

Experimental mixing of a north-temperate lake: testing the thermal limits of a cold-water invasive fish

Zach J. Lawson, M. Jake Vander Zanden, Colin A. Smith, Emily Heald, Thomas R. Hrabik, and Stephen R. Carpenter

Abstract: Species' thermal limits play a key role in determining spatial distributions and understanding their response to changing environments. Manipulation of thermal habitat is a potential avenue of exploration for management of invasive species such as the cold-water rainbow smelt (*Osmerus mordax*), which has adverse effects on native fish communities in central North American inland lakes. In an effort to test the thermal limits and selectively eradicate rainbow smelt, we experimentally mixed Crystal Lake, Wisconsin, USA, during summer of 2012 and 2013 to warm the hypolimnion and eliminate cold-water habitat. This whole-ecosystem manipulation allowed for field testing of published thermal thresholds reported for rainbow smelt. The rainbow smelt population responded to the thermal manipulation by exhibiting unexpected shifts in behavior, intrapopulation divergence in body condition, and significant population declines. Small individuals of each adult age-class tended to survive the manipulation, and the population persisted despite high mortality rates. Our results indicate a high degree of size-based intrapopulation variation in thermal sensitivity for this species. Our findings also raise questions regarding applicability of lab- and model-derived thermal limits to field scenarios, highlighting a need for further field evaluations of species' thermal limits.

Résumé : Les limites de température des espèces jouent un rôle clé dans la détermination de leur répartition spatiale et la compréhension de leur réaction à des milieux changeants. La manipulation de l'habitat thermique est une avenue potentielle à explorer pour la gestion d'espèces envahissantes comme l'éperlan arc-en-ciel (*Osmerus mordax*), une espèce d'eau froide qui a des effets néfastes sur les communautés de poissons indigènes dans les lacs intérieurs du centre de l'Amérique du Nord. Dans un effort visant à vérifier les limites de température et éliminer sélectivement l'éperlan arc-en-ciel, nous avons mélangé expérimentalement le lac Crystal (Wisconsin, États-Unis) durant les étés de 2012 et 2013 pour réchauffer l'hypolimnion et éliminer les habitats d'eau froide. Cette manipulation à l'échelle de l'écosystème a permis la vérification sur le terrain des seuils de températures publiés pour l'éperlan arc-en-ciel. La population d'éperlans arc-en-ciel a réagi à la manipulation thermique par des changements de comportement inattendus, des divergences de l'état d'embonpoint au sein de la population et des baisses significatives de la population. Les petits individus de chaque classe d'âge d'adultes tendaient à survivre à la manipulation et la population a persisté malgré des taux de mortalité élevés. Nos résultats indiquent une forte variation de la sensibilité thermique de cette espèce selon la taille au sein d'une même population. Ils soulèvent également des questions quant à l'applicabilité des limites de température obtenues en laboratoire ou tirées de modèles à des scénarios de terrain, soulignant la nécessité d'autres évaluations sur le terrain des limites de température des espèces. [Traduit par la Rédaction]

Introduction

Abiotic factors such as temperature dictate the within- and among-system spatial distributions of fishes (Jackson et al. 2001). Temperature can act on fishes via several distinct mechanisms. In addition to lethal effects, temperature can directly affect animal metabolic rates, performance, and behavior, as described in the classic "Fry paradigm" (Fry 1947). The concept of thermal niche highlights the idea that a fish species has an optimal temperature, as well as thermal limits beyond which it cannot survive (Magnuson et al. 1979). Thermal tolerances can be estimated from the field by comparing temperature data and species occurrence (Eaton et al. 1995) or in the laboratory by experimentally testing survival in temperature trials (Beitinger et al. 2000). Global change will undoubtedly bring novel environmental and thermal regimes. The question of how species will respond is at the fore-

front of current research. Studies assessing thermal limits underpin current efforts to predict species response to climate and changing thermal regimes (Pörtner and Peck 2010), though predictions of species responses have not often been tested in the field (but see Sellers et al. 1998; Schrank et al. 2003).

Invasive species are a threat to ecosystems (Sala 2000; Carpenter et al. 2011) that can have dramatic ecological and economic consequences (Vitousek et al. 1997; Pimentel et al. 2000, 2005). Rainbow smelt (*Osmerus mordax*; hereinafter referred to as smelt) are a cold-water fish native to northeastern North America (Evans and Loftus 1987; Nellbring 1989) and were introduced into the Laurentian Great Lakes region in the early 1900s (Van Oosten 1937; Evans and Loftus 1987). Smelt have since colonized many inland systems throughout central North America via human transport (Evans and Loftus 1987; Johnson and Goettl 1999) and dispersal through connected waterways (Hrabik and Magnuson 1999). Following in-

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Z.J. Lawson,* M.J. Vander Zanden, C.A. Smith, and S.R. Carpenter. Center for Limnology, University of Wisconsin–Madison, 680 North Park Street, Madison, WI 53706, USA.

E. Heald and T.R. Hrabik. University of Minnesota–Duluth, 207 Swenson Science Building, 1035 Kirby Drive, Duluth, MN 55812, USA.

Corresponding author: Zach J. Lawson (e-mail: zachary.lawson@wisconsin.gov).

*Present address: Wisconsin Department of Natural Resources, 5291 N Statehouse Circle, Mercer, WI 54547, USA.

vasion, smelt commonly cause declines in native fish populations (Hrabik et al. 1998, 2001; Johnson and Goettl 1999; Roth et al. 2010) and are associated with walleye (*Sander vitreus*) recruitment failure (Mercado-Silva et al. 2007). Currently, the principal management tool for smelt is to prevent introductions.

Gaeta et al. (2012) simulated response of smelt to a whole-lake thermal mixing manipulation in a northern Wisconsin lake, and their modeling indicated that it would be possible to extirpate a smelt population by warming all viable cold-water habitat. Thus, a thermal manipulation could provide both a powerful field test of our understanding of thermal tolerances for smelt, as well as a potential management tool for selectively controlling or eradicating an invasive cold-water fish.

Here, we report the results of a 2-year thermal manipulation of a northern Wisconsin lake. We addressed two primary questions: (i) How does a whole-lake mixing manipulation impact the available cold-water thermal habitat within a lake? (ii) How does a smelt population respond to the thermal habitat manipulation? We hypothesized that the whole-lake mixing manipulation would warm all hypolimnetic water within Crystal Lake beyond thermal limits for adult smelt, thereby eradicating all adult year classes (≥ 2 years old). Furthermore, subsequent years of mixing were expected to eradicate younger year classes (0 and 1 years old) of smelt as they transition to cold-water life stages.

Methods

Study site and manipulation

Crystal (46.001°N, 89.610°W; the treatment lake) and Sparkling (46.008°N, 89.701°W; the reference lake) lakes are oligotrophic and mesotrophic lakes, respectively, in Vilas County, Wisconsin, that have been continuously monitored by North Temperate Lakes – Long-Term Ecological Research project (NTL-LTER) from 1981 to the present (Magnuson et al. 2006). Crystal Lake has a surface area of 46 ha, an absolute maximum depth of 20.5 m, a localized maximum depth of 15 m in the western half of the lake, and a mean ice-free Secchi depth of 8 m. Crystal Lake is high in the landscape, has very little groundwater input, and no surface water inlet or outlet (Kenoyer and Anderson 1989). The lake is circular, with a littoral zone composed of a sandy substrate, few macrophytes, and very little coarse woody habitat. Crystal Lake has no recreational fishery, and its fish community is dominated by smelt and yellow perch (*Perca flavescens*). Sparkling Lake (the reference or control lake) is a 68 ha seepage lake with a maximum depth of 20 m and a mean Secchi depth during the ice-free period of 6 m. Its littoral zone is complex and is composed of sand, rocks, coarse woody habitat, and macrophytes. In addition to smelt, Sparkling Lake supports a recreational game fishery composed of smallmouth bass (*Micropterus dolomieu*), walleye, and muskellunge (*Esox masquinongy*).

