

Eradication via destratification: whole-lake mixing to selectively remove rainbow smelt, a cold-water invasive species

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Abstract. Invasive species can have severe effects on aquatic ecosystems. After invasions occur, eradication should be considered whenever the potential loss of ecosystem services outweighs the cost of the eradication method. Here we evaluate the possibility of destratifying Crystal Lake, Wisconsin, USA, to eradicate the invasive fish rainbow smelt (*Osmerus mordax*). We modeled the effects of three destratification scenarios (non-, low-, and high-mixing) using both physical and biological models. Field observations were used to calibrate the models. Water temperatures estimated from 18 unique DYRESM simulations were used in a bioenergetics model to estimate growth of five age classes of rainbow smelt under normal and destratified conditions. Our simulations indicate that destratification can eliminate optimal rainbow smelt thermal habitat resulting in mortality. Destratified lake temperatures also surpassed several physiological critical temperatures. Bioenergetics simulations predicted a weight loss of 45–55% in yearling and adult rainbow smelt. We found that destratification is potentially effective for eradicating cold-water species in temperate lakes.

Key words: aeration; aquatic invasive species; bioenergetics; DYRESM; destratification; eradication; rainbow smelt (*Osmerus mordax*); thermal stress.

INTRODUCTION

Biological invasions are a leading cause of global biodiversity loss (Sala et al. 2000), act as major agents of global change (Vitousek et al. 1996, 1997), and are often associated with significant ecological and economic costs (Vitousek et al. 1996, 1997, Pimentel et al. 2000). Prevention of biological invasions is the preferred management practice, but invasions continue to occur nonetheless (Myers et al. 2000, Lodge et al. 2006, Vander Zanden et al. 2010). Research scientists, management agencies, and the public often view mitigating the negative impacts wrought by invasive species to tolerable levels as our best, if not only, management strategy (Simberloff 2002). Eradication, conversely, is often viewed as impractical due to logistical difficulties and high costs (Dahlsten 1986, Simberloff 2002). However, eradication attempts have been successful across a range of trophic levels and taxonomic groups (Myers et al. 2000, Simberloff 2002). While most successful eradications have addressed small, localized populations (Clout and Veitch 2002, Simberloff 2002), novel technologies and methodologies may expand opportunities for eradication (Clout and Veitch 2002).

Prior to any eradication attempt, the biological and political feasibility as well as the economic costs and ecological risks of eradication must be considered

(Myers et al. 2000, Clout and Veitch 2002, Vander Zanden et al. 2010). Vander Zanden et al. (2010) identified three major factors to consider while assessing whether or not to eradicate an invasive species: (1) The cost of inaction: What are the economic and ecological costs associated with the invasive species? (2) The cost of the eradication: What are the economic and ecological costs of the eradication attempt? (3) The likelihood of success: Is the eradication attempt biologically and politically feasible? Here, we use the framework outlined by Vander Zanden et al. (2010) to evaluate the likelihood of success of a novel eradication method, lake destratification using bubble plume aeration, to selectively remove invasive rainbow smelt in an inland northern Wisconsin lake.

The Laurentian Great Lakes region is one of the most heavily invaded environments on the planet with over 180 established aquatic invasive species (Holeck et al. 2004, Ricciardi 2006, Vander Zanden et al. 2010). Many of these invasive species, including the rainbow smelt, have spread to inland lakes and streams. Some of the invaders cause considerable harm. The economy of Wisconsin's Northern Highland Lake District (NHL), for instance, is strongly reliant on recreational tourism (Peterson et al. 2003). Yet, aquatic invasive species in the NHL have degraded lake food webs and, subsequently, the ecosystem services these lakes provide (Peterson et al. 2003, Wilson and Hrabik 2006). Reducing the spread, mitigating impacts, or even eradicating these invasive species has been identified as a priority for the

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public, management agencies, and researchers (Wilson and Hrabik 2006).

Rainbow smelt are native to freshwater lakes of northeastern North America (Evans and Loftus 1987, Nellbring 1989). They were purposely introduced to the upper Midwest region in 1912, subsequently spread throughout the Great Lakes region (Van Oosten 1937, Evans and Loftus 1987, Nellbring 1989), and now occur across the Great Plains as far west as the Rocky Mountains (Mayden et al. 1987, Johnson and Goettl 1999). Rainbow smelt were first detected in inland Wisconsin lakes during the 1960s and have since invaded at least 26 lakes (Mercado-Silva et al. 2007). Hundreds of other Wisconsin lakes are also vulnerable to invasion (Hrabik and Magnuson 1999, Mercado-Silva et al. 2006). The ecological costs of rainbow smelt invasions include negative impacts on native fishes, including valued game fish, through predation, competition, alteration of food web structure, and shifts in energy flow pathways (Evans and Loftus 1987). Rainbow smelt invasions in the NHLHD have been particularly well studied by the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) project. Researchers have observed declines in yellow perch (*Perca flavescens*) abundance (Hrabik et al. 1998, 2001), recruitment failure in walleye (*Sander vitreus*, a cultural and economic pillar of the NHLHD and other regions), and both recruitment failure and extirpation of cisco (*Coregonus artedii*) following rainbow smelt invasions (Hrabik et al. 1998, Wilson and Hrabik 2006, Mercado-Silva et al. 2007). These invasions not only degrade native food webs, but also have major economic costs in the form of altered fisheries and the need for expensive hatchery-based put-and-take walleye fisheries.

