
North American Journal of Fisheries Management

ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

# Are Yellowstone Lake Temperatures More Suitable to Nonnative Lake Trout than to Native Cutthroat Trout?

Lynn R. Kaeding

**To cite this article:** Lynn R. Kaeding (2012) Are Yellowstone Lake Temperatures More Suitable to Nonnative Lake Trout than to Native Cutthroat Trout?, North American Journal of Fisheries Management, 32:5, 848-852, DOI: 10.1080/02755947.2012.694837

**To link to this article:** http://dx.doi.org/10.1080/02755947.2012.694837

Published online: 14 Sep 2012.

*North American Journal of Fisheries Management* 32:848–852, 2012

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2012.694837

MANAGEMENT BRIEF

# Are Yellowstone Lake Temperatures More Suitable to Nonnative Lake Trout than to Native Cutthroat Trout?

**Lynn R. Kaeding***
*669 Stonegate Drive, Bozeman, Montana 59715, USA*

*Abstract*

**A recent study revealed limitations to the reproduction potential of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (YCT) in Yellowstone Lake, Wyoming, resulting from suboptimal conditions for somatic growth. The present study evaluated the lake as suitable thermal habitat for YCT and lake trout *Salvelinus namaycush*, a highly piscivorous, nonnative species, a reproducing population of which was discovered there in 1994. Because the fundamental thermal niche of lake trout delimits a zone of the lake's annual temperature profile that surrounds the corresponding, separate zone for YCT, the annual growing season and volume of suitable Yellowstone Lake habitat will invariably be larger for lake trout than YCT across the range of cool-to-warm climate years. Ongoing management actions to control lake trout emphasize intensive gill netting, while temporal changes in lake trout catch rates and population structure provide metrics of program success. However, the limits to YCT reproduction potential attributed to the short growing season make the YCT population especially susceptible to lake trout predation, perhaps even from a measurably reduced predator population. Identification of such effects requires that dynamic, age-structured models of the YCT population that incorporate all important population drivers be formulated and used in data analyses and control program assessment.**

Somatic growth and other physiological processes of fish are profoundly affected by ambient water temperature (Brett 1979). A species' "final preferendum" is the narrow range of temperatures that it preferentially occupies when all other environmental conditions are not limiting (Fry 1947). Many physiological processes important to a species' fitness are optimized within its final preferendum (Beitinger and Fitzpatrick 1979; Magnuson et al. 1979; Jobling 1981). Accordingly, Magnuson et al. (1979) proposed that such optimal thermal habitat be considered an ecological resource and the temperature axis of a species' fundamental niche (in the sense of Hutchinson 1957). Christie and Regier (1988) demonstrated the usefulness of that concept by showing that the sustained yields (i.e., long-term commercial harvests) of four fish species that differed in their optimal temperatures were positively associated with the volumes of species-specific, optimal thermal habitat among 21 large North American lakes.

Yellowstone Lake in Yellowstone National Park, Wyoming, lies approximately 2,357 m above mean sea level and has a surface area of 34,100 ha, a shoreline length of 277 km, a mean depth of 43 m, and a maximum depth of 131 m (Gresswell et al. 1994; Morgan 2007). The largest, high-elevation (>2,000-m) lake in North America, Yellowstone Lake mainly lies within an ancient volcanic caldera (Morgan 2007) and has been classified as mesotrophic to moderately eutrophic on the basis of phosphorus concentration, transparency, and primary productivity (Kilham et al. 1996; Theriot et al. 1997). The lake is usually fully ice-covered between late December and late May or early June; a thermocline is completely formed in July at 5–15 m depth and persists into September, although summer surface temperatures rarely exceed 18°C and the water remains well oxygenated to well below the thermocline, i.e., >7 mg/L to at least 30 m depth (Benson 1961). The lake's only native salmonid is the Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (YCT; Behnke 1992).