Physical and biological parameters in Crystal Lake were monitored extensively during premanipulation years (2010 and 2011). During 2011, we designed, constructed, deployed, and tested a semi-autonomous whole-lake mixing system using gradual entrainment lake inverters (GELIs; Read et al. 2011). GELIs are composed of an inflatable air bladder centralized on a geo-membrane that spans a stainless steel frame 8 m in diameter. GELIs are slow moving ($0.07 \text{ m}\cdot\text{s}^{-1}$, $N = 59$) large discs that cyclically travel from the lake bottom to surface under buoyancy and sink when deflated. This oscillation continues until the desired mixing is achieved. Immediately following ice-out in 2012 and 2013, we deployed six GELIs and cycled the GELIs until early September when natural mixing was able to sustain isothermic conditions. The Crystal Lake smelt population was continuously monitored throughout the manipulation. Sparkling Lake was used as a reference system and was monitored by the NTL-LTER program for both physical and biological parameters.

Water temperature

Temperature was monitored in Crystal and Sparkling lakes for the entire ice-free season in all years. Discrete depth-temperature profiles were measured four times per day (minimum frequency) via semi-autonomous environmental sensor buoys deployed in the deepest area of each lake. Vertical resolution of profiles was 1 m for Crystal Lake and 0.5 m (0–5 m), 1 m (5–11 m), 2 m (11–15 m), and 3 m (15–18 m) for Sparkling Lake. A Hydrolab DSX-5 multiparameter profiling sonde was used in Crystal Lake, and NexSens TS110-C and PME Temperature Strings were used in Sparkling Lake. When data were unavailable, linear interpolation was used to estimate temperature at depth.

Potential spatial heterogeneity in Crystal Lake water temperatures was assessed during the 2012 and 2013 thermal manipulation by comparing measurements taken at the primary buoy with those at a spatially distinct secondary buoy, and in 2012 the primary buoy was compared with transects of temperature profiles taken throughout the lake. Crystal Lake's secondary buoy was deployed 400 m west of the primary buoy in a localized 14 m deep bathymetric depression where discrete depth temperature profiles were measured (1 m vertical resolution) on a synchronized schedule with the primary buoy. The secondary buoy was fitted with a string of Onset HOBO Pendant temperature loggers. Manual discrete depth-temperature profiles (1 m vertical resolution) were taken along transects in mid-August and mid-September of 2012, the time period in which the entire lake was at its warmest. August transects consisted of 21 sampling sites (225 m mean distance between sites) along a north-south heading aligned with the deepest area of the lake. September transects consisted of 23 sampling sites (363 m mean distance between sites) along north-south and east-west headings aligned with the deepest area of the lake. Manual temperature profiles were measured with a handheld YSI Pro ODO thermistor sensor. Comparisons between Crystal Lake buoys were made by fitting least-squares regressions to temporally coincident measurements at 13–15 m. Comparisons between the primary buoy and temperature profile transects were made by arithmetic differences of temporally similar measurements observed at the buoy and at all transect depths.

Smelt population dynamics

Smelt population density was estimated via hydroacoustic assessments. Inter-annual trends in smelt densities for Crystal and Sparkling lakes were obtained from the NTL-LTER database (<http://lter.limnology.wisc.edu>; NTL-LTER 2014). Intra-annual time series of smelt densities in Crystal Lake were estimated via hydroacoustic transects conducted 30 min following nautical twilight. We used a 120 kHz Biosonics DTX split-beam echo sounder mounted on a tow body lowered 1 m over the side of the boat. Thresholds for data collection were set to exclude raw echoes below -76 dB for S_v data and -70 dB for target strength (TS) data. Single target analyses were used to estimate sigma values excluding targets below -55 dB , which were applied to S_v data to estimate density of smelt in 200 m segments on each date. We chose 200 m as our segment length based on correlation analyses that demonstrate that segments of that length are not spatially correlated (Holbrook 2011). Segments were then used as samples to estimate variability associated with the density estimates. Monthly overnight vertical gillnet sets (3 m wide; 19, 25, 32, 38, 52, 64, and 92 mm stretch mesh nets) from 0 to 18 m depth were used to calibrate estimates of population densities from acoustic transects. Each acoustic sampling event was divided into 200 m bins using Echoview (version 4.0) software, and all 200 m bins were averaged to compute whole-lake adult smelt density estimates.

We employed our time series of whole-lake smelt population density estimates to estimate population mortality over the course of each sampling season using a model that accounted for smelt that were visible and invisible to our sonar. Boat avoidance by smelt and surface and bottom dead zones required us to ac-

count for smelt that were invisible to sonar. We assumed that the instantaneous mortality rate coefficient m (day^{-1}) for the total smelt population T (including individuals both visible and invisible to sonar) is constant over a time interval:

$$(1) \quad \frac{dT}{dt} = -mT$$

where $T = T_0$, the number of smelt at the beginning of the time series, $t = 0$. Solving eq. 1 yields

$$(2) \quad T_t = T_0 e^{-mt}$$

We assumed that the total smelt population T_t was composed of an observable number of fish P_t and an unobserved number of fish $T_t - P_t$. We assumed that observable fish avoid sonar with rate constant h , and unobservable fish enter the observable pool with rate constant v . Thus, the instantaneous rate of change of observable fish is

$$(3) \quad \frac{dP}{dt} = -hP_t + v(T_t - P_t)$$

We further assumed that exchange between the observable and unobservable pools occurs many times per day. Because this behavior exchange is rapid compared with the rate of mortality, we solved eq. 3 at equilibrium to obtain

$$(4) \quad P_t = \left(\frac{v}{h + v} \right) T_t$$

We then inserted eq. 2 for T_t in eq. 4, which yields

$$(5) \quad P_t = \left(\frac{v}{h + v} \right) T_0 e^{-mt}$$

To fit the model and thereby estimate m , we combined the behavioral term $\left(\frac{v}{h + v} \right) T_0$ into a composite parameter, Q :

$$(6) \quad P_t = Q e^{-mt}$$

Although the parameter Q combines effects of the initial population size and the ratio of movement rates, our interest lies in mortality and not the components of Q . Equation 6 was then fit to sonar time series of adult smelt population densities to obtain intra-annual mortality rate m . Using the observed time series P_t , we estimated m and Q by maximum likelihood. Model parameter error distributions were bootstrapped using 1000 iterations (Efron and Tibshirani 1993). To estimate seasonal mortality M as a proportion of the initial smelt population, we assumed that mortality of visible smelt is the same as mortality of the whole population. Therefore:

$$(7) \quad M = 1 - (P_n/P_1)$$

That is, the proportion of the population that succumbed during the sampling period is one minus the proportion that survived, or the final population (P_n) divided by the initial population (P_1).

Onshore movement

To understand potential activity changes in response to loss of cold-water refugia, trends in smelt onshore movements were monitored using a 3 m tall, 9 m wide, 19 mm stretch mesh gillnet. These nets were set at least biweekly during the summer in the

littoral zone after nautical twilight for no longer than 1 h to avoid major sampling mortality. Catch per unit effort (CPUE) was standardized across all short-term horizontal gillnet sets by taking the total number of individuals in each net set and dividing by the set length (individuals/minute). Individuals were measured to the nearest 1 mm and weighed to the nearest 0.1 g.

