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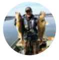

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REVIEW

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Applying Panarchy Theory to 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

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 and Hastings 2010; Cucherousset and 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

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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 and 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 and 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 and Holling 2002). Panarchy theory has been used to explain economic, ecological, and institutional systems and their interactions (Gunderson et al. 1995; Holling and 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 and 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 and 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 and 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 and 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 and 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 and 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 and Smith 1996; Mullon et al. 2005; Pinsky et al. 2011), the control and(or) eradication of invasive species can also be purposefully attempted (Krueger and 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 and 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

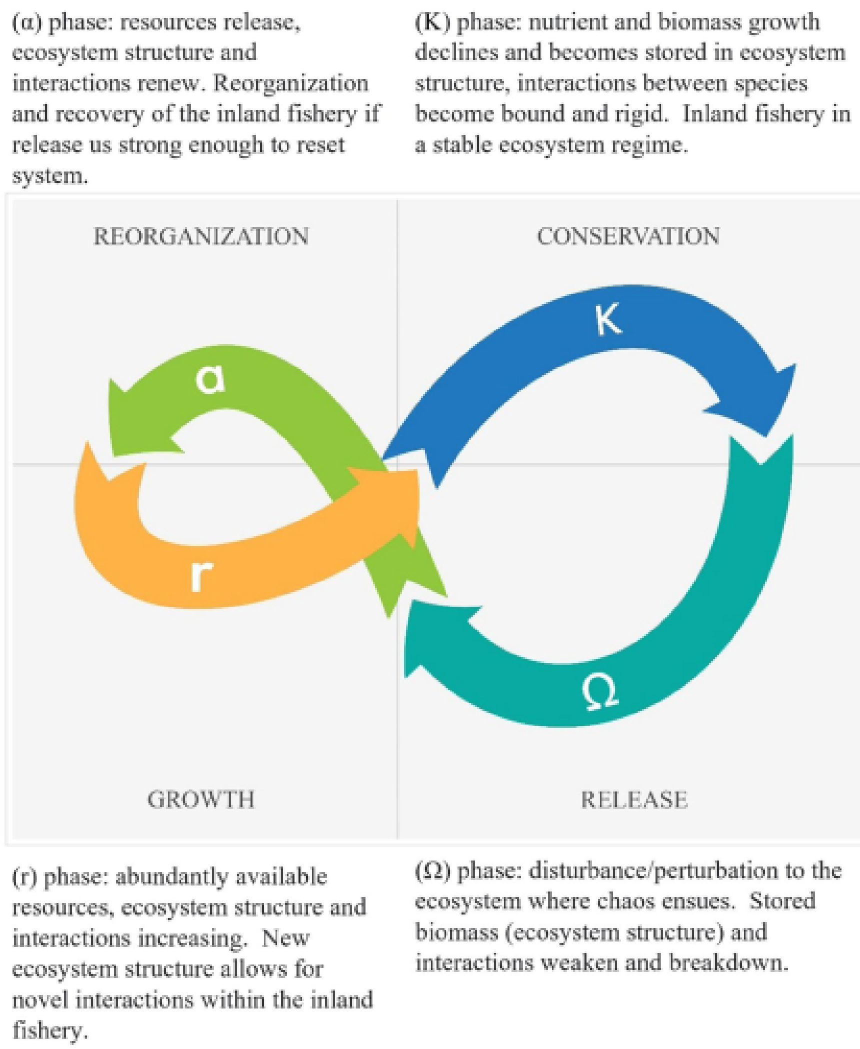

Figure 1. Four phases of a single nested adaptive cycle of a panarchy.

Coregonus clupeaformis; (Evans and Loftus 1987; Johnson and Goettl 1999; Beisner et al. 2003; Rooney and Paterson 2009). Certain piscivorous species (e.g., Atlantic salmon *Salmo salar*, lake trout *Salvelinus namaycush*, walleye) have also benefited from rainbow smelt invasions via increased growth rates (Warner and Fenderson 1963; Maher 1983; Evans and 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 and 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