Recently, Kaeding and Koel (2011) reported that the excised gonads of mature YCT from annual mid-September gill-net catches (years 1977–2007) from Yellowstone Lake indicated that approximately 35% of those fish would not have spawned the next year (∼June) and that this substantial proportion would give rise to a degree of "spawning omission" (in the sense of Rideout et al. 2005), as has been reported for this population (Ball and Cope 1961). (In subsequent analyses, the degree of spawning omission showed no trend across years [L. Kaeding, unpublished data].) Among other fish elsewhere, spawning omission has been attributed to environmental conditions that resulted in slow growth (e.g., a short annual growing season, limited food resources), along with the

*E-mail: kaedingl@aol.com
Received February 5, 2012; accepted May 8, 2012
Published online September 14, 2012

appreciable energy requirements for gonadal development and other activities related to reproduction, which collectively prevented fish from spawning each year when mature (e.g., Rideout et al. 2005). In addition, Kaeding and Koel (2011) showed that YCT longer than ~360 mm total length (TL) from Yellowstone Lake were on average less fecund than YCT of similar length from Idaho streams. Both of these observations indicated measurable limitations to certain components of YCT fitness—specifically, the components affecting reproduction potential—that resulted from suboptimal conditions for somatic growth in Yellowstone Lake.

A reproducing population of lake trout *Salvelinus namaycush*, a highly piscivorous species that inhabits deep, cold, well-oxygenated lakes (e.g., Evans 2007) but that is not indigenous to Yellowstone National Park, was discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996). Because introduced lake trout had elsewhere adversely affected populations of native cutthroat trout (Kaeding et al. 1996), the National Park Service began what became an intensive removal program aimed at controlling the lake trout population (Koel et al. 2005). The efficacy of that program may ultimately be affected by the relative suitability of Yellowstone Lake temperatures to YCT and lake trout. The objectives of the present study were to evaluate the Yellowstone Lake temperature regime as suitable thermal habitat for YCT and lake trout and to describe the importance of those suitabilities to ongoing management actions to control lake trout. The results will show that the temporal window for optimal YCT growth in Yellowstone Lake is short, thus providing a plausible explanation for the limitations to YCT reproduction potential. Moreover, those limitations make the YCT population especially susceptible to lake trout predation, a factor that is important to assessing control program efficacy.

## METHODS

*Lake temperatures*.—The temperatures in the main Yellowstone Lake basin had been measured electronically at 1-m intervals to at least 30 m depth and were available for four years (1957, 1996, 1997, and 1999). The 1957 data were from Benson (1961), who provided profile graphs (but no measurement interval) for 1954–1959, although only the 1957 data were numerous (7 measurement days); those profiles were digitized and the temperatures recorded at 1-m intervals. The 1996 temperature data were those of Interlandi et al. (1999), whereas the data for 1997 and 1999 were collected (and provided to the author, along with those for 1996) by National Park Service personnel at Yellowstone National Park. The 1999 data included concurrent measurements of dissolved oxygen concentration to 60 m depth. These annual temperature and dissolved oxygen data were configured as contour plots (MathWorks 2005) for use in subsequent analyses.

Kaeding (in press) used mean daily air temperatures >0°C at Lake Village (on the lake's north shore) to calculate total water year (1 October–30 September) degree-days for 75 years between 1928 and 2007. The years 1957, 1996, 1997, and 1999 represented the 75th, 15th, 69th, and 26th percentiles of this normally distributed metric, respectively; thus, the data for lake temperatures encompassed a range of cool-to-warm climate years in the Yellowstone Lake region.

*Fundamental thermal niches of the fish*.—Magnuson et al. (1979) examined the statistical distributions of the temperatures selected by various fish species in laboratory tests and thereby quantified the fundamental thermal niche as the species' optimum temperature for growth ±2.0°C and that of lake trout in particular as 8–12°C. (A recent compilation of optimum temperature data for lake trout is provided by Plumb and Blanchfield 2009.) Christie and Regier (1988) set the bounds of the thermal niche at the optimum growth temperature −3°C and +1°C because studies have shown that fish often select somewhat cooler temperatures in nature than in the laboratory. Because application of either criterion would have led to similar conclusions, the approach of Magnuson et al. (1979) was used in the present study.

