

# A whole-lake experiment to control invasive rainbow smelt (*Actinoperygii*, *Osmeridae*) via overharvest and a food web manipulation

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Received: 22 December 2013 / Revised: 12 May 2014 / Accepted: 19 May 2014 / Published online: 6 June 2014  
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**Abstract** Invasive rainbow smelt (*Osmerus mordax*) have spread rapidly throughout inland lakes of North America with detrimental effects on several native fishes. To test for the potential to control this species, we conducted an experimental removal of rainbow smelt in Sparkling Lake, Wisconsin during 2002–2009. We combined intensive spring harvest of rainbow smelt with an effort to increase predation on this invasive through restricted angler harvest of walleye and increased stocking of walleye (*Sander vitreus*). Over 4,170 kg of rainbow smelt were harvested during the experiment; up to 93% of adults

were removed annually. We observed a significant decline in rainbow smelt gillnet catches during the removal. However, rainbow smelt relative abundances began increasing upon cessation of the removal effort. Bioenergetics modeling suggested that despite achieving higher than the regional average walleye densities, walleye consumed only a fraction of the rainbow smelt standing stock biomass. Our findings suggest that removal of rainbow smelt from invaded lakes may be difficult, and reinforce the importance of prevention as a strategy to limit the expansion of this invasive fish.

**Keywords** Bioenergetics · Overharvest · Rainbow smelt (*Osmerus mordax*) · Walleye (*Sander vitreus*)

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Guest editors: Sidinei M. Thomaz, Katya E. Kovalenko, John E. Havel & Lee B. Kats / Aquatic Invasive Species

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## Introduction

Invasive species introductions are a global concern (Vitousek et al., 1996; Pimentel et al., 2000; Sala et al., 2000) and often result in negative consequences for aquatic ecosystems (Leung et al., 2002; Holeck et al., 2004; Vander Zanden et al., 2010). Rainbow smelt (*Osmerus mordax*) are an invasive fish species of particular concern in the Laurentian Great Lakes Basin (Van Oosten, 1937; Evans & Loftus, 1987; Franzin et al., 1994), the Mississippi-Missouri River Basin (Mayden et al., 1987), and as far west as Colorado (Johnson & Goettl, 1999). Invasions of this small anadromous fish native to northeastern North America (Evans & Loftus, 1987) are associated with numerous ecosystem changes. These changes include shifts in food webs (Evans & Loftus, 1987), altered zooplankton community structure (Beisner et al., 2003), and negative effects on native fishes (e.g., Hrabik et al., 1998; Johnson & Goettl, 1999; Mercado-Silva et al., 2007). Observed changes in native fishes associated with rainbow smelt invasions include declines in densities of yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*) (Hrabik et al., 1998, 2001; Johnson & Goettl, 1999; Mercado-Silva et al., 2007; Roth et al., 2010) as well as the extirpation of cisco (*Coregonus artedii*) (Hrabik et al., 1998; Roth et al., 2010). Therefore, methods for control or eradication of rainbow smelt are critical to allow invaded ecosystems opportunities to recover (Lodge et al., 2006; Vander Zanden & Olden, 2008; Vander Zanden et al., 2010).

Overfishing has been used in attempts to control or eradicate numerous populations of freshwater invasive species (e.g., Knapp & Matthews, 1998; Weidel et al., 2007; Hansen et al., 2013; Lathrop et al., 2013). Recruitment overfishing can occur when large portions of the spawning stock are harvested, thereby reducing recruitment potential and population abundance (Allen & Hightower, 2010). Persistent recruitment overfishing can collapse the targeted species and has been implicated in reduced abundances of aquatic invasive species and the subsequent recovery of native plant and fish populations. For example, ecosystem recovery has been observed in whole-lake physical removal efforts of invasive rusty crayfish (*Orconectes rusticus*; see Hein et al., 2007; Hansen et al., 2013) and common carp (*Cyprinus carpio*; see Lathrop et al., 2013). Notably, the removal of rusty crayfish was

augmented with a change in harvest regulations to increase the size structure and density of smallmouth bass (*Micropterus dolomieu*), a known crayfish predator. Such an approach has the potential to favorably alter food webs through increased predation on the invasive species (Isermann & Paukert, 2010). Indeed, increased predation on rainbow smelt by walleye has previously been attributed to significant decreases in rainbow smelt (Krueger & Hrabik, 2005).

Here, we describe the results of eight consecutive years of a whole-lake rainbow smelt removal combined with stocking and regulatory efforts to increase walleye, a known rainbow smelt predator (Krueger & Hrabik, 2005). Our goal was to assess the feasibility of controlling invasive rainbow smelt in a north temperate lake with recruitment overfishing and increased predation. We also discuss the broader implications of our removal effort and the response of the rainbow smelt population.

