I tested whether selective predation on rainbow smelt promotes a greater relative increase in cisco population growth rate and equilibrium population size. I hypothesized that predators will play a critical role in rainbow smelt control and cisco introduction success as predators will help biologically control juvenile and sub-adult rainbow smelt that are not vulnerable to removal gears that target adult spawners. However, system resilience exists along a gradient and is difficult to assess and quantify in the short-term due to the ecological timescales of regime shifts (Magnuson 1990, Carpenter et al. 1998, Scheffer et al. 2001, Scheffer and Carpenter 2003, Hansen et al. 2013). Therefore, I will continue this experimentation through 2029 to adequately test my predator mediation question.

SM.2 Methods

Study area

Experimental lakes (Crystal Lake, 46.000878, -89.612474; Sparkling Lake, 46.007317, -89.700080) are located in Vilas County, Wisconsin, USA and have similar lake characteristics (Table 1. in Shay et al. 2023; Magnuson et al. 2006) but differ in their fish communities. At the beginning of the experiment, Crystal Lake contained invasive rainbow smelt, native yellow perch, and no predators, while Sparkling Lake contained invasive rainbow smelt, native yellow perch and native predators in the form of walleye, muskellunge, and smallmouth bass. Crystal Lake has experienced marked declines in the yellow perch population following rainbow smelt invasion in 1985 (Hrabik et al. 1999; Hrabik et al. 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 non-stocked age-0 walleye collected in fall electrofishing surveys) has been in decline (Wisconsin Department of Natural Resources, *unpublished data*). Similar to other imperiled walleye lakes across the Midwest USA, Sparkling Lake has been stocked with extended growth fingerlings (~150-220mm total length; TL) during the fall of odd years since 1997 (see Elwer et al. 2023).

Mark-recapture surveys

During 2020 – 2023, standardized spring fyke net sampling surveys were conducted to test for changes in the fish communities within the experimental lakes. For Sparkling Lake, sampling began immediately after ice-out (range over study, April 7th – May 5th) with the deployment of eight large frame fyke nets (1.2m x 1.8m, 1.9cm bar mesh) at fixed locations in the lake that were probable walleye spawning sites (Hansen et al. 1991). During these surveys, nets were checked daily after a 24-hr soak, all collected fish were measured for total length (TL; mm), sexed, checked for a uniquely coded passive integrated transponder (PIT), Floy tag, or fin clip (dependent on the year-specific mark and(or) other projects on the lake; e.g., Bright Spots collaboration with University of Wisconsin-Stevens Point). Adult fish were implanted with a PIT tag if one was not present and given a year-specific fin clip. 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). For muskellunge and smallmouth bass, maturity was determined exclusively by the extrusion of gametes. Only adult fish were used for population estimation. When fyke net catches of walleye peaked, an AC boat electrofishing run of the entire shoreline was conducted to capture new fish and recapture previously marked fish. At the conclusion of the walleye spawn (i.e., ~10 days after peak catch), fyke nets were moved to probable smallmouth bass spawning sites. At peak smallmouth bass spawn (noted by peak fyke net catches), a whole-lake angling survey was conducted to capture new fish and recapture previously marked fish. Mark-recapture surveys on Sparkling Lake served two purposes: 1) capture adult walleye, muskellunge, and smallmouth bass to produce an adult population estimate; and 2) to collect length information and estimate relative abundances (fish per net night; CPUE) of commonly observed native fishes.