Body condition

To infer the basis for selective mortality based on body condition, length and mass data were used to compare August and September body condition in each year using ordinary least-squares (OLS) regression. Both length and mass were log-transformed to meet assumptions of normality. Regressions were first fit to length-mass data for individuals sampled during August. This August regression line was then superimposed on the September length-mass data to visually compare divergence between months.

Age structure and length-at-age

Sectioned otoliths were used to compare age and length-at-age characteristics of individuals in the Crystal Lake smelt population before manipulation and those individuals that survived the 2012 manipulation. From 2010 to 2012, otoliths were obtained from individuals sampled during overnight vertical gillnet sets for hydroacoustic calibration and from short-term gillnet sets to assess onshore movements (described above) from June to September. Individuals that survived the manipulation were sampled within 10 days of ice-out in 2013 using vertical gillnets and beach seines. Individuals were euthanized immediately, and otoliths were taken from all individuals collected. Otoliths were prepared in epoxy, sectioned using a slow-speed saw, and aged under a microscope. Annuli were measured along a radial line from the origin to edge. Length-at-age was estimated using the biological intercept method (Campana 1990). We applied the mean smelt otolith radius at time of hatch (Sirois et al. 1998) to our observed linear relationship of natural-log-transformed total otolith radius and total fish length to calculate the biological intercept. Sectioned otoliths were used to assess age and length-at-age characteristics of smelt that survived the manipulation. Length-at-age comparisons between premanipulation smelt and surviving individuals at the beginning of the manipulation (2012) were made by fitting von Bertalanffy Growth Models (VBGM). VBGM parameters were compared using likelihood ratio tests (Kimura 1980).

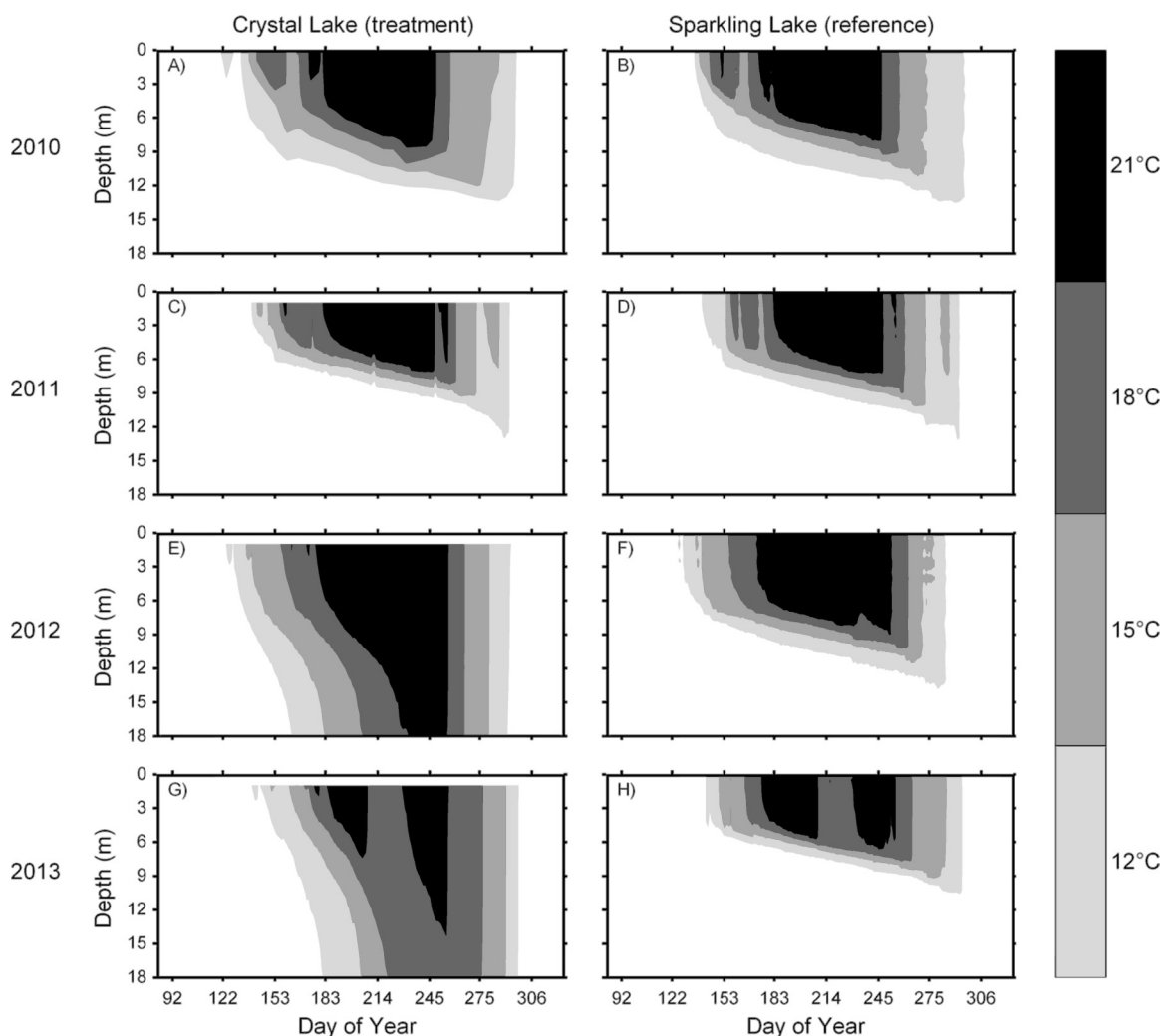
Results

Premanipulation-manipulation and reference-treatment comparisons

The thermal manipulation conducted on Crystal Lake during 2012 and 2013 successfully destratified the water column while simultaneously warming the hypolimnion and removing all cold-water habitat within the lake (Fig. 1). Prior to manipulation, Crystal and Sparkling lakes stratified during spring and remained stratified throughout summer until natural mixing occurred during fall (Figs. 1A–1D). During manipulation years (2012 and 2013) in Crystal Lake, the hypolimnion warmed throughout the summer and reached peak isothermic temperatures in late August (Figs. 1E and 1G). Cooling surface waters in early September sustained isothermic conditions for the remainder of the ice-free season in each manipulation year. The thermal regime of Crystal Lake contrasted sharply with the strong stratification observed in the reference ecosystem, Sparkling Lake (Figs. 1E–1H).

Comparisons of water temperatures measured at the same time and depth by the Crystal Lake buoys show close agreement among buoys in both years of the thermal manipulation. Slopes of least-squares regression fits between buoys were nearly equivalent for 2012 (13 m depth: slope = 0.995, $R^2 = 0.99$; 14 m depth: slope = 1.02, $R^2 = 0.99$; 15 m depth: slope = 1.02, $R^2 = 0.99$) and for 2013 (13 m depth: slope = 0.994, $R^2 = 0.99$; 14 m depth: slope = 0.997, $R^2 = 0.99$; 15 m depth: slope = 1.00, $R^2 = 0.99$).

Fig. 1. Temperature plots for Crystal (left column, manipulation) and Sparkling (right column, reference) lakes show isotherms of critical rainbow smelt temperatures from the literature for premanipulation (2010 and 2011) and manipulation (2012 and 2013) years. Isotherms plotted are as follows: 12 °C ($T_{\text{preferred}}$, light gray; Wismer and Christie 1987), 15 °C ($T_{\text{upper avoidance}}$, medium gray; Ferguson 1965), 18 °C (CT_{Limit} , dark gray; Lantry and Stewart 1993), 21 °C (T_{lethal} , black; Wismer and Christie 1987).



To assess the horizontal consistency of temperature, we compared profiles measured at the primary buoy and cross-lake transects. These comparisons indicated that minimum and maximum differences at all depths and all sites were low (August 2012: min. = 0.2 °C, max. = 0.5 °C, $N = 214$; September 2012: min. = 0.0 °C, max. = 0.1 °C, $N = 227$). The similarity of temperature profiles measured across horizontal transects indicates that the mixing was relatively uniform and did not create cold spots that could serve as thermal refugia for smelt.