## Methods

### Study site

Sparkling Lake is a mesotrophic seepage lake located in the Northern Highland Lakes District of Wisconsin, USA (46.008°N, 89.701°W; Magnuson et al., 2006; Hansen et al., 2013). Fifty percent of this 64 ha lake is >7 m in depth (maximum depth = 20 m) (Hrabik et al., 1998), and the lake has 3.75 km of shoreline. Physical, chemical, and biological characteristics of Sparkling Lake have been monitored since 1981 by the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program (Magnuson et al., 2006). Rainbow smelt were first detected in Sparkling Lake in the early 1980s and are associated with the collapse of native cisco (Hrabik et al., 1998) and the cessation of walleye recruitment in this lake (Mercado-Silva et al., 2007; Roth et al., 2010).

### Experimental manipulation

Our rainbow smelt removal manipulation consisted of three parts during 2002–2009: removal of spawning rainbow smelt (described below), a harvest regulation change on walleye, and stocking fingerling walleye. At high densities, walleye predation on rainbow smelt

has been shown to mitigate negative effects of rainbow smelt such as the decline of native cisco (Krueger & Hrabik, 2005). Walleye harvest was restricted from a daily bag limit of 5 walleye  $\geq 15$  inches (381 mm) to a daily bag limit of one walleye  $\geq 28$  inches (711 mm), which is the most strict walleye regulation in Wisconsin, short of closing the fishery. In an attempt to increase predator densities, walleye extended growth fingerlings ( $\geq 6$  inches or 152 mm) were stocked once annually at  $8.1 \text{ ha}^{-1}$  throughout the duration of the experiment. Our targeted stocking rate was the maximum stocking rate allowed by the Wisconsin Department of Natural Resources. This rate was achieved in all years except for 2002 when extended growth fingerlings were stocked at  $6.6 \text{ ha}^{-1}$ . Prior to 2002, small fingerlings (1.25–2 inches or 32–51 mm) were stocked in 1997, 1999, and 2001, and adults were stocked in 2000 and 2001.

#### Environmental data

We used datasets of abiotic variables to test for changes in rainbow smelt spawning behavior relative to environmental conditions and for a bioenergetics modeling assessment of walleye consumption of rainbow smelt (detailed below). Specifically, the annual ice-off date and daily water temperatures for Sparkling Lake during 2002–2009 were obtained from the NTL-LTER database (NTL-LTER, 2012a, b).

#### Rainbow smelt sampling

Spawning rainbow smelt were intensively harvested in spring with mini-fyke nets during 2002–2009 (NTL-LTER, 2011). Mini-fyke nets are passive trap nets with a 7.62 m or 15.24 m lead net of 3.175 mm mesh bar that guides fish toward either a  $0.91 \text{ m} \times 0.91 \text{ m}$  or a  $0.91 \text{ m} \times 0.61 \text{ m}$  opening on a cone-shaped net bag. Spring netting occurred at or before ice-out to take advantage of their dense spawning aggregations in shallow waters (Evans & Loftus, 1987), during which they are highly vulnerable to capture using fyke nets (Lischka & Magnuson, 2006).

Nets were dispersed around the lake and set for 24-h. The number of nets deployed varied among and within years (Table 1). The ice was manually removed from portions of the shoreline when nets were deployed before ice-out; the nets were checked about 10 h into the set to ensure that ice movement had not

collapsed them. The number of days we sampled for rainbow smelt varied among years due to variability in the duration of the rainbow smelt spawning season (Table 1). Within a season, nets were initially dispersed around the lake with several nets near locations of spawning sites in the previous years (Lischka & Magnuson, 2006). As the spawning run progressed, nets with no or low catches were moved to locations where rainbow smelt were actively spawning to maximize harvest. During 2002–2009, we recorded total weight (g) of the daily catch as well as lengths (mm) and weights (g) for a subset of 50 individuals or the entire daily catch when less than 50 individuals were captured. In order to estimate the total number of individuals caught on a given day, we divided the total weight of the daily catch by the weight of the average individual in the daily subset.

The relative abundance of rainbow smelt was assessed using NTL-LTER gillnet observations during 1982–2013. The type of gillnets used switched from multifilament to monofilament nets starting in 1991. The relative catchability of rainbow smelt in multi- and monofilament nets was examined in 1994 and revealed that monofilament 19 mm nets captured 1.72 times more rainbow smelt than multifilament nets of the same mesh size. This correction factor was applied to all pre-1991 gillnet catches. Gillnet sampling consisted of two 24-h mid-summer gillnet sets using stretched mesh sizes of 19, 25, 32, 38, 51, 64, and 89 mm (NTL-LTER, 2013). Gillnet catch per unit effort (CPUE) was calculated as the number of rainbow smelt  $\text{net}^{-1} \text{ day}^{-1}$ .