Despite preying upon and/or competing with many native fishes, adult rainbow smelt often occupy a different thermal niche than many of the native species they impact. Our goal is to evaluate the likelihood of successful eradication using a methodology that exploits the thermal preferences of rainbow smelt. Rainbow smelt are a eurythermal species with adults, yearlings, and young-of-the-years (YOYs) being cold-, cool-, and warm-water fish having optimal temperature ranges of 10–12°C, 14–16°C, and 16–21°C, respectively (Lantry and Stewart 1993). These preferences suggest that adults are vulnerable to removal of cold-water habitat. Read et al. (2011) destratified a 0.47-ha north temperate bog lake with a maximum depth of 4.3 m in 8 days, resulting in a 13.5°C increase in hypolimnetic temperatures and a reduction of more than 16°C in the surface to bottom temperature differential, indicating that destratification is feasible. Moreover, many of the important game fishes of northern Wisconsin, including those in Crystal Lake, are tolerant of warmer temperatures. These considerations suggest that destratification might succeed in removing rainbow smelt without harming native fishes. However, the likelihood of success should be carefully assessed prior to any eradication attempt (Vander

Zanden et al. 2010). Here we combine a water temperature model with a fish growth model to test the prospect that destratification can be used to successfully eradicate rainbow smelt from Crystal Lake, Wisconsin, USA.

METHODS

Study site

Crystal Lake (46°0.3' N, 89°36.7' W) is located in Vilas County, Wisconsin, USA, in the NHLHD and is one of the primary study lakes of the NTL-LTER project, which has measured physical, chemical, and biological lake variables since 1981 (Magnuson et al. 2006). The lake is an oligotrophic, dimictic lake high in the landscape with minimal groundwater input, an area of 33.8 ha, a light attenuation coefficient of 0.24 m⁻¹ (average ice-free Secchi depth of 8 m), a mean depth of 11.4 m, and a maximum depth of 20.4 m. Crystal Lake is circular with a shoreline development factor very close to 1.0. The littoral zone is fairly homogenous and is dominated by sandy substrate with low macrophyte and coarse woody habitat densities. The fish community has been historically dominated by pelagic yellow perch. However, yellow perch drastically declined after the detection of rainbow smelt in 1985 (Wilson and Hrabik 2006).

Physical sampling and temperature model

Water temperatures for Crystal Lake were simulated with the one-dimensional hydrodynamic model DYRESM (Imberger and Patterson 1981) for each ice-free period from 2003 to 2008. DYRESM is a time-dependent Lagrangian layered water temperature model that simulates the vertical distribution of temperature and salinity in a water body using the combined numerical approaches of energy, water, and turbulent kinetic energy budgets. In addition to modeling expected water temperatures in Crystal Lake during these periods, we used the artificial destratification module of DYRESM to simulate the effects of bubble plumes on predicted water temperatures (Etemad-Shahidi et al. 2010). In practice, these plume sources increase vertical mixing in the lake by bubbling air from multiple diffuser sources located on or near the bottom of the lake.

For each year (2003–2008), we simulated three model scenarios: non-mixing (no artificial destratification), low-mixing (low-coverage aeration), and high-mixing (high-coverage aeration). This resulted in a total of 18 unique DYRESM simulations. The high-mixing scenario was designed to simulate a maximum realistic destratifying effort, after which additional diffusers or increased flow rates would not significantly alter water temperatures. The low-mixing scenario represents a more economical destratification system, using approximately 25% of the air flow needed for the high-mixing scenario. The low-mixing and high-mixing destratification scenarios used individual aeration plume flow rates of 0.01 m³/s for 30 and 100 sources, respectively.

Aeration simulations began 14 days after ice-off (ranging from 25 April to 14 May), and continued for 80 days (low-mixing scenario) and 100 days (high-mixing scenario). The NTL-LTER program began collecting high-resolution meteorological observations in 1989, and the simulation years used in this analysis include the coldest (2004) and second-warmest (2007) mean air temperatures during this record (1989–2010; average of air temperatures recorded during each ice-free period on Crystal Lake). For the purpose of testing the viability of a temperature dependent eradication method, we feel these simulation years (2003–2008) represent an adequate range of meteorological conditions on Crystal Lake.

DYRESM is driven by time-series inputs of water inflows and outflows, radiation, air temperature, wind speed, and relative humidity; these inputs are coupled with in-lake parameters including the diffuse light extinction coefficient and the surface momentum transfer coefficient to predict water temperatures. Because Crystal Lake has no measurable surface inflows or outflows during simulation years, and groundwater can be considered to have negligible effects on the heat budget, these components were left out of the simulations. This practice is analogous to previous model efforts of Sparkling Lake, which is similar in size, location, and hydrology (Lenters et al. 2005). Meteorological inputs for DYRESM were logged as hourly averages from a suite of sensors located off-site at the Noble F. Lee Municipal Airport (approximately 13 km southwest of Crystal Lake, 45°55.7' N, 89°43.9' W). Downwelling longwave and shortwave radiation measurements were recorded using an Eppley PIR radiometer and an Eppley PSP pyranometer, respectively (Eppley Laboratory, Newport, Rhode Island, USA). Wind speed, air temperature, and relative humidity were also recorded at the same temporal resolution. Precipitation data, taken as an hourly sum, were measured using a tipping-bucket rain gauge. The DYRESM model was calibrated independently for each simulation period based on manual water temperature profiles, which were taken at 1-m intervals every two weeks from the lake's deepest point (Carpenter 2009).

Fish sampling and measurements

Rainbow smelt were sampled from Crystal Lake to obtain age and growth estimates. Samples were taken using vertical gillnets and beach seines during late July and early August of 2009. Annual growth was estimated using sectioned sagittal otoliths from 25 individuals spanning the observed length range (31–164 mm). Otoliths were mounted in epoxy and a transverse section was removed using a low-speed saw. Annual growth estimates were measured along a radius from the origin to the edge oriented perpendicular to annual growth rings. Age-specific length was estimated using the biological intercept method of back-calculation (Campana 1990). The biological intercept was calculated by

applying the average rainbow smelt otolith radius at time of hatch, as determined by Sirois et al. (1998), to our observed linear relationship of natural-log-transformed total otolith radius and total fish length. Of the 25 individuals aged using otoliths, 5 were YOYs. As a result, annual growth was only back-calculated using the 20 older individuals. Weight at age was determined from back-calculated lengths using a weight–length relationship derived from 100 individuals captured during late July and early August of 2009.