For Crystal Lake yellow perch, sampling began ~two weeks after ice-out when water temperatures were about 6.5°C (range over study, April 15th – May 11th) with the deployment of six mini fyke nets (0.6m × 1.2m, 0.65cm bar mesh) equally spaced around the lake (e.g., Mrnak et al. 2021; Feucht et al. 2023). During these surveys, nets were picked daily after a 24-hr soak, all adult yellow perch were measured for TL (mm), sexed, and checked for a year-specific fin clip. Yellow perch were defined as an adult if they were ≥ 75 mm TL since all individuals of that length expressed gametes (Mrnak et al. 2021; Feucht et al. 2023). We could not electrofish Crystal Lake due to low water conductivity (13 μS) that could not be overcome with our gear (Mrnak et al. 2021) or angle due to the low catchability of yellow perch in Crystal Lake. Thus, mini fyke nets were the only recapture gear used for Crystal Lake yellow perch population estimation. The marking and recapture period lasted until ≥10% of the marked population was recaptured. Mini fyke nets on Crystal Lake were used to produce an adult yellow perch population estimate and to collect length information and estimate relative abundances (fish per net night; CPUE) over time. For both lakes, population estimates were calculated using the Chapman-modified, continuous Schnabel procedure (Chapman 1951; Ricker 1975). Due to relatively large numbers of recaptures in the walleye and yellow perch surveys (due to prolonging survey effort), we calculated 95% CI for 1/population estimate by using *t*-values from the normal distribution of recaptures. These limits were then inverted to give a 95% CI for the population estimate (Ricker 1975).

SM.3 Results

Extreme variability in the timing of lake phenology (i.e., ice-off date, ensuant warming) resulted in differences in survey effort among years (i.e., number of net nights). Ice-off date for Crystal Lake ranged from April 2nd (2021) to May 4th (2022). Sparkling Lake ice-off date ranged from April 3rd (2021) to May 4th (2022). In 2020, the yellow perch mark-recapture survey started on May 11th and concluded on May 24th with a 11% recapture rate and 84 individual net nights. The 2020 adult yellow perch population estimate (95% LCI – 95% UCI) was 11,051 (9,878 – 12,541; Figure 1). In 2021, the yellow perch mark-recapture survey started on April 15th and concluded on May 3rd with a 9.5% recapture rate and 114 individual net nights. The 2021 adult yellow perch population estimate (95% LCI – 95% UCI) was 5,785 (4,821 – 7,231; Figure 1). In 2022, the yellow perch mark-recapture survey started on May 9th and concluded on May 24th with a 1.8% recapture rate and 96 individual net nights. The 2022 adult yellow perch population estimate (95% LCI – 95% UCI) was 44,812 (34,333 – 64,498; Figure 1). In 2023, the yellow perch mark-recapture survey started on May 5th and concluded on May 18th with a 3.2% recapture rate and 84 individual net nights. The 2023 adult yellow perch population estimate (95% LCI – 95% UCI) was 52,966 (44,387 – 65,655; Figure 1).

The 2020 adult walleye mark-recapture fyke netting surveys on Sparkling Lake started on May 3rd and concluded on May 6th. The boat electrofishing recapture survey occurred on May 18th. At the conclusion of the 2020 survey, we had a 35.4% recapture rate and 48 individual net nights. The 2020 adult walleye population estimate (95% LCI – 95% UCI) was 391 (325 – 491; Figure 1). We did not conduct mark-recapture surveys for other species in Sparkling Lake in 2020. In 2021, the walleye and muskellunge mark-recapture survey started on April 7th and concluded on May 7th with a 45.2% and 33.3% recapture rate for walleye and muskellunge, respectively. There were 248 individual net nights of effort expended for the walleye and muskellunge mark-recapture surveys in 2021. The boat electrofishing recapture survey occurred on April 15th and again on April 22nd. The 2021 adult walleye and muskellunge population estimates (95% LCI – 95% UCI) were 265 (230 – 312) and 16 (8 – 35), respectively. In 2021, the smallmouth bass fyke mark-recapture survey started on May 18th and concluded on May 28th with the angling recapture survey occurring on June 1st. This survey ended with a 28.1% recapture rate and 88 individual net nights. The 2021 adult smallmouth bass population estimate (95% LCI – 95% UCI) was 207 (154 – 283; Figure 1). In 2022, the walleye and muskellunge mark-recapture survey started on May 5th and concluded on May 16th with a 53.6% and 25% recapture rate for walleye and muskellunge, respectively. There were 96 individual net nights of effort expended for the walleye and muskellunge mark-recapture surveys in 2022. The boat electrofishing recapture survey occurred on May 8th. The 2022 adult walleye and muskellunge population estimates (95% LCI – 95% UCI) were 293 (256 – 342) and 20 (9 – 47), respectively. In 2022, the smallmouth bass fyke mark-recapture survey started on May 23rd and concluded on June 3rd with the angling recapture survey occurring the same day. This survey ended with a 33.5% recapture rate and 96 individual net nights. The 2022 adult smallmouth bass population estimate (95% LCI – 95% UCI) was 253 (206 – 328; Figure 1). In 2023, the walleye and muskellunge mark-recapture survey started on May 4th and concluded on May 18th with a 48.9% and 16.6% recapture rate for walleye and muskellunge, respectively. There were 120 individual net nights of effort expended for the walleye and muskellunge mark-recapture surveys in 2023. The boat electrofishing recapture survey occurred on May 11th. The 2023 adult walleye and muskellunge population estimates (95% LCI – 95% UCI) were 432 (386 – 489) and 14 (5 – 33), respectively. In 2023, the smallmouth bass fyke mark-recapture survey started on May 18th and concluded on June 2nd with the angling recapture survey occurring the same day. This survey ended with a 30.7% recapture rate and 128 individual net nights. The 2023 adult smallmouth bass population estimate (95% LCI – 95% UCI) was 274 (219 – 365; Figure 1).