Unlike with lake trout, laboratory data on optimal-growth temperatures for YCT—or any other cutthroat trout—are sparse and often equivocal. Dwyer and Kramer (1975) reported that the scope for activity (i.e., the active minus the standard metabolic rates) of age-1 (71–113-g) "cutthroat trout" held in a respirometer apparatus was greatest at 15°C among the five test temperatures (5, 10, 15, 20, and 24°C). That suggested that 15°C also was the optimal temperature for the growth of these fish. The test fish were of Strawberry Reservoir, Utah, stock (Chris Wilson, Utah Fisheries Experiment Station, Logan, personal communication), which had a Yellowstone Lake YCT ancestry but which may also have been genetically introgressed with rainbow trout *O. mykiss* (Behnke 1992). Ostberg et al. (2011) recently showed that genetic introgression with rainbow trout can affect YCT growth as well as other morphological characteristics.

Meeuwig et al. (2004) examined the effects of constant (12, 18, and 24°C) and cyclical (diel ranges of 15–21°C and 12–24°C) temperatures, each with two replicates, on the growth of nutritionally satiated, age-0 Lahontan cutthroat trout *O. c. henshawi* in four size-classes (mean TL, 20–121 mm; mean weight, 0.2–15.5 g) over a 14-d laboratory period. The growth rate in weight depended upon the initial weight and was reported as most rapid in the 12°C treatment, even though growth at 18°C did not statistically differ from that at 12°C.

Bear et al. (2007) determined the relative growth rate (in weight) of nutritionally satiated, age-0 (9.4–19.3 g; 102–126 mm TL) westslope cutthroat trout *O. c. lewisi* in three replicates at each of six test temperatures (8, 12, 14, 16, 20, and 24°C) over a 60-d laboratory period. Those authors' fit of a quadratic function to the data suggested that the optimum temperature for growth was 13.6°C (i.e., the peak of the fitted curve), even though the most rapid growth was shown by a sample in the 16°C treatment, for which the mean of all samples also appeared to be largest (see their Figure 4).

Collectively, the results of preceding studies suggested an optimal temperature for "cutthroat trout" growth between 12°C and 18°C with its "center of mass" near 15°C, which is similar to the optimal-growth temperatures of three other oncorhynchids reviewed by Brett (1979; sockeye salmon *O. nerka*, 15°C; Chinook salmon *O. tshawytscha* and pink salmon *O. gorbuscha*, 15.5°C). Moreover, the apparent cutthroat trout growth optimum clearly was warmer than 8–12°C, the fundamental thermal niche of lake trout. In the present study, I considered the fundamental thermal niche of YCT to be 15 ± 2.0°C.

*Quantification of suitable thermal habitat in the lake*.—The suitability of the Yellowstone Lake temperature regime as thermal habitat for YCT and lake trout was assessed by delineating the area and temporal extent of each species' fundamental thermal niche on contour plots of lake temperatures. Individual areas were quantified by weighing (±0.01%) their cutouts from hard copies of plots. As discussed by Magnuson et al. (1990), this approach does not assume that the growth of either species is restricted to temperatures within their respective fundamental thermal niches. Slower, suboptimal growth would occur at somewhat warmer or cooler temperatures, including during "shoulder" seasons. The approach assures comparability between species in assessments of temperature regime suitability. Because the comparisons were between species and among years within a single lake rather than across multiple lakes, it was not necessary to estimate the volumes of species-specific, optimal thermal habitat (e.g., Christie and Regier 1988).