We obtained estimates of adult rainbow smelt diet proportions from 116 individuals captured via short-term vertical gillnet sets (30–100 minutes) in August 2009, May 2010, June 2010, and July 2010. Fish were euthanized upon capture; stomach contents were removed and stored on ice until further analysis in the laboratory. In the laboratory, gut contents were separated into the lowest taxonomic unit using a dissecting scope. Wet weights were measured to determine diet proportions (Appendix).

Bioenergetics modeling

A fish bioenergetics model is an energy budget in which energy consumed is allocated among metabolism, waste, or growth (Hanson et al. 1997). This partitioning of energy is dependent upon temperature (Kitchell et al. 1977). The primary model components used here include temperature as well as age-specific physiological parameters, estimations of annual growth, and diet proportions.

Annual consumption (g/yr) was estimated using the bioenergetics model developed by Kitchell et al. (1977), the software created by Hanson et al. (1997), and the physiological parameter estimates from Lantry and Stewart (1993) for 74 back-calculated annual growth estimates from 20 rainbow smelt individuals. The models were fit to end weight when estimating consumption. Simulations were initiated on 10 April (spawning date) for yearling and adult annuli observations and on 5 May (hatch date) for YOY annuli observations (Hrabik et al. 2001). Simulations ended on 9 April of the subsequent year.

Model input data included diet proportions, growth, and temperature. Diet proportions of YOY rainbow smelt were obtained from Hrabik et al. (2001). LaBar (1993) reported that yearling rainbow smelt annual diet proportions were nearly identical to mid- to late-summer YOY diets. We therefore assumed all yearling diet proportions in Crystal Lake were the same as the mid-July YOY diet proportions reported in Hrabik et al. (2001). Adult diet proportions were obtained during the summers of 2009 and 2010 using methods indicated above. Prey energy densities for diet proportions were obtained from Hanson et al. (1997), Lantry and Stewart (1993), and Cummins and Wuycheck (1971). Observed annual change in weight (g) was determined from otolith back-calculation and the observed weight–length relationship. The average weight at time of hatch (5 May)

for all YOY individuals was assumed to be 0.0616 g as indicated in Lantry and Stewart (1993). Daily temperatures were estimated using DYRESM output for the ice-free season, and were linearly interpolated from NTL-LTER measurements during the ice-on season (Carpenter 2009). In our model simulations, smelt were assumed to occupy waters closest to their optimal temperature (16, 14, and 10°C for YOY, yearling, and adult smelt, respectively; Lantry and Stewart 1993). Consumption for each annuli observation was fit using year-specific temperatures, i.e., growth from 2003 was fit using 2003 non-mixing temperature data.

After establishing the median, minimum, and maximum age-specific start weight (established from the distribution of weights at age derived from otolith back-calculations) and annual consumption (predicted from the distribution of 74 unique bioenergetics model calibration runs), we derived the mean, maximum, and minimum growth trajectories for each age class under the non-mixing, low-mixing, and high-mixing temperature scenarios. Age-specific growth trajectories were simulated using the median observed start weight and the median observed total annual consumption for each age class (age 0–4) during each simulation year (2003–2008). These year-specific growth trajectories were averaged within each age class to yield the mean age-specific growth trajectory from 2003–2008. This procedure was performed under the non-, low-, and high-mixing scenarios totaling 90 bioenergetics model runs that yielded five age-specific mean growth trajectories per mixing scenario. Each age-specific maximum growth trajectory was estimated using the greatest observed start weight and the greatest observed consumption during the best simulation year (i.e., the year that yielded the largest end weight) for each age class. Likewise, the minimum growth trajectory was estimated using the lowest observed start weight and the lowest observed consumption during the worst simulation year. These procedures were repeated under each mixing scenario (non-mixing, low-mixing, high-mixing) totaling 30 bioenergetics model runs to yield the maximum and minimum growth trajectories.

Very little is known about the impacts of thermally induced starvation or the lethal weight loss limits of rainbow smelt. Laboratory studies have, however, indicated that the lethal maximum temperature (i.e., the temperature at which smelt lose locomotive activity and the ability to escape from a temperature that will lead to death) for rainbow smelt is 23.5°C (Wisner and Christie 1987). Those studies also determined that 21°C is lethal after 7 hours of exposure as is 22°C after only 1.5 hours of exposure.

Several studies have investigated starvation independent of thermal stress in different species and found a continuous seasonal weight loss of 30–74% to be lethal, the range of which depends on the species. Based on empirical data, Trebitz (1991) estimated mortality of adult largemouth bass (*Micropterus salmoides*) at 55%

weight loss. In a literature survey of studies on several species of larval and juvenile fishes, Letcher et al. (1996b) found mortality to occur between 46% and 74% weight loss. In their own laboratory study of larval and juvenile yellow perch, they found mortality to occur between 46% and 55% weight loss (Letcher et al. 1996a). A study that included thermal stress, however, observed adult gizzard shad (*Dorosoma cepedianum*) mortality at 30% weight loss relative to a control group (Adams et al. 1985). Based on these studies, we considered a continuous seasonal weight loss of 45–55% to be lethal in our simulations.