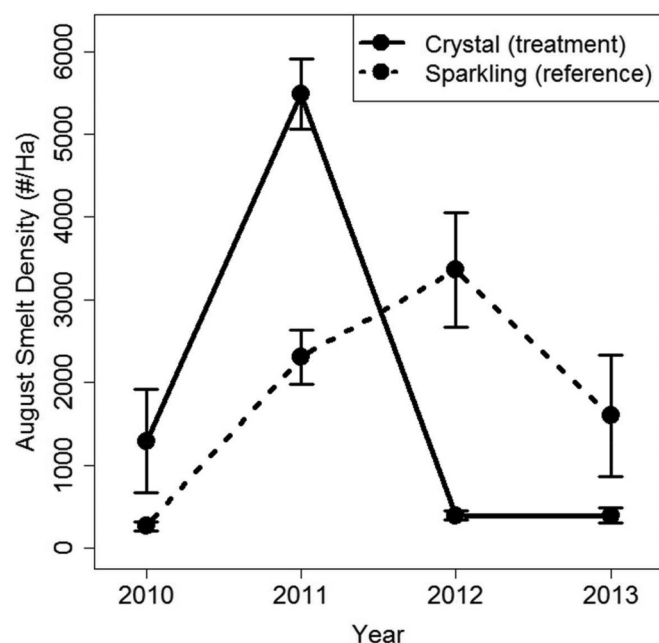
Crystal Lake water temperatures observed throughout the manipulation, at the primary buoy, were representative of temperatures observed elsewhere in the lake. Locations likely to accumulate cold water (i.e., the deepest area of the lake and the localized bathymetric depression to the west of it) were observed to increase in temperature at nearly the same rate. Additionally, potential cold-water thermal refuge from annual groundwater inputs to Crystal Lake are low (0.8% of lake volume; Kenoyer and Anderson 1989), and the associated water table reaches a seasonal low in midsummer, further reducing the chances of groundwater input during the thermal manipulation (NTL-LTER database; <http://lter.limnology.wisc.edu>; NTL-LTER 2014). We employed numerous sampling techniques to search for cold-water refuge and were unsuccessful in finding any. Therefore, we are confident that

all smelt in Crystal Lake were subject to the same extreme thermal habitats created by the manipulation.

Although Crystal Lake was completely destratified during both manipulation years, the maximum temperature achieved was higher in 2012 than in 2013 (21.6 and 20.8 °C, respectively), and the length of time that isothermic conditions exceeded 20 °C was greater in 2012 than in 2013 at 38 and 13 days, respectively. Manipulation year temperatures surpassed most critical temperature estimates for smelt from the literature for extended periods of time: $T_{\text{preferred}} = 12$ °C (Wismer and Christie 1987; 2012: 122 days, 2013: 115 days), $T_{\text{upper avoidance}} = 15$ °C (Ferguson 1965; 2012: 96 days, 2013: 86 days), $CT_{\text{Limit}} = 18$ °C (Lantry and Stewart 1993; 2012: 60 days, 2013: 55 days), and $T_{\text{lethal}} = 21$ °C (Wismer and Christie 1987; 2012: 22 days, 2013: 0 days).

Removal of cold-water habitat in Crystal Lake was associated with reductions in adult smelt population density, which were not noted in Sparkling Lake. In Crystal Lake, late summer adult smelt density increased in premanipulation years, followed by a decline in 2012 and 2013 manipulation years (Fig. 2). The Sparkling Lake adult smelt population showed an overall increasing trend from 2010 to the end of the manipulation in 2013 (Fig. 2).

Fig. 2. Population density estimates for adult rainbow smelt obtained via hydroacoustic surveys conducted during mid-August in Crystal (treatment) and Sparkling (reference) lakes (solid and dashed lines, respectively). 2010 and 2011 were premanipulation years; Crystal Lake was experimentally mixed during 2012 and 2013. Error bars represent 95% confidence intervals.



Smelt populations before and during manipulation

As cold-water habitat in Crystal Lake warmed during manipulation years, smelt exhibited extreme shifts in behavior. During premanipulation years, smelt were rarely observed in the littoral zone following the onset of summer stratification, as shown by short-term gillnet sets (Fig. 3A). During the manipulation, however, smelt were consistently nearshore at night in the warmest water in the lake (Figs. 3B and 3C). The timing of this onshore movement coincided with the entire water column exceeding the upper avoidance temperature of 15 °C for smelt (Ferguson 1965). This onshore movement was accompanied by smelt splashing at the surface at all times of the day. When maximum temperatures were achieved during late August in 2012, we observed smelt coming to the surface. Some individuals appeared lethargic, exhibited compromised locomotion, or lay motionless at or near the surface. However, we were unable to obtain stressed individuals at the surface with any consistency because large flocks of ring-billed gulls (*Larus delawarensis*) consumed vulnerable individuals from the surface before we could recover them.

Annual mortality estimates using each year's time series of smelt population density estimates from acoustic surveys showed significantly higher mortality in manipulation years (Fig. 4). Instantaneous mortality rate (m) of smelt in Crystal Lake prior to manipulation (2010) was 0.396 (interquartile range 0.364–0.417; Table 1). During the manipulation years of 2012 and 2013, the instantaneous mortality rate was 0.921 (interquartile range 0.867–0.957) and 0.898 (interquartile range 0.854–0.950), respectively (mortality rate from reference Sparkling Lake provided in Appendix A). Seasonal mortality associated with the manipulation during 2012 and 2013 was higher than observed prior to the manipulation ($M = 0.921$ and 0.898 , respectively; Figs. 4B and 4C). Bootstrapped median mortality estimates were similar to the nominal least-squares estimates (Table 1), suggesting that the estimation procedure is unbiased (Efron and Tibshirani 1993).

The body condition of smelt had a greater response during the 2012 manipulation than in 2013. In 2012, we observed what ap-

peared to be two distinct groups of individuals in the August length–mass regressions (Fig. 5C): those that exhibited elevated body condition (above August OLS regression line, $N = 66$) and those that exhibited poor body condition (below August OLS regression line, $N = 43$; Table 2; Fig. 5C). However, in September, all smelt sampled exhibited a body condition above the same August OLS regression line (Fig. 5G); only the group with elevated body condition in August remained. Divergence in smelt body condition was most apparent in 2012 (Table 2; Fig. 5).

Characteristics of smelt that survived the 2012 manipulation

Length-at-age relationships for premanipulation individuals and length-at-age of surviving individuals at the beginning of the manipulation (2012) were significantly different (Fig. 6). Although individuals from almost all adult age-classes survived the manipulation (Fig. 7), the largest fish within these age-classes did not (Fig. 6). Yearling smelt that survived the manipulation were larger at the beginning of the manipulation than yearling smelt during premanipulation years (VBGM parameter $K = 1.16$ and 0.10 , respectively; Fig. 6). However, for adult year classes (>2years old), only shorter individuals survived the 2012 manipulation compared with premanipulation fish of the same age (VBGM parameter $L_{\infty} = 258$ and 143 , respectively; Fig. 6). VBGM parameters computed for premanipulation years and for surviving smelt at the beginning of 2012 were significantly different via likelihood ratio test (L_{∞} : $\chi^2 = 18.03$, $df = 1$, $P < 0.001$; K : $\chi^2 = 15.05$, $df = 1$, $P < 0.001$; t_0 : $\chi^2 = 10.73$, $df = 1$, $P = 0.001$). This finding does not suggest that smelt grew differently before manipulation and during the manipulation; rather, our results suggest that smaller individuals of adult year classes survived the manipulation.