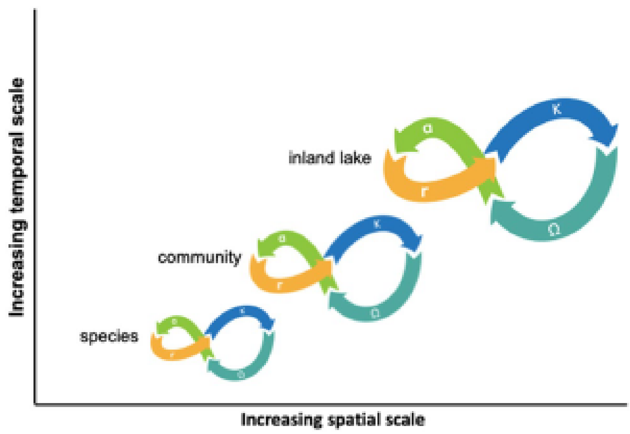

Figure 2. Species-, community-, and inland lake-level nested adaptive cycles comprising a panarchy for a north-temperate inland lake ecosystem.

smelt invasions in inland lakes (e.g., Evans and Loftus 1987; Rooney and 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 and 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.

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 and 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 and 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 and Carpenter 2003; Garmestani 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 and 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 and Panetta 2009; Green and 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 and Holling 2002; Holling and 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 and 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 and 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 and 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.

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.

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 and 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 and 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 et al. 2011; Gamble 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 and 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 and Loftus 1987; Hrabik and Magnuson 1999). The further expansion of rainbow smelt in Wisconsin waters was predicted to be incipient (Hrabik and 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 and 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 and 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 and Loftus 1987; Franzin et al. 1994; Rooney and 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 and Paterson 2009). When left unchecked, rainbow smelt are efficient at rapid dispersal and establishment across these north-temperate landscapes.

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 and 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 > 6.1 m), 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 and 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 – 10 mg/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 and 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 and 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 and 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.

Ecological effects of rainbow smelt invasions

Colonization of invasive rainbow smelt in inland lakes and waterbodies has resulted in negative, benign, or

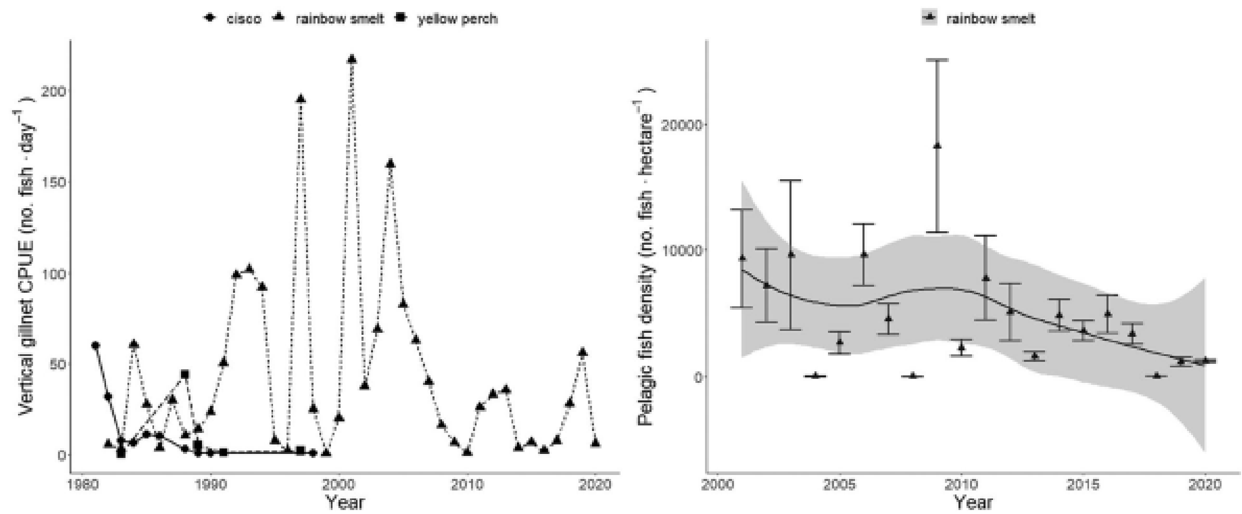

Figure 3. Long-term trends in cisco Coregonus artedi, rainbow smelt Osmerus mordax, and yellow perch Perca flavescens vertical gillnet catch per unit effort (no. fish · day^{-1}; left) and rainbow smelt mean ± SE pelagic density (no. fish · hectare^{-1}; right) for Sparkling Lake (Vilas County, Wisconsin)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

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-Silva 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 and Leach 1977; Colby et al. 1987; Jones et al. 1994; Johnson and 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 and Loftus 1987; Rooney and 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