RESULTS

Water temperature simulations

DYRESM water temperature simulations indicated that the destratification effort would drastically alter the thermal habitat of the lake during the mid-summer months (1 July–31 August). Under non-mixing conditions, Crystal Lake is dimictic with strong seasonal stratification in the summer, with surface temperatures reaching an average maximum of 23.9°C and bottom temperatures reaching an average maximum of 11.9°C for all simulated seasons (Fig. 1A). A low-mixing effort to destratify the lake greatly altered the stratification strength of the lake, as the estimates of bottom temperatures reached an average maximum of 21.1°C for all simulation years (Fig. 1B). Increasing the mixing effort to a high-mixing scenario further limited the cold water habitat, as bottom temperatures were predicted to reach an average of 22.5°C for all simulation years (Fig. 1C). In all years, increased destratification efforts resulted in warmer bottom waters at the expense of surface waters, as average mid-summer surface waters were reduced from a maximum temperature of 23.9°C in the non-mixing scenario to 23.5°C, and 23.3°C for the low- and high-mixing scenarios, respectively (Fig. 1).

Under the high-mixing scenario, several temperature thresholds important to rainbow smelt physiology were surpassed. The maximum bottom temperature (averaged from 2003 to 2008) under the high-mixing scenario (Fig. 1C) surpassed the water temperature above which rainbow smelt consumption ceases (the critical thermal maxima for consumption, henceforth referred to as the CTM; Hanson et al. 1997) by 10.5°C, 6.5°C, and 1.5°C from adults, yearlings, and YOYs, respectively (Fig. 2). However, the achieved maximum bottom temperature under the high-mixing scenario was well below the CTM of several native fishes normally impacted by rainbow smelt invasions (i.e., walleye, yellow perch, and cisco) or commonly found in invaded lakes (e.g., northern pike or smallmouth bass; Fig. 2). Additionally, laboratory studies have indicated that rainbow smelt will survive for less than 7 hours at 21°C, less than 1.5 hours at 22°C, and have an average lethal maximum temperature of 23.5°C (Wisner and Christie 1987). One or more of these lethal thresholds were surpassed under the high-mixing scenario during all simulated years (Table 1).

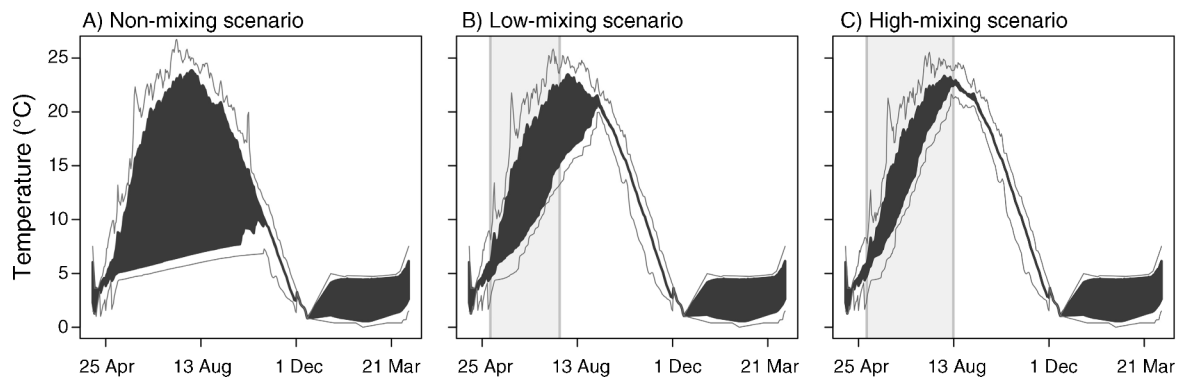


FIG. 1. Simulated temperature range in Crystal Lake, Wisconsin, USA, from 10 April to 9 April of the following year for the (A) non-, (B) low-, and (C) high-mixing scenarios. The dark gray polygon represents the mean maximum and minimum daily temperatures averaged over 2003–2008. The lines represent the range of maximum and minimum temperature observed on a given day from 2003–2008. The light gray box represents the periods of destratification for the manipulation scenarios. Ice-free temperatures were estimated using the DYRESM model. Ice-on temperatures were linearly interpolated between North Temperate Lakes Long-Term Ecological Research (NTL-LTER) temperature observations.

Bioenergetics model

A total of 194 bioenergetics model runs were used to calibrate the model as well as estimate median, minimum, and maximum age-specific growth trajectories. The bioenergetics model was calibrated using 74 annuli observations (observations of ages 0–4 were 20, 19, 15, 12, and 7 annuli, respectively) from 20 individuals fit to the DYRESM non-mixed temperature scenario from 2003 to 2008 (Fig. 3A and B). The median annual consumption was 22.2 g/yr for YOYs, 52.9 g/yr for yearlings, and ranged from 92.0 to 139.7 g/yr for adults (Fig. 3C). The median proportion of maximum consumption (henceforth referred to as PMC; a value that scales from 0 to 1.0 representing zero feeding to the

maximum possible governed by body size, thermal history, and diet; Kitchell et al. 1977) was 0.51 for YOYs and ranged from 0.33 to 0.35 for yearlings and adults (Fig. 3D).

Yearling and adult rainbow smelt exhibited a greater maximum consecutive weight loss under both low- and high-mixing scenarios relative to the non-mixing scenario (Figs. 4 and 5). Additionally, the timing of the consecutive weight loss shifted from winter in the non-mixing scenario to late summer and early fall in both mixing scenarios (Fig. 4). Summer weight loss occurs as abnormally high water temperatures exceeded the CTM. The average YOY rainbow smelt, however, does not lose any weight regardless of the scenario