Discussion

We completely mixed Crystal Lake during 2012 and 2013 and warmed the hypolimnetic temperatures beyond many published thermal tolerances for smelt. Smelt exhibited extreme shifts in behavior in response to the experiment during both 2012 and 2013. Thermal stress was associated with significant population declines and a rapid divergence in body condition in 2012. The manipulation did not completely remove adult year classes as hypothesized. Rather, smaller adult individuals at the beginning of 2012 ultimately survived the manipulation, whereas larger individuals died.

Smelt exhibited extreme shifts in behavior during the lake-mixing manipulation. We observed smelt consistently jumping at the surface during the day and moving onshore at night. In both cases, smelt moved from the coolest habitat available (hypolimnion) into the warmest thermal habitats in the lake (~24 °C; exceeding published lethal limits). Plausible explanations for these behavioral observations include thermal effects on locomotion, attempting to evade extreme conditions, searching for foraging opportunities to sustain elevated metabolism (Robinson and Pitcher 1989), or potentially seeking warmer water to acclimate as conditions worsen. Studies have documented jumping fish in thermally stressful environments (Davenport and Woolmington 1981) and suggested that this behavior is related to loss of locomotive capability (Huntsman 1942; Bailey 1955). While jumping can be associated with foraging or predator avoidance, these explanations seem unlikely given the simplicity of the Crystal Lake food web. Alternatively, extreme thermal stress may have triggered a flight-type response to escape from an extreme environment (Wingfield 2003). Movements allow for rapid adjustments in localized thermal habitat use (Heggenes 1988), and thermally stressed fish are known to emigrate from stressful environments to seek more favorable conditions (Kaya 1977; Berman and Quinn 1991; Garrett and Bennett 1995). Finally, since acclimation temperature can have an important impact on thermal tolerance (Beitinger et al. 2000), it is possible that these smelt were seeking warmer

Fig. 3. Short-term horizontal gillnet catch per unit effort (CPUE, fish/minute) for rainbow smelt sampled in the littoral zone of Crystal Lake at night during (A) premanipulation (2010 and 2011) and manipulation years: (B) 2012 and (C) 2013.

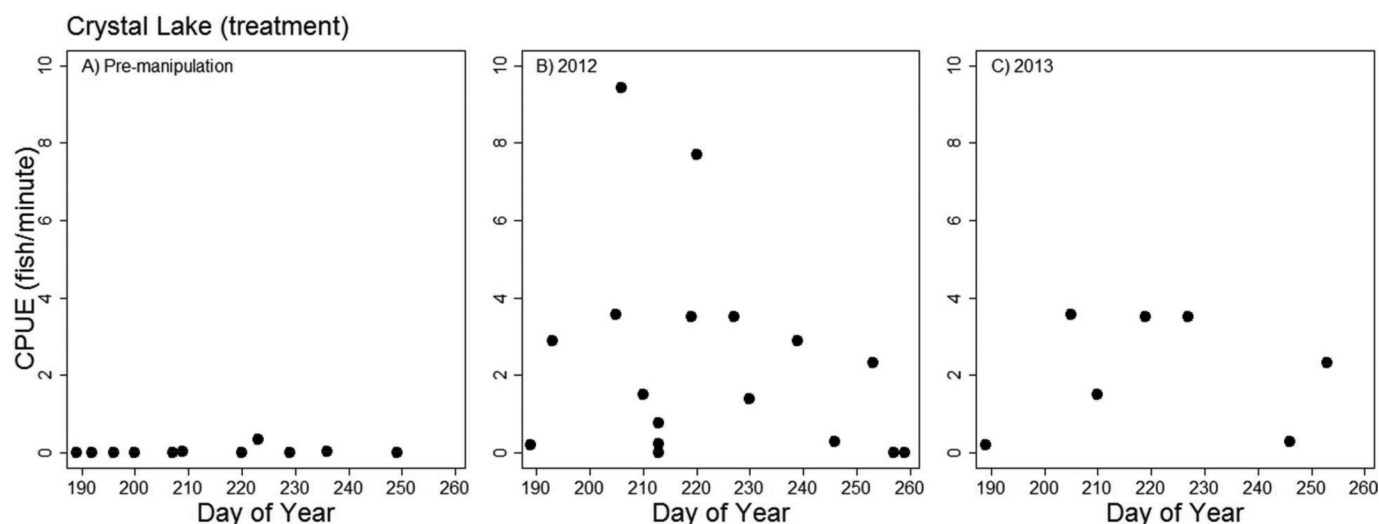
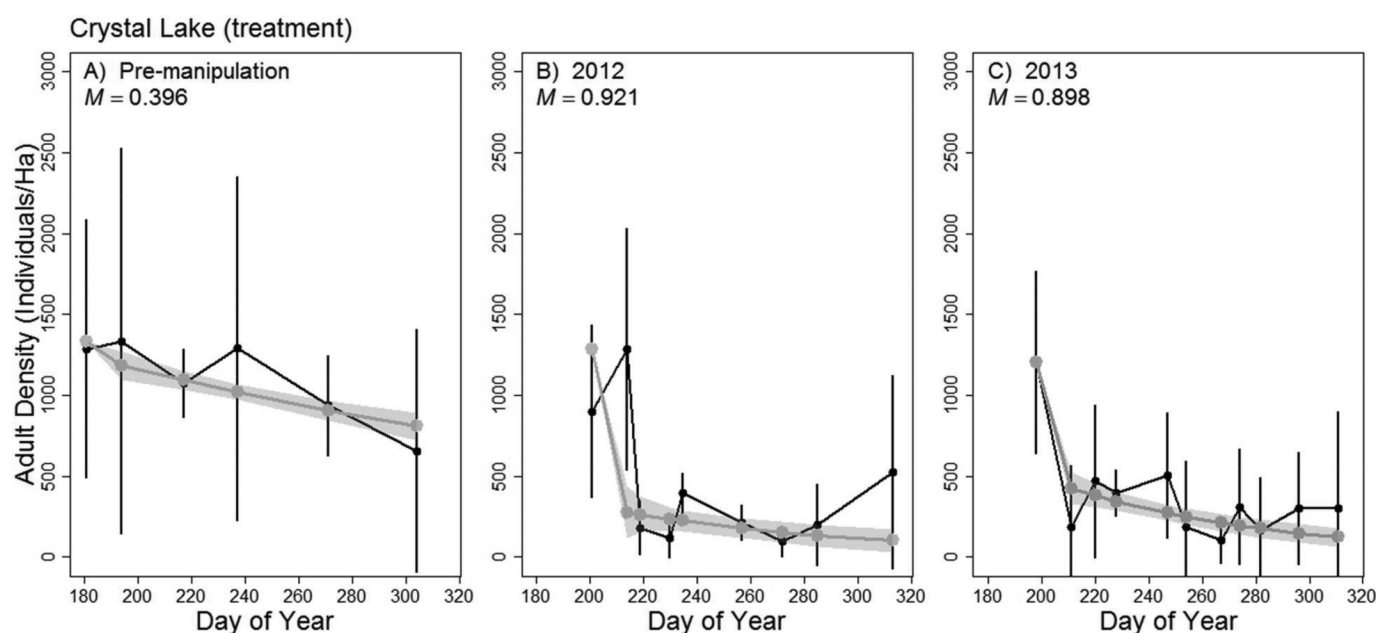


Fig. 4. Rainbow smelt seasonal adult population dynamics in Crystal Lake for (A) premanipulation (2010) and manipulation years: (B) 2012 and (C) 2013. Solid black circles and lines denote adult smelt density estimates from hydroacoustic surveys (\pm SD). Solid gray circles and lines denote model fits used to compute adult smelt mortality (M) over the season (\pm SD of bootstrapped density estimates).



water to acclimate as thermal habitats became warmer. These results provide a rare account of pelagic cold-water fish behavioral response to the loss of cold-water habitat and how fish respond to compromised thermal habitats.

