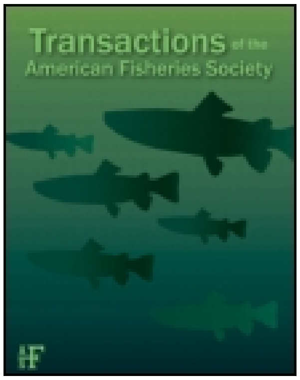

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Survival of Apache Trout Eggs and Alevins under Static and Fluctuating Temperature Regimes

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ARTICLE

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Abstract
Increased stream temperatures due to global climate change, livestock grazing, removal of riparian cover, reduction of stream flow, and urbanization will have important implications for fishes worldwide. Information exists that describes the effects of elevated water temperatures on fish eggs, but less information is available on the effects of fluctuating water temperatures on egg survival, especially those of threatened and endangered species. We tested the posthatch survival of eyed eggs and alevins of Apache Trout *Oncorhynchus gilae apache*, a threatened salmonid, in static temperatures of 15, 18, 21, 24, and 27°C, and also in treatments with diel fluctuations of ±3°C around those temperatures. The LT50 for posthatch survival of Apache Trout eyed eggs and alevins was 17.1°C for static temperatures treatments and 17.9°C for the midpoints of ±3°C fluctuating temperature treatments. There was no significant difference in survival between static temperatures and fluctuating temperatures that shared the same mean temperature, yet there was a slight difference in LT50s. Upper thermal tolerance of Apache Trout eyed eggs and alevins is much lower than that of fry to adult life stages (22–23°C). Information on thermal tolerance of early life stages (eyed egg and alevin) will be valuable to those restoring streams or investigating thermal tolerances of imperiled fishes.

The egg stage is arguably the most sensitive life stage in fish, and temperature is one of the most critical environmental factors affecting ontogeny and early stage development (Klimogianni et al. 2004). Incubation temperatures can affect hatch time, sex, and survival of salmonids (Baird et al. 2002; Wedekind and Küng 2010). Temperature also influences size at hatching, feeding onset, and yolk consumption (Wang et al. 1987; Polo et al. 1991; Koumoundouros et al. 2001). Salmonid embryos and alevins have both upper and lower lethal temperature tolerances (Stonecypher et al. 1994; Crisp 1988). Within these limits of tolerance, eggs of salmonids develop and hatch at different rates related to both temperature and species (Crisp 1981, 1988; Velsen 1987). As temperature increases, hatch time shortens (Crisp 1981, 1988; Beacham and Murray 1990) until an upper lethal temperature is reached (Beacham and Murray 1990). Both upper and lower lethal temperatures vary by species. For example, Coho Salmon *Oncorhynchus kisutch* eggs experienced 100% mortality when incubated at 15°C, whereas those of Rainbow Trout *O. mykiss* exhibited 7% mortality at 16°C (Velsen 1987). Furthermore, fluctuations commonly occur in stream and river temperatures, potentially adding another source of stress to developing eggs (Geist et al. 2006). The difference in thermal tolerance for eggs of different trout species makes an examination of each on a case-by-case basis important.

Stream temperatures are increasing throughout the world due to global climate change (Solomon et al. 2007), livestock

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grazing (Platts 1991; Trimble 1994), loss and removal of riparian cover (Chamberlin et al. 1991; USFWS 2009), and reduction of stream flow (Deacon et al. 1987; Hoerling and Eischeid 2007). These increases are particularly important for threatened coldwater species such as southwestern trouts that inhabit restricted ranges in mountainous terrain and other high elevation areas in the southwestern United States and Mexico (Williams and Carter 2009).