## RESULTS

The Yellowstone Lake thermocline formed in July of all years and persisted at 10–20 m depth into September 1996 and 1999, the years when temperature measurements extended into October (Figure 1). The maximum recorded surface temperatures were 17.5, 16.3, 15.6, and 15.4°C in 1957, 1996, 1997, and 1999, respectively. The thermocline dissipated in September 1996 and 1999, the cool climate years, but

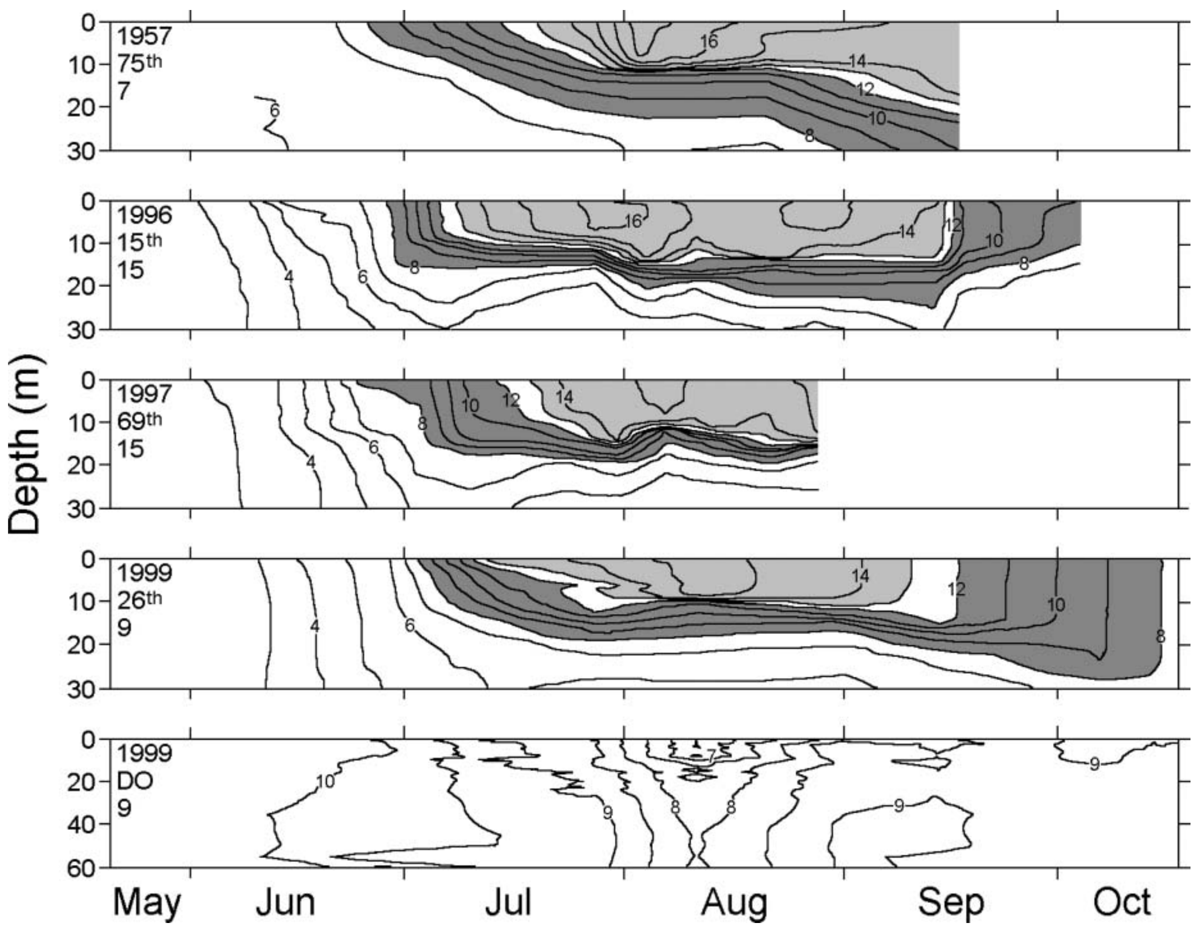


FIGURE 1. Contour plots of seasonal Yellowstone Lake temperatures in 1957, 1996, 1997, and 1999. The contour interval is 1°C; the shaded areas are the spatiotemporal zones constituting the fundamental thermal niches of Yellowstone cutthroat trout (light shading) and lake trout (dark shading). Total water year degree-day percentiles (see Methods) and the number of measurement days are given for each year. The last panel shows concurrent dissolved oxygen concentrations to 60 m depth in 1999; the contour interval is 0.5 mg/L.

measurements ended before thermocline dissipation in fall 1957 and 1997, the warmer climate years.