Erratic behavior made it difficult to assess population densities. The model we derived to account for changes in visibility to sonar of smelt (eq. 6 from Methods) produced relatively precise estimates of intra-annual mortality rate (m) and total mortality for each year (M) using a time series of acoustic density estimates. This model could also be used by researchers and managers assessing pelagic fish population mortality over the course of a sampling season when fishes move rapidly in and out of the sonar field. However, this model is not intended for application to populations that exhibit large-scale seasonal migrations. Although application of this model requires effort to obtain a time series of population density estimates, it allows for an effective assessment

of a single seasonal mortality rate for a fish population exhibiting rapid movements among habitats in a lake. The model showed that cold-water habitat removal was associated with a more than twofold increase in mortality rate of adult smelt in Crystal Lake.

Smelt likely experienced mortality throughout the entirety of each manipulation year (as shown by our mortality model); however, we detected one specific time period during 2012 in which a group of individuals disappeared from the population. When hypolimnetic temperatures peaked in August 2012, body condition of the smelt population increased in variability; within weeks (in September), low-conditioned individuals were no longer present (Figs. 5C and 5G). This suggests that individuals with lower body condition did not survive the manipulation or that individuals lost mass and eventually died. We believe that this rapid change in body condition in the smelt population may indicate selective removal of less resilient individuals. Genetic studies have suggested

Table 1. Estimates of smelt mortality in Crystal Lake before manipulation (2010) and in 2 years when the lake was mixed (2012 and 2013).

Year	Estimated quantity	Q (composite parameter for effects of initial smelt population and movement rates)	m (instantaneous mortality rate, day ⁻¹)	M (seasonal mortality, proportion of population)
2010	Nominal least squares	1355.890	0.004	0.396
	Bootstrap median	1352.165	0.003	0.397
	Bootstrap interquartile range	1281.032–1435.279	0.003–0.004	0.364–0.417
2012	Nominal least squares	520.660	0.010	0.921
	Bootstrap median	501.161	0.011	0.925
	Bootstrap interquartile range	287.010–950.038	0.004–0.017	0.867–0.957
2013	Nominal least squares	774.964	0.012	0.898
	Bootstrap median	810.989	0.013	0.894
	Bootstrap interquartile range	585.918–1136.454	0.008–0.017	0.854–0.950

Note: For each year, we present estimates of the composite parameter Q, instantaneous mortality rate (m), and cumulative seasonal mortality (M) from the nominal least squares estimates and bootstrapping (median and interquartile range).

Fig. 5. Rainbow smelt body condition (length–mass relationship; log-transformed for normality) in Crystal Lake associated with peak temperatures during each summer from 2010 to 2013. Each column represents a year, with body condition for August shown in the top row and September in the bottom row. The August ordinary least-squares (OLS) regression line is shown in the August plot (dashed black line) and is reproduced in the September plots for reference (gray dashed line).

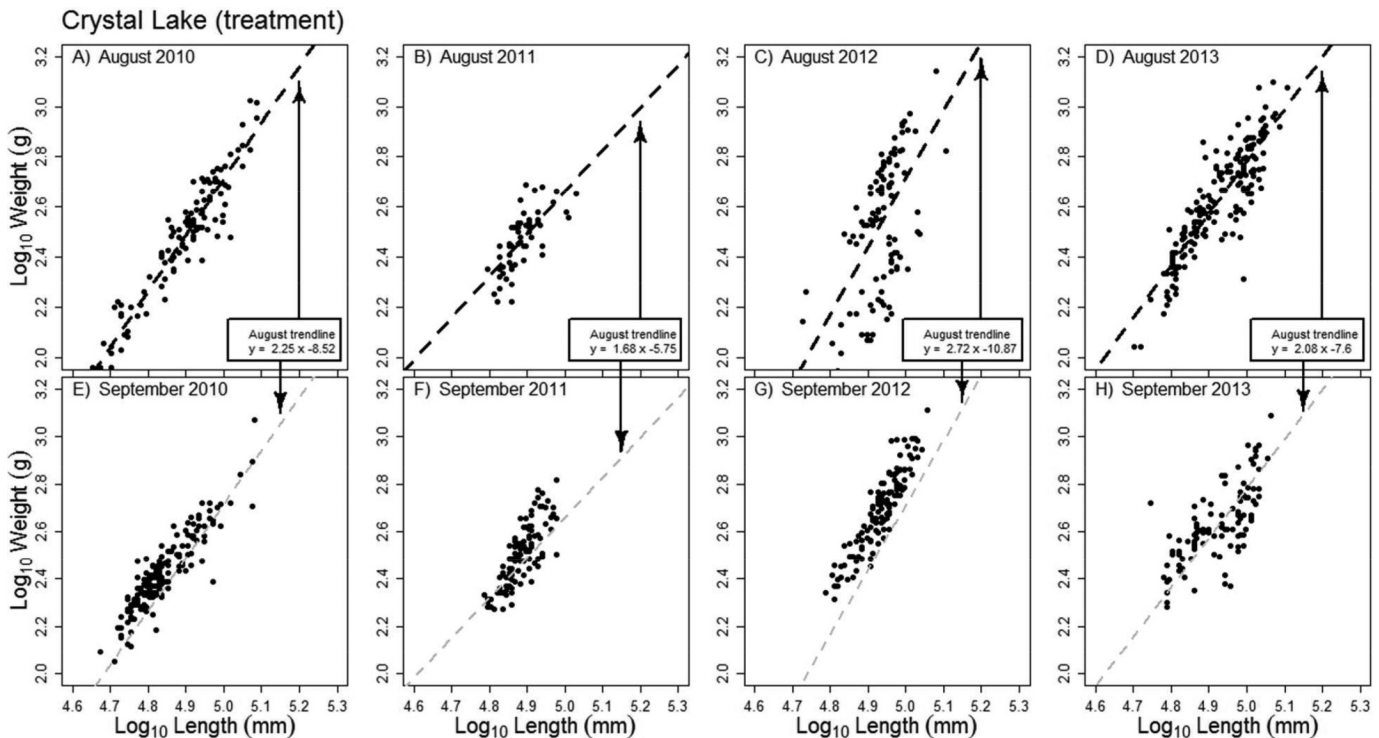


Table 2. Statistical results for ordinary least squares regression of rainbow smelt body condition (length–mass relationship; log-transformed for normality) in Crystal Lake during August for years 2010–2013.

Year	Model	df	R ²	P
2010	$y = 2.25x - 8.52$	1, 106	0.90	<0.001
2011	$y = 1.68x - 5.75$	1, 58	0.50	<0.001
2012	$y = 2.72x - 10.87$	1, 107	0.20	<0.001
2013	$y = 2.08x - 7.60$	1, 173	0.76	<0.001

that variation in thermal tolerance can be responsible for inter-population genetic divergence (Taylor 1991; Waples 1995; Healey and Prince 1995), but few studies have investigated intrapopulation variation in temperature tolerance (Stitt et al. 2014). Alternatively, this body condition divergence could be a manifestation of intensified intraspecific competition under extreme conditions at

a discrete time point. More specifically, we hypothesized that smelt would gradually lose mass and expire during late summer (Gaeta et al. 2012), and it is possible that the group of smelt exhibiting lower body condition lost mass simultaneously over a 2-week period and expired at the same time. Some smelt may have increased their consumption rate to accommodate an elevated metabolism, though we have no direct evidence for this. We cannot speak to the underlying mechanism for the apparent intrapopulation divergence in body condition; however, the group of low-conditioned individuals was removed from the population during the warmest period of the 2012 manipulation, consistent with temperature-mediated mortality.