Rainbow smelt pelagic biomass and density were assessed annually in mid-summer during 2001–2011 using hydroacoustics (NTL-LTER, 2012c). Sonar data were collected using a Biosonics DT-6000 Echosounder with a 120 kHz split beam transducer (2001–2003) and a Biosonics DT-X echosounder with a 70 kHz split beam transducer (2004–2011) using pulse duration of 0.04 ms. Minimum thresholds for volumetric backscattering strength were  $-65$  decibels (dB), and single target thresholds were  $-55$  dB for each frequency. Calibration was performed prior to each survey and never deviated more than 1 dB from the expected target strength for each unit. Post-processing of acoustic data collected with each frequency was performed using Ecoview v. 4.1 (Myriax Inc.). Density estimates were apportioned to species based on numerical proportions, and mean sizes from

**Table 1** Summary of fyke netting effort and harvest among years in Sparkling Lake, WI from 2002 to 2009

Year	Number of days with nets deployed	Number of days of days catching fish	Total net days	Number of nets deployed (maximum)	Number of nets deployed (minimum)	Number of nets deployed (mean)	Biomass removed (kg)
2002	11	10	161	16	10	14.6	1,727.2
2003	8	7	88	16	5	11	374.8
2004	11	11	203	30	5	18.5	909.9
2005	10	7	129	18	1	12.9	34.5
2006	9	7	95	13	5	10.6	72.3
2007	7	6	89	15	6	12.7	32.6
2008	17	11	178	15	4	10.5	1,003.1
2009	10	8	93	14	2	9.3	16.5

vertical gillnet samples were collected within days of sampling with hydroacoustics. Densities were obtained for the entire rainbow smelt population and for spawning adults. Individuals were considered adults if they were  $\geq 25$ th percentile of observed lengths of rainbow smelt captured in fyke nets ( $\geq 115$  mm). The proportion of rainbow smelt removed annually was estimated as a ratio of the number removed relative to the number removed plus the number of spawning adults as estimated by the summer hydroacoustics assessment.

#### Walleye sampling

We sampled walleye to assess the potential effects of their predation upon rainbow smelt. Walleye length-weight data were obtained from 24-h mid-summer gillnet sets using stretched mesh sizes of 19, 25, 32, 38, 51, 64, and 89 mm during 1981–2012 ( $n = 724$  for all years; NTL-LTER, 2013). Scales and dorsal fin spines collected from Sparkling Lake walleye during spring fyke netting in 2012 were used to estimate length-at-age (Wisconsin Department of Natural Resources, unpublished data). Walleye population estimates for Sparkling Lake were also calculated in 2002 and 2006 (Wisconsin Department of Natural Resources, unpublished data). Walleye diets were sampled (May–September) from 2000 to 2004 via gastric lavage performed on individuals collected using pulsed-DC electrofishing (Roth, 2005). Stomach contents were sorted by taxon, dried at 57°C, and weighed to the nearest 0.001 g.

#### Statistical analysis

To assess the effectiveness of the whole-lake manipulation, we tested for changes in the rainbow smelt population and evaluated the role of predation in controlling this invasive species. We used a breakpoint analysis of a 32-year time series of gillnet CPUEs, a surrogate for abundance, to test whether the removal effort was associated with altered rainbow smelt densities. Gillnet CPUE values were compared to hydroacoustic estimates of spawning adult abundance from 2002 to 2011. We also evaluated an apparent shift in the timing of spawning relative to ice-off throughout the course of the manipulation. Finally, we performed a bioenergetics analysis for walleye to estimate the relative role of predation in controlling this invasive species.

We tested whether CPUE from 1982 to 2013 in the NTL-LTER rainbow smelt gillnet time series changed using a breakpoint segmented regression analysis with R Cran package “segmented” (version 0.2–9.4; Muggeo, 2003). We tested for one and two break points ( $\alpha = 0.05$ ) and compared the breakpoint analyses to a simple, zero break point, linear regression. These CPUE data were also compared to the hydroacoustics data (2001–2011) using Spearman’s rank correlation to test whether gillnet CPUE and hydroacoustics yielded similar trends in rainbow smelt population abundance. All statistical analyses were performed using R Cran statistical package version 3.0.1 (R Development Core Team, 2013).

We tested for a shift in the peak of the rainbow smelt spawn relative to ice-off over time using simple linear regression (Gelman & Hill, 2008). Sampling date was

converted to “day relative to ice-off” by subtracting the day-of-year of the sampling event from the ice-off day-of-year. The peak day of the spawning run was considered the day of the greatest mass of rainbow smelt removed during that spawning season. The “day relative to ice-off” of the peak of the spawning run was regressed against year to test for a change in the timing of the peak of spawn relative to ice-off. In 2003 and 2007, the peak day of spawning occurred on the first day of sampling indicating that the actual peak may have occurred earlier. To account for potential biases associated with the peak occurring on the first day of sampling, we performed our regression analysis on the peak of spawn relative to ice-off among years for years when the peak occurred after our first day of sampling (i.e., 2002, 2004–2006, 2008, and 2009) as well as in all years. We also used linear regression to test for relationships between the day-of-year of ice-off and both year and the peak day of the run relative to ice-off ( $\alpha = 0.05$ ).