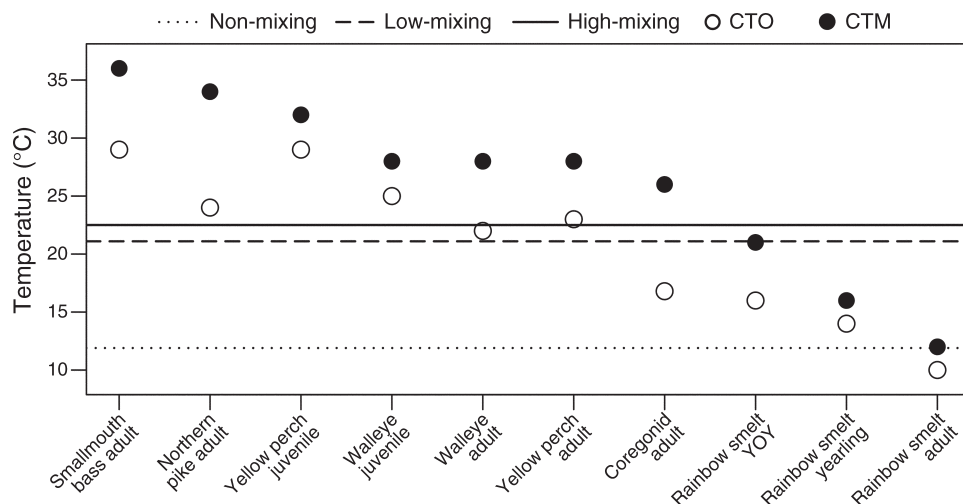


FIG. 2. The optimum and maximum temperatures for consumption: data are presented for rainbow smelt and for commonly impacted species (yellow perch, *Perca flavescens*; walleye, *Sander vitreus*; coregonid species) and common game fishes (smallmouth bass, *Micropterus dolomieu*; northern pike, *Esox lucius*) in invaded lakes, relative to the maximum observed minimum temperatures under the non-, low-, and high-mixing scenarios (averaged across 2003–2008). “YOY” stands for young of the year. The optimum temperature is the laboratory temperature preferendum for consumption (CTO). The maximum temperature is the maximum water temperature above which consumption ceases (CTM). Data are from Hanson et al. (1997).

TABLE 1. The maximum percentages of the volume of Crystal Lake, Wisconsin, USA, predicted to occur at three physiologically critical temperatures shown with the duration for which the temperature is maintained as predicted by the DYRESM model for the high-mixing scenario from 2003–2008.

Year	Maximum lake volume ≥ 21°C (%)	Time at ≥ 21°C (h)	Maximum lake volume ≥ 22°C (%)	Time at ≥ 22°C (h)	Maximum lake volume ≥ 23.5°C (%)	Time at ≥ 23.5°C (h)
2003	100	1088	100	658	100	98
2004	100	284	100	61	11.8	3
2005	100	1376	100	755	100	78
2006	100	1004	100	723	100	402
2007	100	784	100	304	11	4
2008	100	547	55.3	5	1	3

Notes: Temperatures were identified from laboratory studies that indicated 21°C, 22°C, and 23.5°C are lethal to rainbow smelt after less than 7 h, after less than 1.5 h, and immediately, respectively (Wismer and Christie 1987).

(Figs. 4 and 5). Under the non-mixing scenario, the mean yearling and adult rainbow smelt lose 4.7% and 9.4% of their body weight, respectively. However, yearlings and adults lose 34.9% and 43.3% of their body weight under low-mixing conditions, respectively, and lose 59.7% and 57.4% under high-mixing conditions, respectively.

DISCUSSION

Eradication via destratification?

Our simulated whole-lake destratification effort predicted that minimum water temperatures would increase during the normally stratified season, and thereby eliminate the optimal thermal habitat for yearling and