One such species, the Apache Trout *O. gilae apache*, is restricted to a few cool, high elevation streams in the White Mountains of east-central Arizona (Behnke 1992; USFWS 2009; Williams and Carter 2009). Apache Trout spawning activity begins in the White Mountains when water temperatures reach approximately 8°C in the late spring (Harper 1976). The time from egg deposition until hatching is about 30 d, and the total time until fry emergence is approximately 60 d (Harper 1976). Increased stream temperatures may have profound effects on hatching success of Apache Trout eggs, potentially leading to lower survival and faster hatch rates and triggering earlier onset of spawning. If eggs hatch earlier, adequate food may be unavailable to support young fish (Teletchea and Fontaine 2010). For example, mayflies (order Ephemeroptera), an important food of Apache Trout fry (Harper 1978), can exhibit altered life histories due to increased stream temperatures (Sweeney 1978; Burgmer et al. 2007; USFWS 2009; Scherr et al. 2010). Furthermore, at heightened temperatures coldwater fishes such as Apache Trout tend to have poor yolk sac use as evidenced by lower lipid levels at yolk depletion (Wang et al. 1987). The challenges associated with increased stream temperatures make a thorough understanding about the thermal requirements and limitations of the early life stages of Apache Trout important.

Our objective was to document the effects of various water temperature regimes on hatching success and posthatch survival of Apache Trout eggs. We studied the effects of long-term static and fluctuating water temperatures on egg and alevin survival, concentrating on the upper thermal limits because those are of immediate concern in the Southwest. Knowledge of how water temperature regimes affect hatching rates of Apache Trout eggs and survival of alevins can be used to identify streams optimal for Apache Trout. This information can also be used by hatchery managers to provide optimal conditions for survival of Apache Trout eggs and alevins during hatching operations. Furthermore, understanding how static and fluctuating temperature regimes affect survival of early life stages will allow better management of both wild Apache Trout populations threatened by projected increases in stream temperature.

METHODS

Apache Trout eggs used in tests were acquired from the Arizona Game and Fish Department (AZGFD) Tonto Creek Fish Hatchery and transported using AZGFD recommended methods, which were similar to those of Kincaid (1910). Eggs were in the eyed stage. Eggs were placed in between damp paper towels on top of mesh solar screen fabric that was supported by 1-cm^2 plastic grid material elevated by polyvinyl chloride (PVC) elbows 4 cm off the bottom of an insulated cooler. Another mesh sheet was placed 25 cm above the eggs and supported by more plastic grid material elevated by 3.3-cm-diameter PVC pipe. Ice was placed on the top mesh sheet. As ice melted, dripping cold water moistened eggs without danger of eggs suffocating or drying.

We transported eggs for approximately 3.5 h to the Environmental Research Laboratory (ERL) at the University of Arizona, Tucson. Upon arrival at the ERL, eggs were tempered from 12°C to 15°C over a 30-min period in a clean 1-L bucket and treated in a formalin (Rid-ich, Kordon, Hayward, California) bath. We used a standard dosage of 10 drops of Rid-ich per 3.79 L of water for 10 min to kill fungus or parasites that eggs may have been carrying or acquired during transport or handling. We wore rubber gloves when handling to prevent any additional contamination. After the 15°C bath treatment, eggs were rinsed and randomly placed, 30 per tank, in each of 30 egg baskets within test tanks held at 15°C, which is the upper temperature currently encountered at Arizona fish hatcheries that raise Apache Trout (AZGFD, unpublished data). We used a temperature-controlled recirculating system developed by Widmer et al. (2006b) to maintain tank water temperatures within 0.5°C of the 15°C acclimation temperature. The recirculating system consisted of 36 aluminum tanks (122 × 36 cm × 25 cm tall) lined with a polyurethane material known to be nontoxic to fish. Tank temperatures were measured using thermocouples integrated with a computer program that also controlled Hass k-series intellifaucets (Hass Manufacturing, Averill Park, New York). Intellifaucets mixed hot and cold water to desired temperatures and pumped that water into each tank on a set schedule, thus enabling complete control of each tank temperature to within ±0.5°C. A PVC standpipe, which was separated from the rest of the tank by a stainless steel screen to keep fish out of the drain, was located near the end of each tank. The standpipe allowed overflow to run into an 1,800-L biofilter sump tank built on-site where water was then pumped through numerous biological and mechanical filters including bioballs, a series of four polyester filter pads, two Pentair cartridge filters (CC75, Moonpark, California), and a ultraviolet sterilizer (COM6390-UL, Emperor Aquatics, Pottstown, Pennsylvania) before being pumped back to tanks that heated and chilled the water. The system was programmed to pump for 3 min every half hour resulting in approximately half the water being changed every hour.