Sparkling Lake's fish community was more diverse than Crystal Lake's fish community (Figure 2; Figure 3). During these surveys, we encountered 29 fish species in Sparkling Lake and 12 in Crystal Lake. Of those 12 species, four were observed only one time (walleye, smallmouth bass, northern pike *Esox lucius,* and pumpkinseed *Lepomis gibbosus*). Yellow perch dominated the catches on Crystal Lake, while fyke net catches on Sparkling Lake most often contained bluegill, largemouth bass, muskellunge, rock bass, smallmouth bass, walleye, or yellow perch (Figure 2; Figure 3).

SM.4 Conclusion

Mark-recapture surveys are foundational to fisheries management – the bread of butter of this discipline. After student training and mentoring, spring fyke netting is my favorite part of my job. Observing and experiencing the phenological progression of these lakes and species is a special and magical thing. I am fortunate and grateful to have conducted these surveys with such amazing humans (and dogs).

SM.5 References

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SM.6 Figures

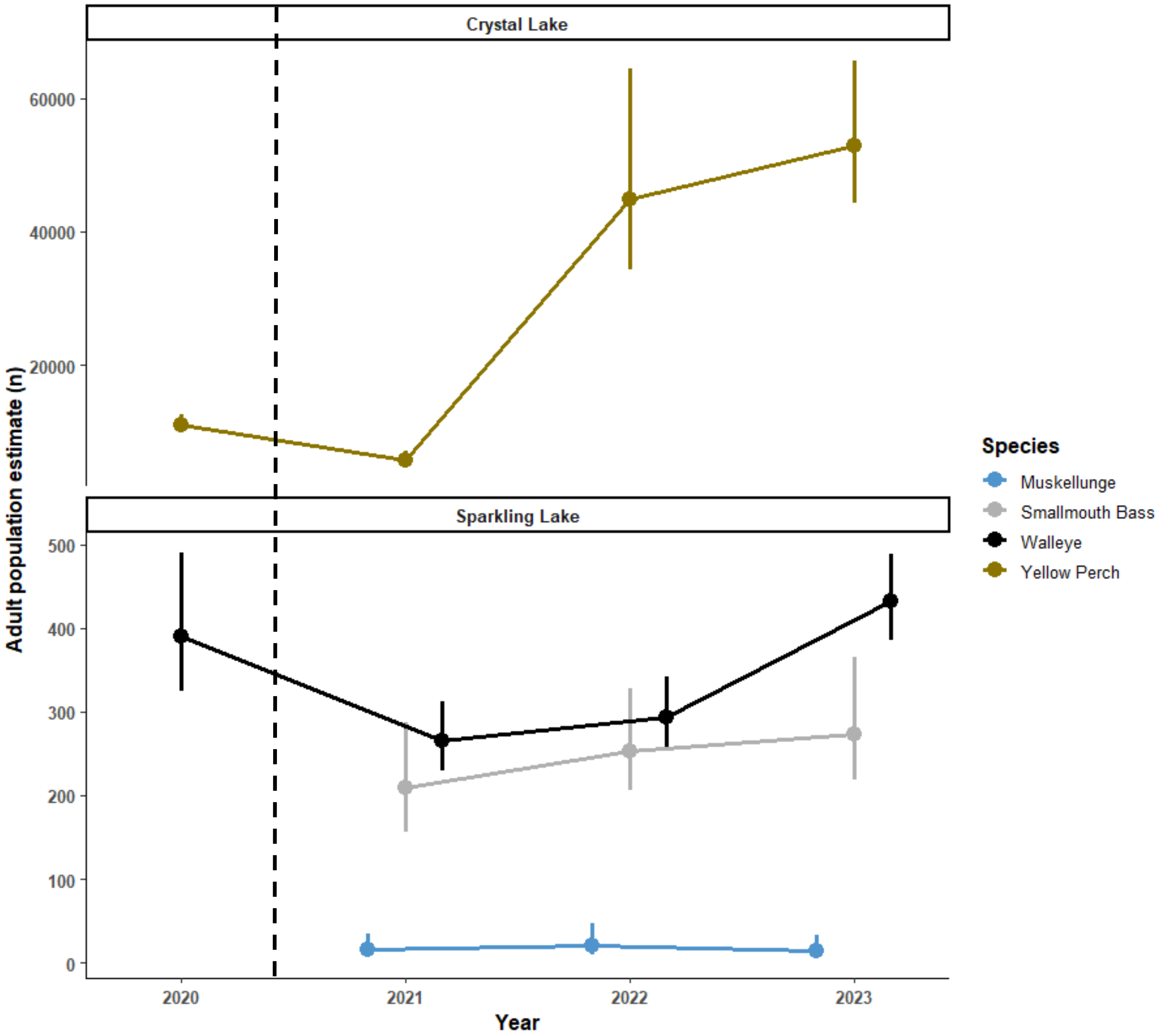

Figure 1. Yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), muskellunge (*Esox masquinongy*), and smallmouth bass (*Micropterus dolomeiu*) adult population estimates (n) for Crystal (top) and Sparkling (bottom) lakes during 2020 – 2023. Error bars represent 95% confidence intervals. The vertical dotted line at 2020.5 indicates the time period prior to the invasive rainbow smelt (*Osmerus mordax*) removal and native cisco (*Coregonus artedi*) introduction ecosystem manipulations. Values offset along x-axis for clarity.