We characterized the individuals that survived the 2012 manipulation through investigating age structure and length-at-age relationships. Our hypotheses were based on model results from Gaeta et al. (2012), predicting that whole-lake mixing would extirpate adult year classes (≥ 2 years old) in the first year of treatment,

Fig. 6. Back-calculated length-at-age (median, first and third quantiles, and 1.5 times the interquartile range) for rainbow smelt in Crystal Lake during premanipulation years (panel A; $N = 589$) and for individuals who ultimately survived the 2012 manipulation (beginning of 2012, panel B; $N = 144$). von Bertalanffy Growth Model (VBGM) fits for premanipulation years (solid line; parameters: $L_{\infty} = 257.7$, $K = 0.10$, $t_0 = -2.921$) and for surviving individuals (dashed line; parameters: $L_{\infty} = 143.2$, $K = 1.162$, $t_0 = -3.580$) are shown. All VBGM parameters are significantly different based on likelihood ratio test (L_{∞} : $\chi^2 = 18.03$, $df = 1$, $P < 0.001$; K : $\chi^2 = 15.05$, $df = 1$, $P < 0.001$; t_0 : $\chi^2 = 10.73$, $df = 1$, $P = 0.001$).

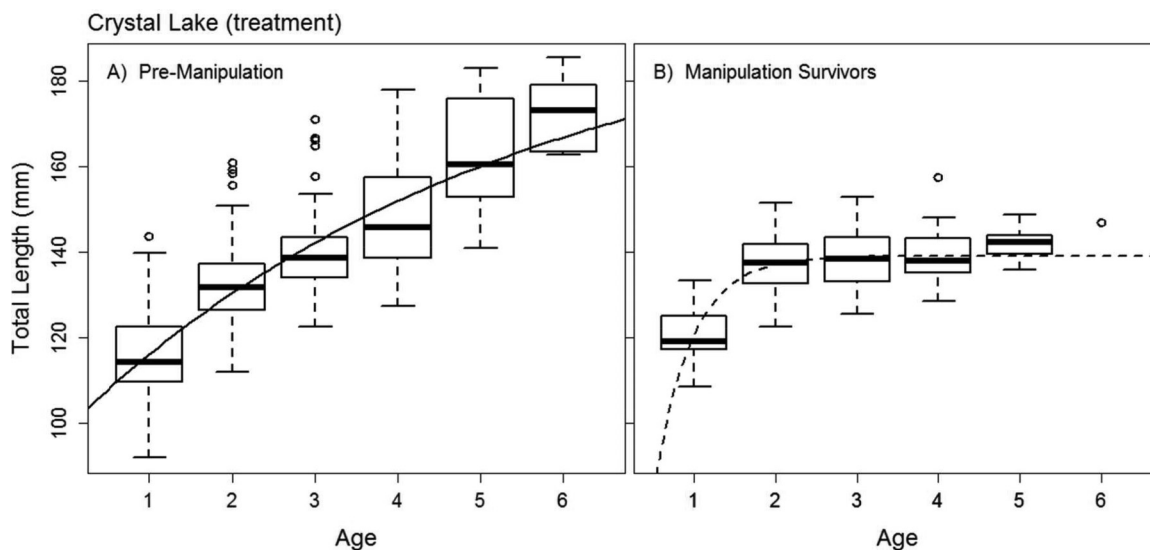
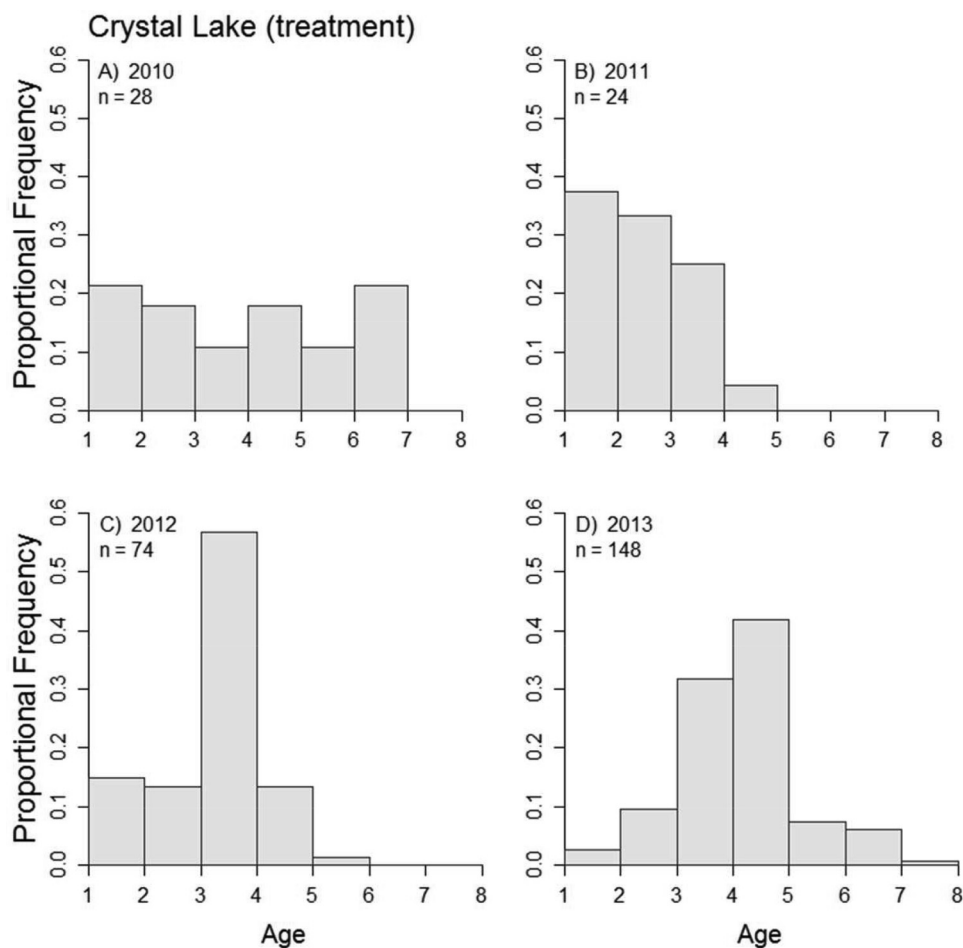


Fig. 7. Rainbow smelt age structure in Crystal Lake obtained via aging sectioned otoliths for premanipulation years (A, 2010; and B, 2011) and manipulation years (C, 2012; and D, 2013) (sample size " n " listed for each year).



and subsequent treatment years would extirpate juvenile age classes (0 and 1 years old) after they age into cold-water life stages (smelt exhibit a eurythermal life history with warm-water tolerance in young age classes; Evans and Loftus 1987). Results from our experiment indicate that adults of all ages survived the 2012 manipulation (ages 1–7). Interestingly, for adult year classes (>2), only shorter individuals survived the 2012 manipulation compared with premanipulation fish of the same age (Fig. 6). Therefore, our results suggest that our thermal manipulation did not selectively remove particular age classes, but rather removed the larger individuals from each adult age class. Other investigations of thermally induced large-scale fish die-offs suggest that larger individuals expire before the smaller individuals (Huntsman 1942; Hart 1952). Additionally, lab studies have shown negative relationships between total length and upper thermal limit, suggesting that shorter individuals for some species might be more resilient in extreme thermal habitats (Recsetar et al. 2012).