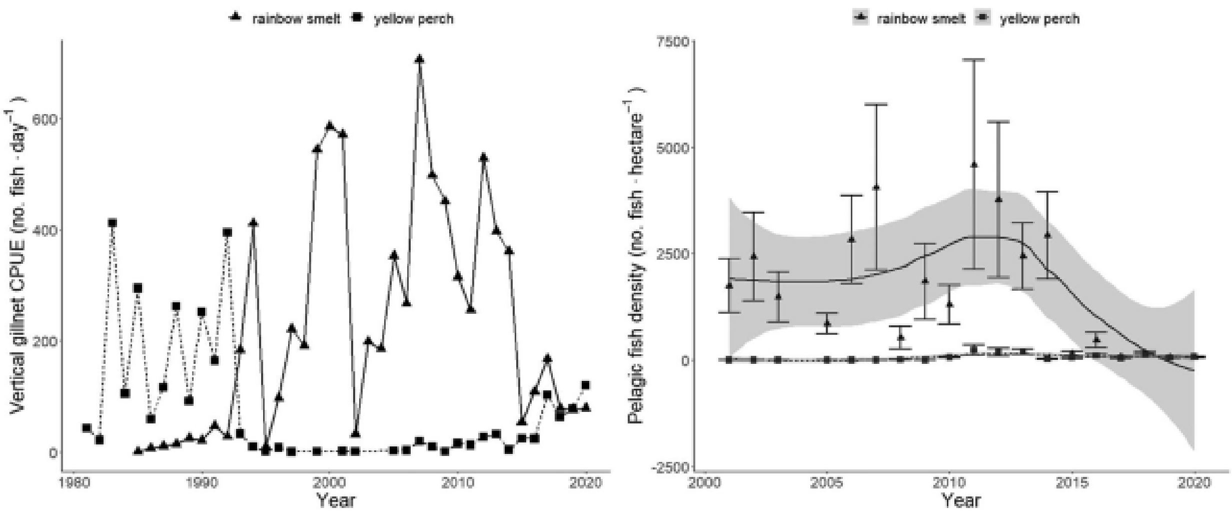

Figure 4. Long-term trends in rainbow smelt Osmerus mordax and yellow perch Perca flavescens vertical gillnet catch per unit effort (no. fish · day^{-1}; left) and mean ± SE pelagic fish density (no. fish · hectare^{-1}; right) for Crystal Lake (Vilas County, Wisconsin) during 1980 – 2020 and 2001 –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

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 and Loftus 1987; Rooney and 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 and 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 toward 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.

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 and 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 and 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 and 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 and Hrabik 2005). The biomanipulation focused on increasing walleye abundance and biomass, and thus predation pressure (i.e.,