#### Bioenergetics modeling

Annual consumption (kg) of rainbow smelt by the walleye population in Sparkling Lake was estimated using Bioenergetics 3.0 (Hanson et al., 1997) modified to run in R version 3.0.1 (R Development Core Team, 2013). The approach we used involved first estimating size-specific annual walleye consumption of rainbow smelt. Size-specific estimates were then applied to the known walleye population structure and density in Sparkling Lake to estimate the biomass of rainbow smelt consumed by the standing stock of walleye.

A bioenergetics model is a simple energy budget equation in which information on fish growth and relative proportions of diet items can be used to estimate the quantity of each diet item an individual consumed over a given time period (Hanson et al., 1997; Kitchell et al., 1977). To estimate consumption of an individual walleye, the analysis requires information on walleye growth ( $\Delta g$ ), walleye diets including the proportion of rainbow smelt in walleye diets, water temperature, and a suite of physiological parameters. The physiological parameters we used for walleye were temperature dependent functions for consumption, respiration, and egestion/excretion rates and were acquired from Hanson et al. (1997) and Kitchell et al. (1977).

Several bioenergetics model inputs were specific to Sparkling Lake including walleye growth and diets. Annual walleye growth (change in length) was determined by applying length-at-age estimates from scales and dorsal fin spines of walleye captured in 2012 from Sparkling Lake by the Wisconsin Department of Natural Resources ( $n = 148$ ) to a von Bertalanffy length-at-age model (Ricker, 1975; Isely and Grabowski, 2007) with R Cran package “fishmethods” (version 1.5-0). The analysis yielded the following von Bertalanffy length-at-age model:

$$\text{walleye length} = 648.83 \cdot \left(1 - e^{-(0.28 \cdot (\text{walleye age} + 0.29))}\right). \quad (1)$$

Since the growth metric for bioenergetics modeling is weight, we applied our length-at-age model to a walleye length-weight model to estimate weight-at-age and, subsequently, annual change in weight.

We developed a length-weight relationship for walleye caught in Sparkling Lake during 1981–2012 by the NTL-LTER ( $n = 724$  for all years; detailed above). The relationship was developed using 50th percentile (median) quantile regression (Cade & Noon, 2003) with R Cran package “quantreg” (version 5.01). The length-weight relationship was transformed using a power function (log–log), and the analysis yielded the following model:

$$\text{walleye weight} = e^{-12.69 + 3.18 \cdot \log_e(\text{walleye length})}. \quad (2)$$

The length-weight relationship (Eq. 2) was applied to the von Bertalanffy length-at-age model (Eq. 1) to estimate weight-at-age, which was used as the growth input for the bioenergetics model.

Diets were obtained from 281 Sparkling Lake walleye (Roth, 2005). Diet item taxonomic groups included amphipods, crayfish, other aquatic invertebrates, terrestrial invertebrates, rainbow smelt, and other fishes (predominantly cyprinids). Diet proportions (% by dry mass) were calculated for each taxon with rainbow smelt representing 23.3%. Prey energy densities for invertebrates and fishes were obtained from Cummins & Wuycheck (1971) and amphipods from Hanson et al. (1997). Dry to wet weight ratio of rainbow smelt was assumed to be 14.5% based on the relationship between percentage dry weight and wet weight caloric density developed in Lantry & Stewart (1993) as applied to their mean estimate of energy densities of 96–140 mm rainbow smelt.

Daily Sparkling Lake water temperatures during 2001–2009 were used as a bioenergetics model input (NTL-LTER, 2012a). We identified the maximum and minimum daily water temperatures from thermal profiles and used the extreme daily values observed during 2001–2009 to estimate the range of temperatures available on a given day. We assumed walleye behaviorally thermoregulated to live at their optimal temperature (22°C) for growth when available (Kitchell et al., 1977). When unavailable, we assumed that they behaviorally thermoregulated to live at the temperature nearest to 22°C.

Bioenergetic analyses were performed on walleye size classes ranging from 175 to 625 mm at 50 mm increments. To estimate population-level consumption of rainbow smelt, the size-specific estimates were applied to the walleye population size structure of individuals caught during 2001–2009 ( $n = 106$  for all years) in Sparkling Lake by the NTL-LTER using a variety of sampling methods (NTL-LTER, 2013). We then used the population size structure, size-specific estimates of consumption, and walleye density estimates (5.1–10.3 walleye  $\text{ha}^{-1}$ ) to estimate walleye consumption of rainbow smelt. These walleye consumption estimates across the observed range of densities were compared to the mid-summer pelagic biomass of all ages of rainbow smelt observed using hydroacoustics.