Oxygen and capacity-limited thermal tolerance provides a mechanism for understanding thermal tolerance as it relates to fish size (Pörtner and Knust 2007; Pörtner and Peck 2010). All organisms live within a limited range of body temperatures that allows for optimal functioning of molecular, cellular, and systemic processes. When temperatures deviate far from the optimal range, limiting capacity for oxygen supply may cause hypoxemia (Pörtner 2002; Pörtner and Knust 2007). Beyond low and high critical temperatures, only a passive, anaerobic existence is possible. Therefore, environments enabling optimal aerobic scope allow individuals to perform higher functions (muscular activity, behavior, growth, and reproduction), while environments beyond low or high critical temperatures minimize aerobic scope. Survival beyond these thermal thresholds, then, is time-limited and supported by anaerobic metabolism. Thermally induced mortality ensues when oxygen circulation falls below basal demands for an organism; thus, larger individuals are more thermally sensitive owing to progressively falling oxygen supply capacity in relation to demand (Pörtner and Peck 2010). Our results corroborate earlier work suggesting that organisms do not effectively function beyond oxygen-dependent size limits set by temperature (Pörtner and Knust 2007).

Differential thermal capacities in small and large individuals also have implications for intrapopulation interactions. Although smaller individuals have higher mass-specific metabolic rates, they also have higher mass-specific aerobic scope, making them relatively less sensitive to elevated temperatures and therefore are less sensitive to negative effects of extreme temperature than larger individuals of the same species (Fowler et al. 2009; Breau et al. 2011). Disproportionately higher temperature effects on metabolic rates of larger fish (or reduced aerobic scope) may limit the growth of larger individuals (Hamrin and Persson 1986; Pörtner and Farrell 2008) and allow for competitive release of smaller cohorts in warmer environments (Hamrin and Persson 1986). Ultimately, metabolic limitations of larger individuals in critical thermal habitats can result in smaller population size structures (Daufresne et al. 2009; Cheung et al. 2013). Although we did not specifically test for intraspecific competition among cohorts, disproportionate thermal effects on larger individuals undoubtedly altered competitive interactions with smaller individuals, which may explain the survival of smaller size-at-age adult smelt in our manipulation. While our results provide evidence for differential thermal effects on small and large individuals driving size-at-age relationships over a short time scale, perpetually warmer habitats may be driving reduced size structures of populations over longer time scales as well (Daufresne et al. 2009; Cheung et al. 2013).

Thermal tolerance as it relates to size can also impact fish populations and communities on larger geographic scales (Pörtner 2001; Rijnsdorp et al. 2009; Pörtner and Peck 2010). For smelt specifically, dwarf populations have been noted in warmer lakes (Rupp 1959), while populations inhabiting large, deep lakes gen-

erally mature later and grow to larger size than those in shallower, warmer lakes (Nellbrink 1989). For other species, cool and cold-water fishes tend to be smaller at equatorial latitudes and increase in size towards the poles, suggesting that individuals are larger in cooler environments (Rypel 2014). Although little work has been done relating body size to thermal limits, our results provide support for patterns observed for smelt on a larger geographic scale and provide insight for future research regarding thermal effects on body size in a geographic context.

Application of lake-mixing as a management tool for a cold-water invasive species

Despite removing a substantial portion of the population in 2012, the smelt population persisted. Our results show that hypolimnetic warming could potentially be used as a management technique to reduce smelt population densities, especially if used with trophic manipulation (Krueger and Hrabik 2005) and (or) overharvesting (Gaeta et al. 2015). However, eradication seems unlikely. There have been many nonselective fish eradication attempts using piscicides (Britton and Brazier 2006; Britton et al. 2011) and dewatering (Britton et al. 2008). These practices are nonselective and impose collateral effects on desirable species. Other studies have successfully eradicated a targeted species from a system using size-selective overharvesting methods (gillnets), although these methods may only be effective on systems <3.0 ha (Knapp and Matthews 1998; Parker et al. 2001; Kolar et al. 2010). While other selective eradication methods have been proposed, such as reproductive disruption (Bergstedt et al. 2003; Sorensen and Stacey 2004) and genetic manipulation (Thresher 2008; Thresher et al. 2014), they remain undeveloped. Experimenting with novel eradication methods is important for developing new management tools (Clout and Veitch 2002) and also allows for field testing predictive laboratory and computer modeling studies.

Our study highlights the challenges of evaluating thermal habitat suitability in natural systems. Both lab and bioenergetics models incorporating published thermal thresholds (Gaeta et al. 2012) failed to predict the resilience of the smelt population in Crystal Lake and would never have predicted indirect mortality (i.e., predation by gulls, etc.). Lab-derived critical thresholds predict temperatures ranging from 21 to 23.5 °C as lethal within hours (Wismer and Christie 1987), and bioenergetics models predicted a 43.3% mass loss in adults under low-mixing conditions (with a maximum mean bottom temperature of 21.1 °C; Gaeta et al. 2012). Although we observed significant mortality after exceeding these critical temperatures, uniform mass loss was not observed, and many individuals survived. Despite caveats concerning extrapolation of lab- and model-derived thermal limits to natural systems (due to varying acclimation temperatures, behavioral thermoregulation, and prey availability), the reality is that lab-derived values are a key means for addressing scientific questions at broad spatial or temporal scales. Thus, management and conservation efforts tend to rely on extrapolations that use laboratory values (along with niche modeling based on correlations between distribution and environmental data), even though thermal limits are not usually tested in the field. To our knowledge, this manipulation is the first experimental field test of published thermal limits. Schrank et al. (2003) observed Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) persisting in habitats surpassing published thermal limits for extended periods of time. Our results corroborate observations from Schrank et al. (2003), providing another example of cold-water fish surviving in environments predicted to be lethal based on the literature. While predicted niche boundaries for some cold-water fishes have inadequately described critical habitat use (Sellers et al. 1998), we suggest that the difference between lab- and model-derived (as described above) thermal limits to species' resilience in the field may be larger than we anticipated. Thus, it is important to better

understand how thermal limit estimates relate to living organisms in real ecosystems.

In conclusion, the smelt population in Crystal Lake persisted in extreme thermal habitats throughout the manipulation, highlighting the resilience of invasive smelt and the importance of preventing future invasions. As such, our results raise awareness about the field application of lab- and model-derived critical thermal limits. Future research should test field-, lab-, and model-derived thermal limits in real ecosystems. These experiments are needed to increase accuracy of predictive models and expand our understanding of mechanisms underlying fishes' resilience to changing thermal regimes. Whole-ecosystem experiments allow for testing of theory, models, and mechanisms in real systems (Carpenter and Kitchell 1993) and in this context might provide a more appropriate scale to address such questions. Moving forward, we must improve our understanding of fishes' thermal limits in the environment to better prepare for changing ecosystems.

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Appendix A. Intra-annual smelt population dynamics in Sparkling Lake 2013

Appendix Fig. A1 and Table A1 appear on the following pages.

Table A1. Adult smelt population mortality model (eq. 6 of main text) nominal values and bootstrapped statistical results for 1000 model simulations of Sparkling Lake in 2013.

Year	Estimated quantity	Q (composite parameter for effects of initial smelt population and movement rates)	m (instantaneous mortality rate, day ⁻¹)	M (seasonal mortality, proportion of population)
2013	Nominal least squares	1941.134	0.016	0.724
	Bootstrap median	1922.594	0.016	0.719
	Bootstrap interquartile range	1721.902–2170.353	0.013–0.019	0.666–0.767

Fig. A1. Seasonal population dynamics for rainbow smelt in Sparkling Lake during 2013. Black circles and black lines denote observed density estimates from hydroacoustic surveys (\pm SD). Gray circles and gray shaded region denote model fits of adult mortality rate in the smelt population over the course of the season (\pm SD).