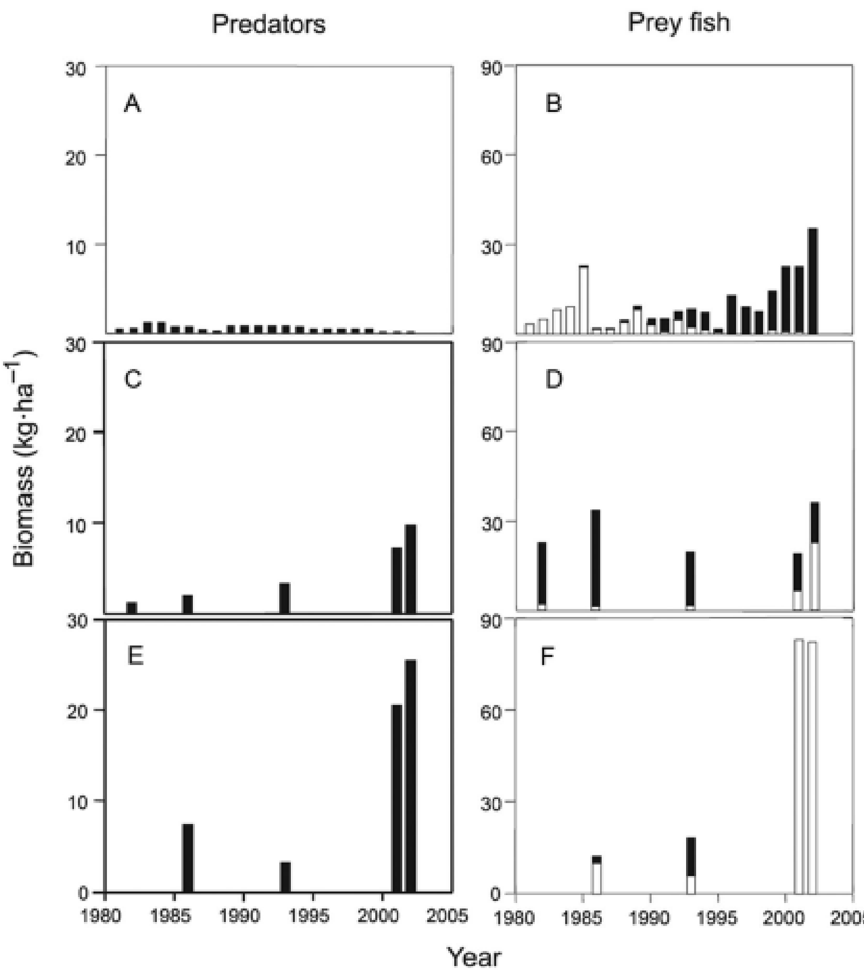

Figure 5. The estimated biomass of predator and prey species in each study lake from 1982 to 2002. (A) The biomass of predatory fish in Crystal Lake represented as a combined estimate of lake trout (Salvelinus namaycush) and walleye (Stizostedion vitreum). (B) The biomass of rainbow smelt (Osmerus mordax; 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 and Hrabik 2005). Reprinted with permission from D.M. Krueger and T.R. Hrabik.

consumption rates) on rainbow smelt through protective fishing regulations (recreational and tribal) and walleye stocking (Krueger and Hrabik 2005). During the biomanipulation, walleye biomass increased from 3.2 and 3.1 kg·ha^{-1} to 9.7 and 25.4 kg·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 and 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

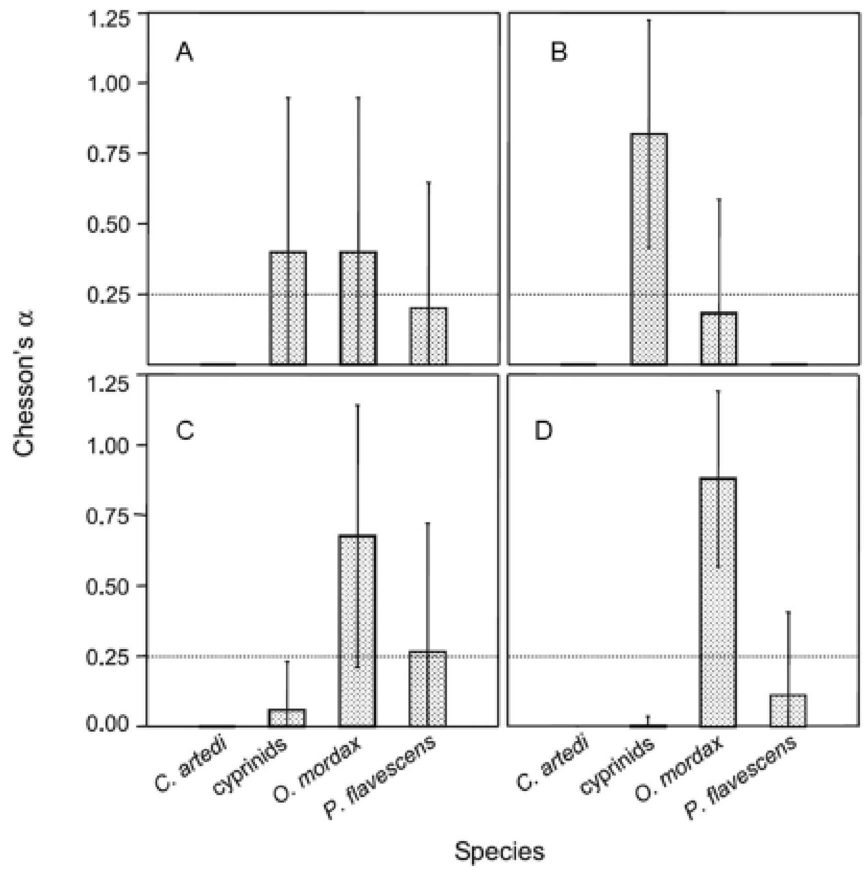

Figure 6. Chesson's index of prey selection for walleye (Stizostedion vitreum) caught in Fence Lake in (A) May, (B) June, (C) July, and (D) August of 2002. Error bars indicate 95% confidence intervals; the dotted horizontal line in each box represents neutral selection (Krueger and Hrabik 2005). Reprinted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