## Results

The effort of our experimental removal varied among years (Table 1). The number of nets deployed daily in a given year ranged from 1 to 30 with an annual average ranging from 9.3 to 18.5 nets  $\text{day}^{-1}$ . The duration of removal also varied among years with the number of days with nets deployed ranging from 7 to 17 days. Deployed nets did not always catch rainbow smelt; therefore, the number of days during which rainbow smelt were captured ranged from 6 to 11 days.

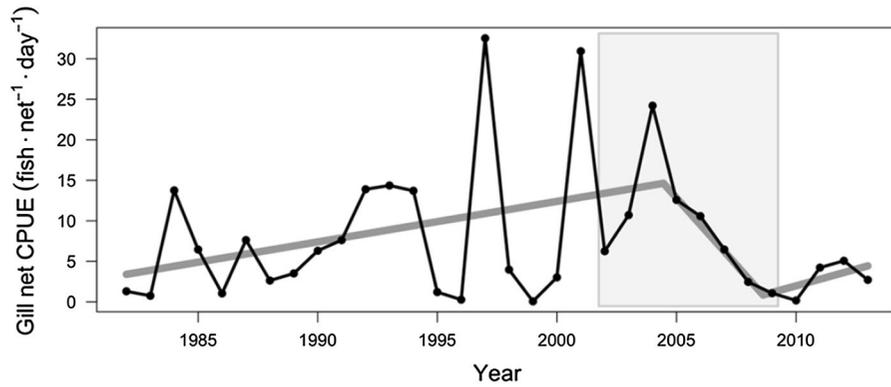
Significant changes in rainbow smelt CPUE trajectories were observed following the onset and cessation of experimental spring removals (Fig. 1). Prior to the removal, rainbow smelt CPUE was variable (which is not uncommon for gillnet catches; i.e., see Krueger & Hrabik, 2005), but generally increased through time. A significant decline in rainbow smelt CPUE was observed in 2004, two-years after the onset of removal.

Rainbow smelt CPUE increased significantly following the cessation of the removal effort. The single-breakpoint analysis identified a change in 2004. However, the slope and intercept were not significant ( $P > 0.05$ ,  $R^2 = 0.19$ ). The double-breakpoint analysis identified significant changes in 2004 (SE 2.2 years) and 2009 (SE 2.6 years) and had significant intercept ( $P = 0.04$ ) and slope ( $P = 0.04$ ) coefficients ( $R^2 = 0.24$ ). The break-points improved the model fit over a simple linear regression ( $R^2 < 0.01$ ), which was not statistically significant ( $P > 0.05$ ). The CPUE data were positively correlated with spawner hydroacoustic abundances estimates (Spearman's  $\rho = 0.71$ ) reinforcing the likelihood that while the gillnet CPUE estimates were variable, they reflect similar relative rainbow smelt abundances as the hydroacoustic estimates.

The magnitude of the rainbow smelt spawning run varied among years, with the biomass removed on the peak day ranging from 7.4 to 496.8 kg (Fig. 2). Annual biomass of rainbow smelt removed during the experiment ranged from 16.5 kg in 2009 to 1727.2 kg in 2002 (Table 1). The standing stock of rainbow smelt estimated with hydroacoustics varied over time. Before the experiment, in 2001, the mid-summer standing stock of rainbow smelt was about 900,000 individuals with a biomass of about 3,000 kg. During the experiment, the mid-summer standing stock of rainbow smelt ranged from about 450,000 individuals in 2002 to <60,000 in 2008 (Fig. 3). The standing stock of adults ( $\geq 115$  mm) ranged from >213,000 in 2001 to <12,000 in 2010. The proportion of adults removed annually ranged from 0.02 in 2007 to 0.93 in 2008, with <8% of spawning rainbow smelt removed in half of the removal years and more than 40% removed in three of 8 years.

The peak of the rainbow smelt spawning run shifted earlier relative to ice-off (Fig. 4;  $P = 0.03$  and  $R^2 = 0.68$  for peak observed data only,  $n = 6$ ;  $P = 0.03$  and  $R^2 = 0.58$  for all years,  $n = 8$ ). The peak of the spawning run occurred 8 days after ice-off at the onset of the removal and occurred 1–2 days before ice-off by 2009. No relationships were observed between the day-of-year of ice-off and year ( $P = 0.54$ ) or between the day-of-year of ice-off and the peak day of the run relative to ice-off ( $P = 0.70$ ).