As one would expect, the water temperatures within the fundamental thermal niche occurred earlier in the season and extended later for lake trout in 1996 and 1999, as they would have in 1957 and 1997 had temperature measurements extended into late fall (Figure 1). The fundamental thermal niche of lake trout encompassed areas approximately 1.46, 1.11, 1.09, and 2.94 times that of YCT in 1957, 1996, 1997, and 1999, respectively; however, the lake temperature data encompassed the entire thermal niches of both species only in 1999. In 1999, niche temperatures extended over about 2 months for YCT and about 3.5 months for lake trout. Dissolved oxygen concentration was $>7$ mg/L to 60 m depth throughout the 1999 recording period (Figure 1).

## DISCUSSION

The analyses used data from four differing climate years and showed how Yellowstone Lake temperatures were more suitable to lake trout than to YCT. Moreover, the data for dissolved oxygen concentration show that seasonal hypoxia did not occur and thus was not a factor affecting habitat availability within the fundamental thermal niche of lake trout (Evans 2007). Because the fundamental thermal niche of lake trout delimits a zone of the lake's annual temperature profile that surrounds the corresponding, distinct zone for YCT, both the annual growing season and volume of suitable Yellowstone Lake habitat will invariably be larger for lake trout than for YCT across the range of cool-to-warm climate years. Furthermore, lake trout are not confined to their fundamental thermal niche but can make forays into warmer waters to prey upon YCT (e.g., Morbey et al. 2006). Thus, lake trout benefit from waters within the thermal niches of both species. Because their Yellowstone Lake growing seasons are short, the production of both lake trout and YCT would likely increase under climate warming, as concluded by Magnuson et al. (1990) for lake trout and coho salmon *O. kisutch* in Lake Michigan; however, climate warming also may reduce the reproductive success of the exclusively stream-spawning YCT (Kaeding, in press).

Yellowstone Lake has been described as "the core of the remaining undisturbed natural habitat" for YCT (Kaeding et al. 1996); however, that description should not imply near-optimal conditions for YCT in the lake. Trotter's (2008) review of the literature indicated that at the end of the Pinedale alpine glaciation of the Yellowstone region (10,000–12,000 years ago), YCT from a Snake River refugium in Idaho followed waters spanning Two Ocean Pass and thereby accessed and colonized Yellowstone Lake as well as the downstream Yellowstone River drainage in eastern Montana. Thus, Yellowstone Lake is recent habitat for YCT and likely provides suboptimal conditions for YCT somatic growth and reproduction.

Ongoing management actions to control lake trout in Yellowstone Lake emphasize intensive gill netting to reduce the population, particularly juvenile and mature fish (Koel et al. 2005). Temporal changes in lake trout catch rates and the age and size structures of the lake trout population provide key metrics of program success. The present study shows that the temporal window for optimal YCT growth in Yellowstone Lake is short, thus providing a plausible explanation for the limitations to YCT reproduction potential reported by Kaeding and Koel (2011). Importantly, such limitations make the maintenance and growth of the YCT population especially vulnerable to lake trout predation, perhaps even from a lake trout population measurably reduced by gill netting or other methods. Moreover, the dynamics of the YCT population are likely driven by a multitude of factors, including both lake trout predation and climate variation (Kaeding, in press). Identification of such effects—necessary for a thorough assessment of removal program efficacy—requires that pertinent data for the YCT population be regularly collected and examined using dynamic, age-structured models that incorporate all factors known to be important drivers of the population.