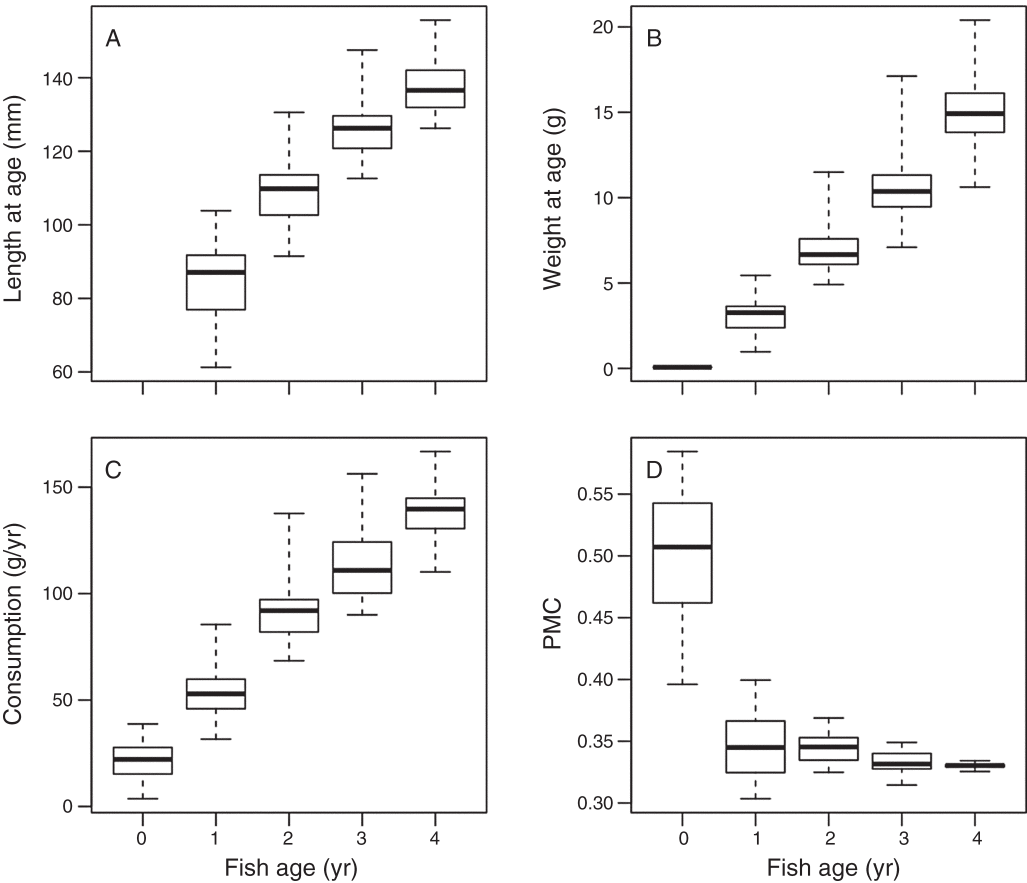


FIG. 3. Bioenergetics model calibration inputs and outputs. (A) Length (mm) at age estimates back-calculated from otoliths. (B) Weight (g) at age estimated from back-calculated lengths at age and a weight–length relationship; weight at time of hatch (age 0) was assumed to be 0.0616 g for each individual (Lantry and Stewart 1993). (C) Annual consumption (g/yr) and (D) proportion of maximum consumption values (PMC) estimates from bioenergetics calibration runs. Box plots are shown with medians, first and third quartiles, and error bars, which represent the total observed range.

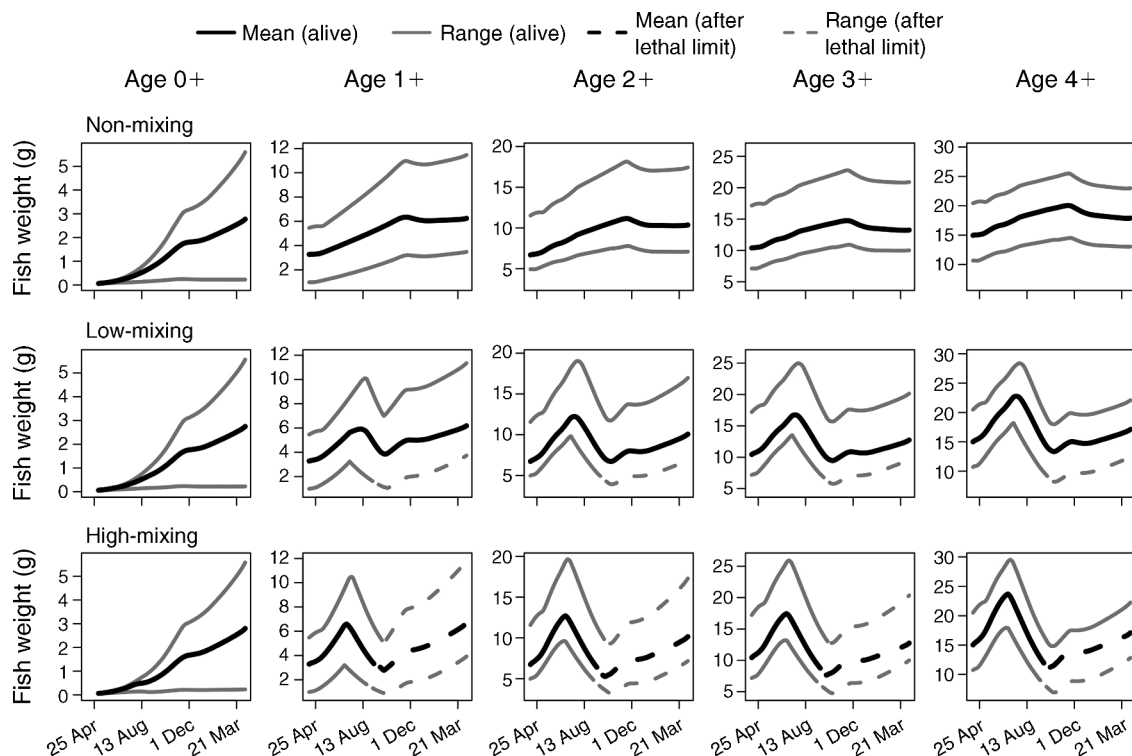


FIG. 4. Predicted age-specific rainbow smelt growth trajectories in the non-, low-, and high-mixing scenarios. Black lines represent the mean age-specific growth trajectories from 2003–2008 (i.e., the median observed start weight and median observed consumption averaged across all years). The gray lines represent the minimum and maximum age-specific growth trajectories (i.e., extreme observed age-specific consumption rate paired with the most extreme observed start weight during the most extreme simulation year). Solid lines represent growth trajectories that have not reached the lethal limit of 50% weight loss (living fish); dashed lines represent growth trajectories after reaching the lethal limit (dead fish). Simulations for age 0 individuals were initiated at the time of hatch (5 May), and age 1–4 individuals were initiated at spawning (10 April).

adult rainbow smelt. These simulations indicate that several physiologically critical temperature thresholds (Wisner and Christie 1987) will be surpassed. However, it is not uncommon for organisms to exceed laboratory thresholds in the wild, for instance rainbow smelt have been reported in large numbers in an isothermal system at 20°C and a single smelt was observed in a system with bottom temperatures that reached 21°C (Franzin et al. 1994). Based on laboratory experiments alone, these temperatures should be lethal after 27 and 7 hours, respectively (Wisner and Christie 1987). Therefore, surpassing laboratory predicted critical temperature thresholds might not be enough to eradicate rainbow smelt from an ecosystem. We therefore used bioenergetics models to predict rainbow smelt growth in the face of prolonged thermal stress.

The bioenergetics simulations predicted that the high-mixing scenario will result in lethal weight losses (a maximum consecutive weight loss of $\geq 45\%$) for both yearling and adult rainbow smelt. The YOY rainbow smelt were not susceptible to the destratification efforts, as simulated increases in minimum water temperatures had negligible effects on growth. Indeed, if our predicted weight loss threshold is lethal to the entire age class, the

complete eradication of rainbow smelt from Crystal Lake would require two consecutive manipulation years. The YOY age-class that was not susceptible to warming in the first year of mixing would become susceptible to warming in the second year of mixing. The findings suggest that, in principle, lake destratification could be used to eliminate thermal refuge and potentially eliminate a cold-water fish species from lake ecosystems. While these results are specific to rainbow smelt, the general approach could potentially be applied to other current or future nuisance cold-water species or, perhaps, warm-water nuisance species with winter mixing.