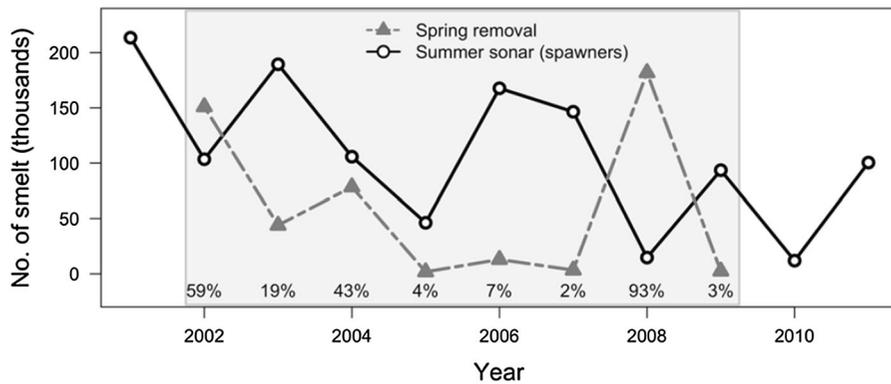
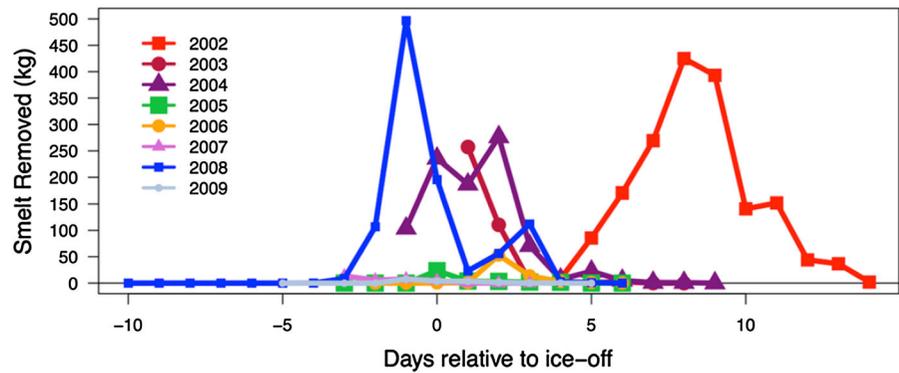
We achieved walleye densities of 5.1–10.3 walleye  $\text{ha}^{-1}$  in Sparkling Lake through stocking and restricted harvest; however, our bioenergetics analysis indicated that these densities were not high enough to



**Fig. 1** Rainbow smelt (*Osmerus mordax*) mid-summer gillnet catch per unit effort (fish net<sup>-1</sup> day<sup>-1</sup>) from the North Temperate Lakes Long-Term Ecological Research program during 1982–2013 (Black line and points). The gray region represents the period of experimental removal. Shown with

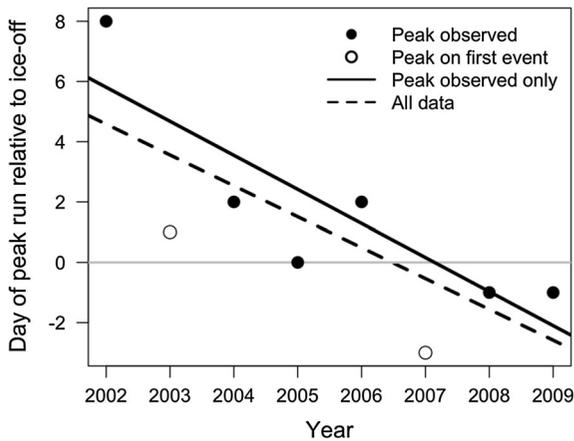
double-breakpoint (solid light gray line) segmented regression analysis. The double-breakpoint segmented regression analysis identified break points at 2004 (SE 2.3 years) and 2010 (SE 1.8 years); the slope and intercept were significant at  $P \leq 0.05$  ( $R^2 = 0.23$ )

**Fig. 2** Annual time series of daily mass (kg) of spawning adult rainbow smelt (*Osmerus mordax*) removed from Sparkling Lake, WI during 2002–2009 using fyke nets. Days are relative to annual ice-off date



**Fig. 3** Number of rainbow smelt (*Osmerus mordax*) removed from Sparkling Lake, WI during 2002–2009 using fyke nets in the spring (gray two-dashed line with gray triangles) and the number detected in the late summer using hydroacoustics. The hydroacoustic estimates are shown for spawning adults

( $\geq 115$  mm; black line with open circles). The gray region represents the period of experimental removal. Shown with the percent of spawning adults removed annually (i.e., No. removed/(No. removed + No. spawning adults))