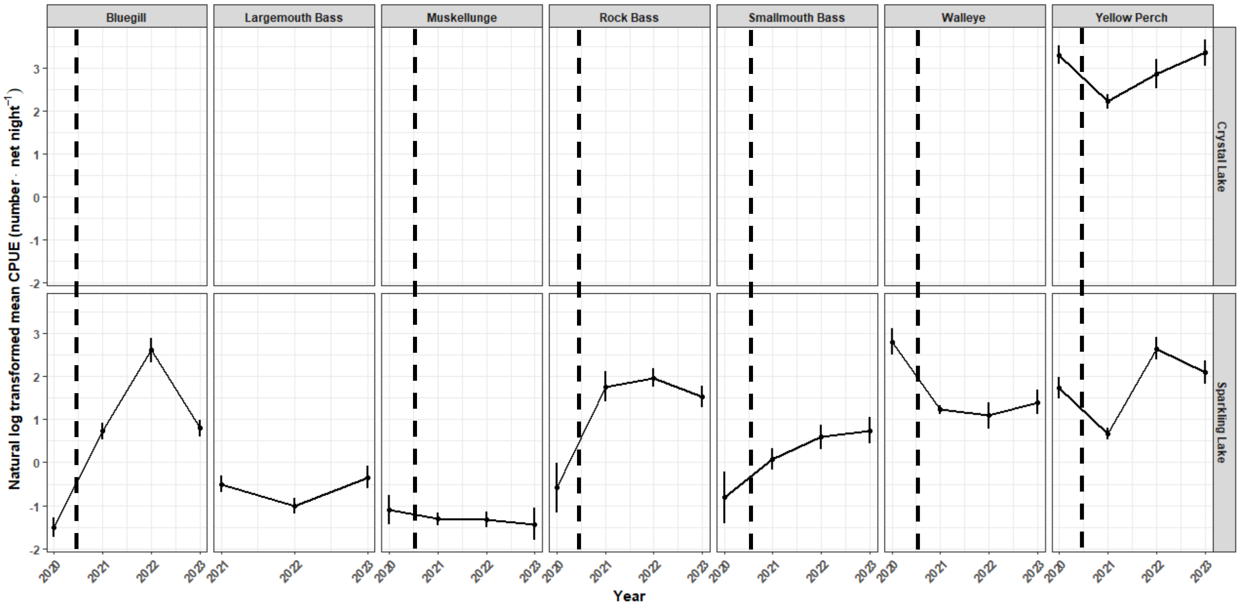

Figure 2. Species-specific $\log_e$ transformed mean (±SE) CPUE (catch per unit effort; number per net night) for frequently observed species in Crystal (top) and Sparkling (bottom) lakes during 2020 – 2023 spring mark-recapture fyke net surveys. The vertical dotted line at 2020.5 indicates the time period prior to the invasive rainbow smelt (*Osmerus mordax*) removal and native cisco (*Coregonus artedi*) introduction ecosystem manipulations (excluding the largemouth bass panel as we did not capture largemouth bass prior to 2021.

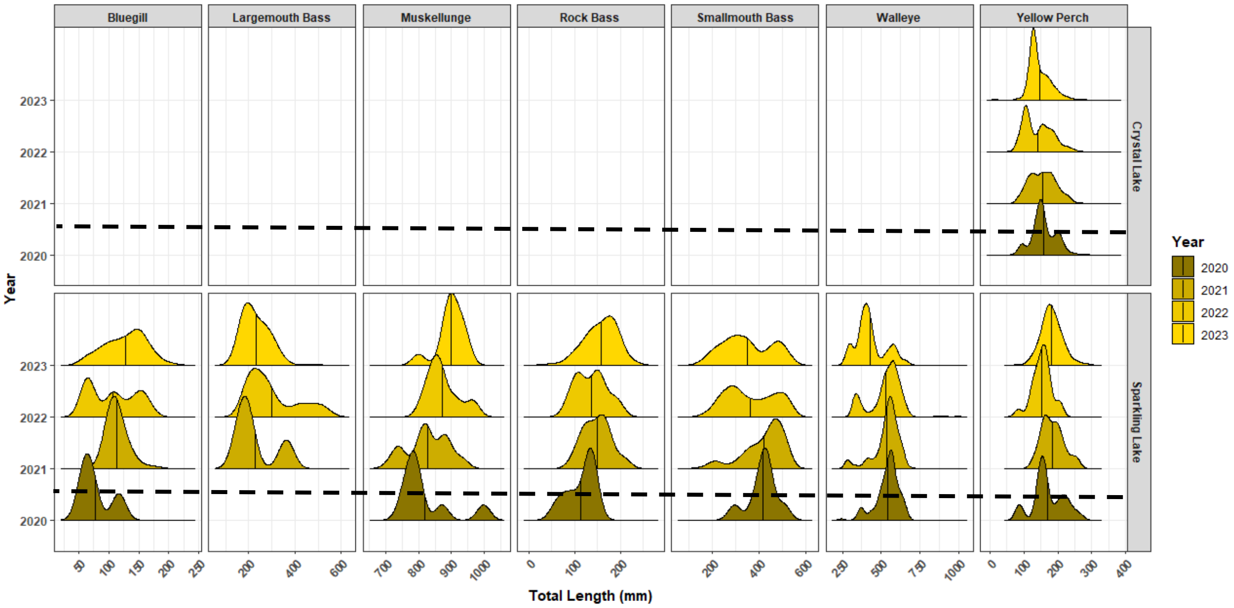

Figure 3. Species-specific total length (mm) density distributions for frequently observed species in Crystal (top) and Sparkling (bottom) lakes during 2020 – 2023 spring mark-recapture fyke net surveys. The upper row corresponds to Crystal Lake and the lower row corresponds to Sparkling Lake. Vertical black lines in each distribution correspond to the mean total length value. Color corresponds to year. The horizontal dotted line at 2020.5 indicates the time period prior to the invasive rainbow smelt (*Osmerus mordax*) removal and native cisco (*Coregonus artedi*) introduction ecosystem manipulations.