Evaluating factors of assumed mortality

The bioenergetics modeling approach employed here was intentionally conservative and likely underestimated the potential for the eradication of smelt. The minimum and maximum growth trajectories were plausible but biased toward smelt survival. Indeed, rather than using a measure of statistical dispersion (e.g., interquartile range) as model inputs, the extreme observed age-specific consumption rates (i.e., the largest and smallest for maximum and minimum growth trajectories, respec-

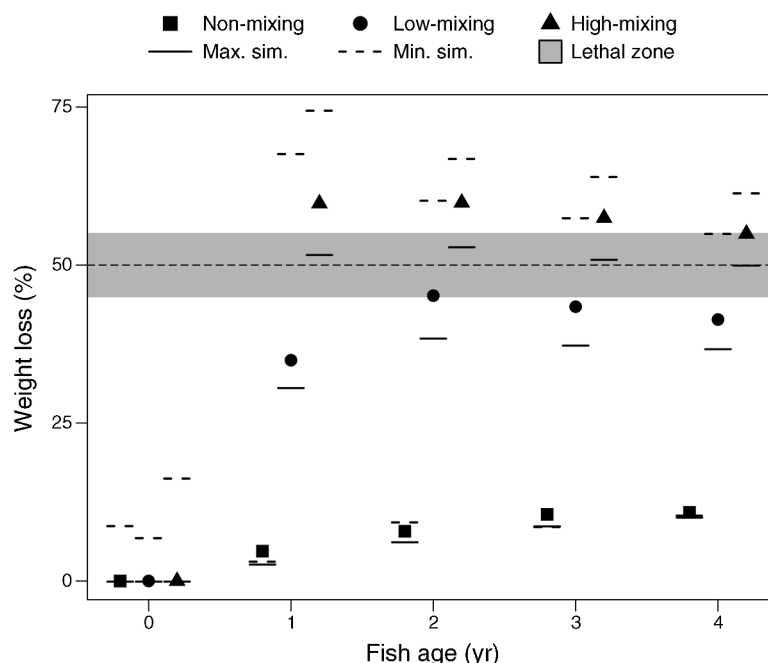


FIG. 5. The predicted mean age-specific consecutive weight loss (%) in the non-mixing (squares), low-mixing (circles), and high-mixing (triangles) scenarios. Lethal weight loss of 45–55% is shown in gray. Dotted and solid lines are the age-specific weight loss (%) of the minimum (Min. sim.) and maximum (Max. sim.) growth trajectory simulations, respectively (i.e., extreme observed age-specific consumption rate paired with the most extreme observed start weight during the most extreme simulation year).

tively) were paired with the most extreme observed start weights during the most extreme simulation years (i.e., the years that yielded the most extreme end weights; Fig. 3B and C) inflating the maximum and minimum growth trajectories.

The bioenergetics simulations were also fit to consumption (i.e., total weight consumed per year), regardless of the PMC. In order to annually consume the amount of food required by the model, yearling and adult individuals were forced to forage at a PMC greater than 0.55 in the high-mixing scenarios, i.e., a value that was well above what we observed for these ages during model calibration (Fig. 3D). This occurred because as temperatures reached and surpassed the CTM during mid-summer, prey consumption was greatly reduced or stopped altogether (Fig. 6; Windell et al. 1976, Hanson et al. 1997) causing rapid mid-summer weight loss (Fig. 4; Kitchell et al. 1977). To compensate for the reduction in mid-summer consumption, the model forced rapid and likely unrealistic increases in consumption (Fig. 6B and C) and weight (Fig. 4) in early summer and again over winter when temperatures were below the CTM. We allowed consumption to be inflated to nearly unrealistic levels to account for unpredictable environmental variability associated with lake destratification and to maximize the conservative nature of our analysis. Nonetheless, the weight gain that preceded reaching the CTM was insufficient to prevent lethal weight loss for yearling and adult rainbow smelt during high-mixing scenarios (Figs. 4 and 5).

The critical lethal threshold of a consecutive weight loss of 45–55% was derived from a literature survey of other species and may be larger than the actual threshold in the field. The threshold of 45–55% was observed in laboratory starvation experiments that did not include the thermal stress that rainbow smelt would be subjected to in our simulations (Trebitz 1991, Letcher et al. 1996a). Looking into the additive effects of starvation and thermal stress on gizzard shad, Adams et al. (1985) identified a critical weight loss limit of 30%, suggesting that smelt may die well before the targeted weight loss of 45–55%.

A limit of the modeling approach employed here, however, is that we can only use weight loss as a metric for mortality, not the interaction of thermal stress and weight loss. Indeed, under the high-mixing scenario, rainbow smelt are predicted to surpass several physiologically lethal temperature thresholds by mid-August (Wisner and Christie [1987] report survival at less than 7 hours at 21°C, less than 1.5 hours at 22°C, and have an average lethal maximum temperature of 23.5°C; Fig. 1), but do not reach a weight loss limit of 50% until late September or early October (Fig. 4). This suggests that the additive effects of thermal stress and starvation may be lethal before the weight loss threshold is reached, adding to the conservative nature of our bioenergetics results.