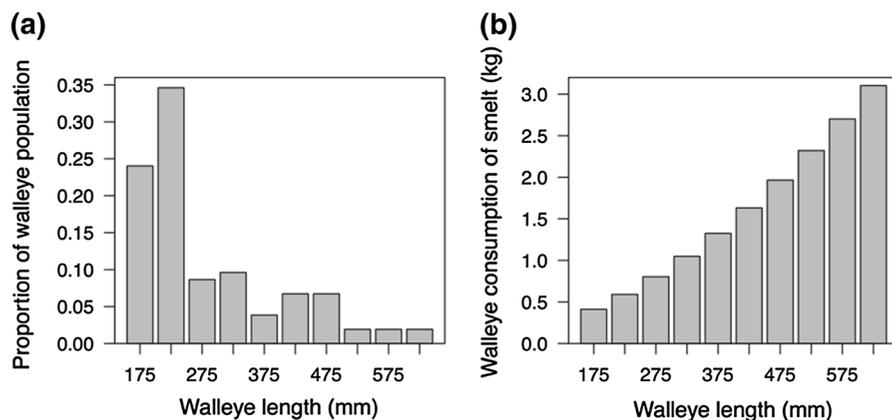
**Fig. 4** The day of peak rainbow smelt (*Osmerus mordax*) spawning relative to ice-off date during 2002–2009. *Solid circles* represent years in which peak spawning occurred after the first sample day. *Open circles* represent years in which peak spawning was observed on the first sample day, indicating that these years could be an overestimate of the peak day. Shown with linear regression models based on only years during which the peak was observed ( $P = 0.03$  and  $R^2 = 0.68$ ; *dashed line*) and all data, including years during which the peak occurred on the first day of sampling ( $P = 0.03$  and  $R^2 = 0.58$ ; *solid line*)

consume the mid-summer standing stock biomass of rainbow smelt. During the experiment, the mid-summer rainbow smelt standing stock total biomass ranged from just over 1,700 kg in 2008 to about 4,100 kg in 2004. Modeled size-specific consumption rates of walleye increased linearly from about 0.4 to 3.1 kg year<sup>-1</sup> for

the 175 mm to 625 mm size classes, respectively (Fig. 5b). When applied to the population size structure (Fig. 5a), we estimated that walleye consumed only between 300 and 611 kg of rainbow smelt given the observed density range of 5.1–10.3 walleye ha<sup>-1</sup>, which fell well below the mid-summer standing stock of rainbow smelt.

## Discussion

Fisheries theory suggests that high fishing mortality in conjunction with low spawning stock biomass can collapse fish populations (Hansen et al., 2010). Our three-pronged approach of intensive spring harvest of rainbow smelt; reduced harvest of walleye, a native predator of rainbow smelt; and predator stocking was correlated with an overall decline in rainbow smelt gillnet CPUE, a surrogate for abundance (Fig. 1). However, we were unable to collapse the population of rainbow smelt in Sparkling Lake even though we removed as much as 93% of the spawning individuals in a given year (Fig. 2). Indeed, our rainbow smelt harvest effort was successful at removing a sizable portion of the population in a matter of days for three of eight removal years. Overall, <8% of the spawning rainbow smelt were removed in half of the study years with an average annual removal of 29% of spawning individuals. Factors related to rainbow smelt spawning behavior (specifically, broadcast spawning potentially



**Fig. 5** Bioenergetics modeling size-specific evaluation of walleye (*Sander vitreus*) predation on rainbow smelt (*Osmerus mordax*). **a** The observed size distribution of walleye (>175 mm) caught in Sparkling Lake, WI by the North Temperate Lakes Long-Term Ecological Research program

using a variety of sampling methods during 2001–2009 ( $n = 106$ ). **b** Bioenergetics modeling derived size-specific estimates of rainbow smelt biomass (kg) consumed annually by walleye in a given size class based on 2000–2004 average diet composition ( $n = 281$ )

enabling successful spawning even while trapped in fyke nets) and fecundity (i.e., a single rainbow smelt can deposit 4.1–40.9 thousand eggs with hatch success of 0.03–7.2%; Nellbring, 1989) may make this species more resilient to eradication via spring netting than other species successfully eradicated via traps and nets (e.g., trout species; Knapp & Matthews, 1998).

Our removal efforts may have been further hampered as the timing of spawning shifted, and rainbow smelt began spawning under the ice (Fig. 4). This change in rainbow smelt spawning behavior proved to be problematic as breaking through ice to set nets is logistically challenging, and shifting ice can decrease net effectiveness. Our removal effort could have exerted a heavy selective pressure, recognizing that invasive species can evolve rapidly in the face of control efforts (Lee, 2002). Phenological changes, such as a change to spawning under the ice, can be associated with overharvest (Lewin et al., 2006). However, causation cannot be inferred from our study due to potential unmeasured confounding variables (Swain et al., 2007). Nonetheless, the temporal correlation between our removal effort and the shift in timing of peak spawn relative to ice-off is intriguing and warrants further investigation.

Trapping and netting removals alone are rarely successful at eradicating invasive fishes (Kolar et al., 2010), and efforts may require increased predation to supplement removal efforts (Hein et al., 2007). Successful eradication attempts of lentic fishes via trapping and netting alone have only occurred in small lakes less than a few hectares in surface area, such as high mountain lakes (e.g., Knapp & Matthews, 1998; Parker et al., 2001; Vredenburg, 2004) or pools (e.g., Lozano-Vilano et al., 2006). However, native fishes have recovered from rainbow smelt invasions following changes in predator harvest regulations and augmented stocking programs, which together increased predator densities (Krueger & Hrabik, 2005).