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 and Olden 2008; Seekamp et al. 2016; Seekamp 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 and Suttle 2001; Terborgh and 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

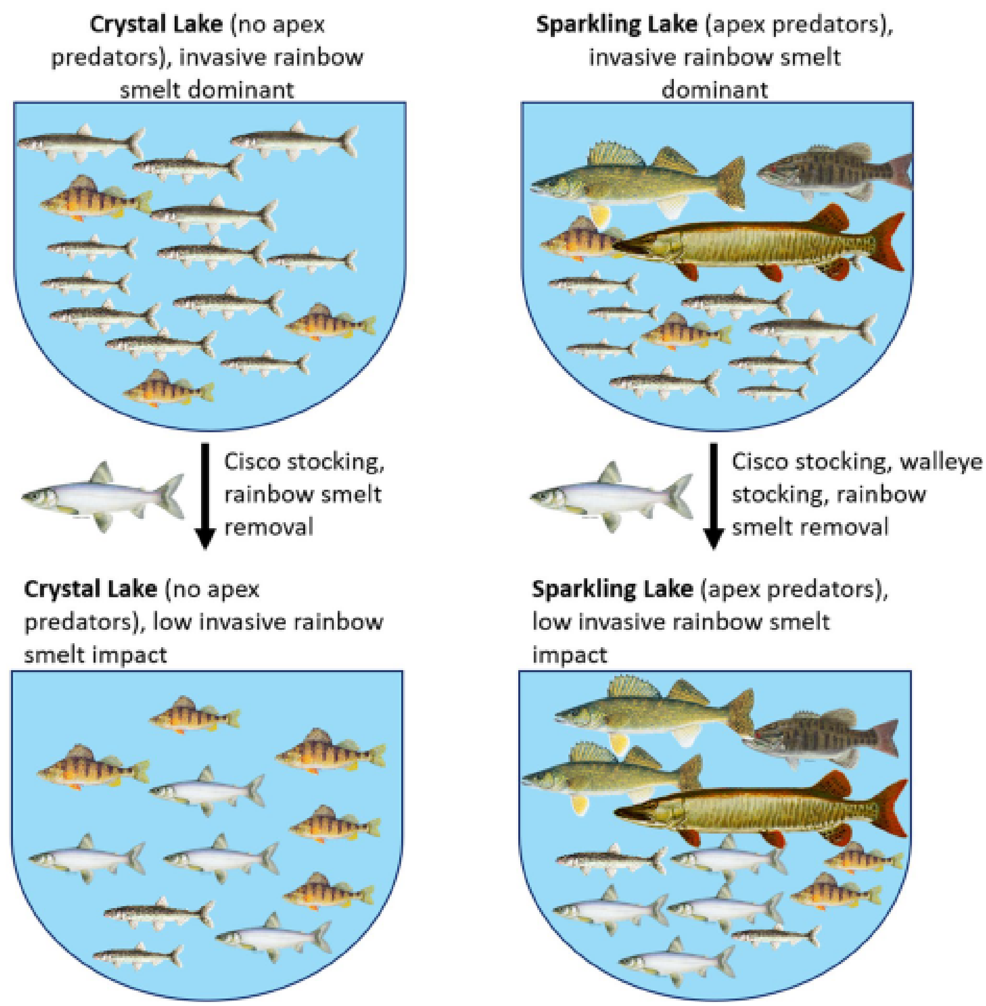

Figure 7. Experimental reintroduction of native cisco Coregonus artedi and control of invasive rainbow smelt Osmerus mordax in Crystal and Sparkling Lakes (Vilas County, Wisconsin) by leveraging panarchy theory. Crystal Lake contains no apex predators and a native planktivore in the form of yellow perch 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.

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 and 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 and 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 and 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 and 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.

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 and Estes 2010). This can include mediating interactions among prey species (Abrams 1987a, 1987b), which has been reported for rainbow smelt-cisco interactions (Krueger and 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 (Figures 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 (Figures 1 and 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 $>10\,\mathrm{kg{\cdot}ha^{-1}}$ and consumption rate $> 12\,\mathrm{kg{\cdot}ha{\cdot}year^{-1}}$ (Krueger and 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 and 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 Sparling 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., Figures 1 and 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.

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 toward 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 orientated 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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