If a weight loss of 45–55% is sublethal and these physiologically critical temperatures fail to induce mortality in a natural system, overwinter survival is

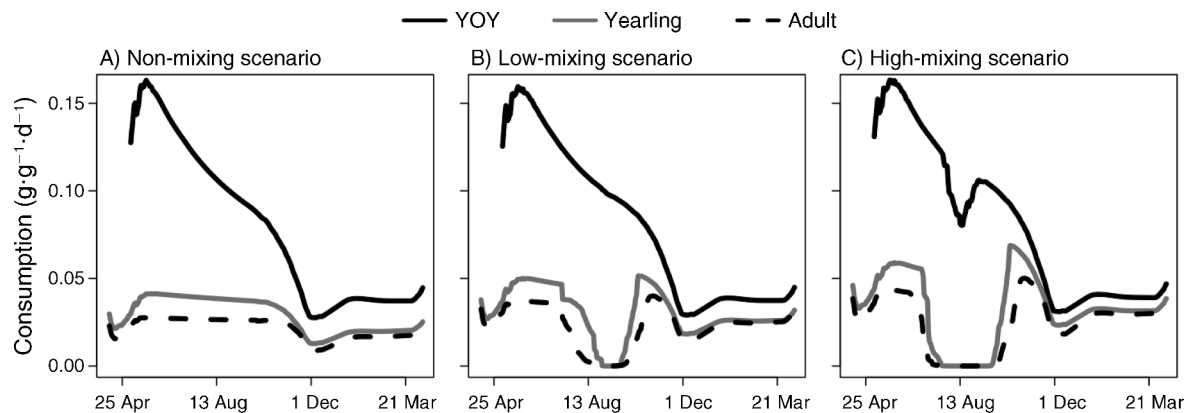


FIG. 6. The mean consumption estimates ($[g \text{ food consumed}] \cdot [g \text{ fish}]^{-1} \cdot d^{-1}$) for YOY (solid black line), yearling (solid gray line), and age-4 adult (dashed black line) rainbow smelt under the (A) non-, (B) low-, and (C) high-mixing scenarios averaged across the 2003–2008 simulation years.

possible. We hypothesize that the additive effects of thermal stress and starvation will prevent the development of adequate energy stores for successful reproduction if yearling and adult individuals survive (Adams et al. 1985). Windell (1966) determined that, after prolonged periods of starvation, the stomachs and digestive tracts of fishes shrink and result in slower recovery rates than expected. This suggests rainbow smelt recovery rates and, therefore, energy storage after starvation would be much lower than those predicted by our simulations (Fig. 4), further hindering gonadal development. Therefore, repeating high-mixing destratification for approximately 6 years would allow all age classes to senesce through the system without successful reproduction, eradicating rainbow smelt from Crystal Lake.

Eradication or mitigation?

While the negative impacts of rainbow smelt invasions have been most extensively studied in Wisconsin, issues involving rainbow smelt introductions and invasions are far from exclusive to inland Wisconsin lakes. Indeed, rainbow smelt have been observed as far west as Colorado (Johnson and Goettl 1999), throughout the Mississippi–Missouri River basin as far northwest as Montana and as far south as Louisiana (Mayden et al. 1987), and have been documented throughout the Canadian Shield Lakes of Minnesota, Ontario, and Manitoba (Campbell et al. 1991, Franzin et al. 1994). Wisconsin's NHL, in particular, is a high-risk region for the continued spread of rainbow smelt (Hrabik and Magnuson 1999, Mercado-Silva et al. 2006). Rainbow smelt dispersal could occur rapidly in lake rich regions, such as the NHL, with a low gradient landscape and neighboring lakes in close proximity (Hrabik and Magnuson 1999). Furthermore, Hrabik and Magnuson (1999) note that downstream invasions from lakes high in the landscape are nearly impossible to stop due to the tendency of rainbow smelt to spawn in streams where they rapidly disperse small, abundant, eurythermal

larvae. Several invaded lakes in the NHL are high in the landscape, where increased connectivity during high-water years could result in rapid spread to other lakes.

Due to potentially high ecological and economic costs associated with eradication efforts, it is critical not only to evaluate the cost of eradication (Vander Zanden et al. 2010), but also to identify and focus eradication efforts on high-risk systems. Crystal Lake, for example, is isolated high in the landscape; however, past high-water events have formed a stream channel that has served as a surface-water connection to lakes lower in the watershed. A high-water year connecting Crystal Lake surface waters to the watershed during spring spawning could, therefore, result in downstream spread of rainbow smelt. Such an event would give these invaders unimpeded access to numerous lakes lower in the landscape, including nearby Trout Lake, a large water body (1568.2 ha) considered to be one of the NHL's most successful walleye fisheries. The downstream spread of rainbow smelt from Crystal Lake, therefore, has the potential to shift many of the region's economically critical walleye fisheries from naturally reproducing to expensive put-and-take systems (e.g., Sparkling Lake; Mercado-Silva et al. 2007).

Mitigating the effects of a rainbow smelt invasion can help improve local fisheries, but does not prevent further spread. For instance, stocking of the hybrid between striped bass (*Morone saxatilis*) and white bass (*Morone chrysops*) increased predation on rainbow smelt in Horsetooth Reservoir, Colorado (Johnson and Goettl 1999) and changes in harvest regulations increased adult walleye densities in Fence Lake and Crawling Stone Lake, Wisconsin (Krueger and Hrabik 2005). However, these mitigation efforts do not reduce the risk of dispersal to nearby lakes. Lake destratification, in contrast, has the potential to eliminate rainbow smelt and thereby prevent future dispersal to other lakes. Since prevention is the best management practice (Myers et al. 2000, Lodge et al. 2006, Vander Zanden

et al. 2010), eradication efforts such as the one described here should be considered whenever the potential loss of ecosystem services outweighs the cost of the eradication method. Indeed, as Simberloff (2002) eloquently states, “we are not doomed to the biotic homogenization of the Earth, but we will surely lose this war if we do not aim high.”

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SUPPLEMENTAL MATERIAL

Appendix

Adult rainbow smelt diet proportions (*Ecological Archives* A022-044-A1).