In Sparkling Lake, walleye harvest regulation changes and stocking resulted in a maximum walleye density ( $\geq 178$  mm) of 10.3 walleye  $\text{ha}^{-1}$ , which, while above the regional norm (Beard et al., 2003; Sass et al., 2004), bioenergetic analyses indicate that the walleye population consumed only a fraction of the rainbow smelt standing stock. However, complete eradication of the rainbow smelt population may be unnecessary as native communities often recover at reduced invader densities (e.g., Krueger & Hrabik,

2005; Hansen et al., 2013; Lathrop et al., 2013). Unfortunately, the increase in rainbow smelt gillnet CPUE following our eradication effort suggests that rainbow smelt may recover from relatively low population sizes (Fig. 1). This capacity is consistent with their tendency to successfully invade new environments during their spreading invasion of North America, which likely propagated from small populations. Additional research is needed to assess the long-term response of the rainbow smelt population to the removal effort and to test whether our efforts reduced the rainbow smelt population enough to allow aspects of the native community, such as natural walleye recruitment, to recover.

### Conclusions and management implications

Several existing management strategies could be implemented to mitigate the effects of rainbow smelt invasions; however, these strategies are not without drawbacks and are not desirable to many stakeholders. For instance, managers may mitigate walleye recruitment failure, one major negative ecological consequence of a rainbow smelt invasion, through stocking and restrictive harvest regulations. Adult walleye densities may be elevated by implementing an intensive and expensive extended growth walleye fingerling stocking program while minimizing walleye harvest. Such an approach may increase walleye predation on juvenile and adult rainbow and constrain densities of this invasive species as demonstrated by Krueger & Hrabik (2005) in Fence and Crawling Stone Lakes, Vilas Co. Wisconsin, USA. While such regulatory changes can increase walleye densities, and subsequently predation on rainbow smelt, this management strategy may reduce catch rates of harvestable fish to near zero, effectively eliminating the fishery. Alternatively, managers may choose to accept the negative effects of a rainbow smelt invasion and simply turn the invaded system into an extensive put-and-take fishery where extended growth walleye fingerlings are stocked with the sole purpose of providing anglers with walleye harvest opportunities. Finally, managers may resort to piscicides followed by restocking of entire fish communities (McClay, 2000).

Our research was motivated by the drawbacks of traditional methods and the need to develop a novel strategy to manage invasive rainbow smelt in hopes of restoring invaded ecosystems. However, selectively

removing spawning adults in conjunction with increasing walleye densities to greater than the regional average (Beard et al., 2003; Sass et al., 2004) did not collapse invasive rainbow smelt in Sparkling Lake. Despite high walleye densities, we found that walleye predation removed only a small fraction of the rainbow smelt biomass. Furthermore, our findings support previous studies suggesting that trapping and netting are not enough to collapse or control an aquatic invasive species in larger lakes (i.e., >3 ha; Knapp & Matthews, 1998). Thus, overharvest does not appear to be a feasible control method as this species potentially exhibits strong compensatory recruitment dynamics at low spawning stocks. For example, the removal of 93% of spawning individuals in 2008 reduced midsummer spawning individual densities to <230 ha<sup>-1</sup>. Yet, 1 year later, the densities had increased to >1,462 ha<sup>-1</sup>.

Prevention is the optimal management practice (Myers et al., 2000; Lodge et al., 2006; Vander Zanden et al., 2010), and managers are left with few viable options once rainbow smelt invasions occur. The persistence of rainbow smelt despite our efforts highlights the need to consider novel, alternative management strategies after rainbow smelt invasion. For example, Gaeta et al. (2012) found that experimental lake destratification could potentially remove critical thermal refuge and eradicate rainbow smelt populations, an experiment currently being field tested in Crystal Lake, Vilas County, Wisconsin. Ultimately, our research and studies by others indicate that the outcome for native fishes and fisheries is likely bleak once rainbow smelt establish. Indeed, without prevention or novel management strategies, management options after a rainbow smelt invasion are limited and often unfavorable.

**Acknowledgments** We thank Steve Carpenter, Tim Kratz, Stacy Lischka, and John Magnuson for guidance and help in the development of this project and comments on earlier versions of the manuscript. We also thank two anonymous reviews for helpful comments. Our research was supported by the National Science Foundation (NSF) North Temperate Lakes Long-Term Ecological Research program and a NSF Biocomplexity award as well as a Graduate Engineering Research Scholars Fellowship to J. Gaeta. B. Roth and G. Sass were supported by a NSF Integrated Graduate Research and Education Traineeship. We thank Jeff Bode of the Wisconsin Department of Natural Resources for help in changing the fishing regulations on Sparkling Lake. We also thank David Gilroy, Jeff Hinke, Damon Krueger, Katie Lee, Liz Leavitt, Steve Martell, Pam Montz, Brad Ray, Jim Rusak, Laura Smith, Scott Van Egren, and

Michelle Woodford for help with field data collection and laboratory analysis.

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