## ACKNOWLEDGMENTS

I thank Pat Bigelow, National Park Service, Yellowstone National Park, for providing the data for 1996, 1997, and 1999; Jim Mogen, U.S. Fish and Wildlife Service, Bozeman, Montana, for his help in preparing the figure; Beth Kaeding for her editorial assistance; Thomas E. McMahon, Ecology Department, Montana State University, for his constructive comments on a preceding version of this report; and an anonymous reviewer for his useful comments on the manuscript submitted for publication.

## REFERENCES

Ball, O. P., and O. B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service Research Report 55.

Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of westslope cutthroat trout and rainbow trout: implications for species interactions and development of thermal protection standards. Transactions of the American Fisheries Society 136:1113–1121.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Beitinger, T. L., and L. C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. American Zoologist 19:319–329.

Benson, N. G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service Research Report 56.

Brett, J. R. 1979. Environmental factors and growth. Pages 599–675 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume VIII: bioenergetics and growth. Academic Press, New York.

Christie, G. C., and H. A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45:301–314.

Dwyer, W. P., and R. H. Kramer. 1975. The influence of temperature on scope for activity in cutthroat trout, *Salmo clarki*. Transaction of the American Fisheries Society 104:552–554.

Evans, D. O. 2007. Effects of hypoxia on scope-for-activity and power capacity of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 64:345–361.

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55. Publication of the Ontario Fisheries Research Laboratory 68:1–62.

Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries Aquatic Sciences 51(Supplement 1):298–309.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Interlandi, S. J., S. S. Kilhamn, and E. C. Theriot 1999. Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone ecosystem. Limnology and Oceanography 44:668–682.

Jobling, M. 1981. Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology 19:439–455.

Kaeding, L. R. In press. A climate-based index of historic spawning-stream hydrology. River Research and Applications. DOI: 10.1002/rra. 1606.

Kaeding, L. R., G. D. Boltz, and D. G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21(3): 16–20.

Kaeding, L. R., and T. M. Koel. 2011. Age, growth, maturity, and fecundity of Yellowstone Lake cutthroat trout. Northwest Science 85:431–444.

Kilham, S. S., E. C. Theriot, and S. C. Fritz. 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnology and Oceanography 41:1052–1062.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout declines and impacts to bears and anglers. Fisheries 30(11):10–19.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19:331–343.

Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Transactions of the American Fisheries Society 119:254–264.

MathWorks. 2005. MATLAB: the language of technical computing, version 7.1.0.124 (R14). MathWorks, Natick, Massachusetts.

Meeuwig, M. H., J. B. Dunham, J. P. Hayes, and G. L. Vinyard. 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. Ecology of Freshwater Fish 13: 208–216.

Morbey, Y. E., P. Addison, B. J. Shuter, and K. Vascotto. 2006. Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*. Journal of Fish Biology 69:1675–1696.

Morgan, L. A., editor. 2007. Integrated geoscience studies in the greater Yellowstone area—volcanic, tectonic, and hydrothermal processes in the Yellowstone geoecosystem. U.S. Geological Survey Professional Paper 1717. Available: http: //pubs.usgs.gov/pp/1717/. (December 2011).

Ostberg, C. O., J. J. Duda, J. H. Graham, S. Zhang, K. P. Haywood III, B. Miller, and T. L. Lerud. 2011. Growth, morphology, and developmental instability of rainbow trout, Yellowstone cutthroat trout, and four hybrid generations. Transactions of the American Fisheries Society 140:334–344.

Plumb, J. M., and P. J. Blanchfield. 2009. Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 66:2011–2023.

Rideout, R. M., G. A. Rose, and M. P. M. Burton. 2005. Skipped spawning in female iteroparous fishes. Fish and Fisheries 6:50–72.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Arctic and Alpine Research 29:304–314.

Trotter, P. 2008. Cutthroat: native trout of the West, 2nd edition. University of California Press, Berkeley.