Egg incubators or baskets were designed similarly to upwelling incubators commonly used in trout hatcheries (Hinshaw and Thompson 2000) and consisted of 10-cm-diameter PVC pipe that rose 2 cm above the water level in each tank. Each PVC basket was placed in a thin, mesh filter bag that covered the bottom of the basket and went up to the midpoint of each. The mesh kept eggs contained within the basket. Air diffusers were placed in each egg basket to provide constant oxygen. Two 1-cm-diameter holes were drilled directly across from each other 1 cm from the bottom of each egg basket. Air was pumped through the two holes using small Rio water pumps (HyperFlow, TAAM, Camarillo, California) to create water flow through the egg basket for stirring eggs and facilitating oxygen transport.

Apache Trout eggs propagated at hatcheries hatch successfully and survive through the alevin (sac fry) stage at water temperatures of 8–11°C (AZGFD, unpublished data). Therefore, we tested effects of static temperatures of 15, 18, 21, 24, and 27°C on Apache Trout egg hatching success and posthatch survival over a 14-d test period to see how eggs would fare in warmer conditions. We also wanted to estimate an LT50 (the median temperature lethal to 50% of a population) for Apache Trout eggs and alevins.

Because southwestern streams containing Apache Trout exhibit diel temperature fluctuations, we also tested effects of ± 3°C diel water temperature fluctuations around the same static temperature midpoints. Here temperature treatments were designed to fluctuate sinusoidally by ± 3°C from each midpoint within a 24-h period. Therefore, our fluctuating treatments were 15 ± 3, 18 ± 3, 21 ± 3, 24 ± 3, and 27 ± 3°C. We chose those temperatures so we could compare static and fluctuating temperatures with equivalent midpoints.

After eggs were placed in tanks, experiments commenced and eggs were allowed to acclimate at 15°C for 12 h. Temperatures of all tanks except the 15°C tanks were then increased at rates so that all tanks reached test temperatures in 36 h. Specifically, 27°C static and 24 ± 3°C fluctuating treatments were reached at a rate of 0.33°C/h; 24°C static and 21 ± 3°C fluctuating treatments were reached at a rate of 0.25°C/h; 21°C static and 18 ± 3°C fluctuating treatments were reached at a rate of 0.17°C/h; and 18°C static and 15 ± 3°C fluctuating treatments were reached at a rate of 0.08°C/h. Because eggs were eyed and already beginning to hatch at the start of the experiment, the temperatures were ramped to treatment temperatures more rapidly than 1°C/d, which is the method commonly used in other acclimated chronic exposure (ACE) type experiments (Zale 1984; Selong et al. 2001; Widmer et al. 2006a; Carveth et al. 2007). After all tanks reached desired test temperatures, temperature regimes were maintained for 2 weeks (14 d) to observe posthatch survival. Survival was monitored over the 14-d test period by conducting daily counts of surviving eggs and newly-hatched larvae. Dead eggs and larvae could be easily distinguished because they turned white, became stuck to the sides of the egg baskets, or both. Dead eggs were removed via a siphon each day. All eggs had either hatched or died by the end of the 14-d test period, and no larvae had fully consumed their yolk sacs by that point.

Data analyses.—We plotted survival and mortality data for static and ± 3°C fluctuating treatments using logistic regression for binomial counts (Hosmer and Lemeshow 2000) and estimated the 14-d LT50, which is the temperature survived by 50% of fish after 14 d. As a further check of the data, we also conducted a probit analysis to ensure LT50s calculated using both methods were similar (Finney 1971; Cramer and Maywright 2008). Adequacy of the models was evaluated by a likelihood ratio R^2, calculating the proportion of deviance explained by the logistic model compared with the null model ([null deviance − residual deviance]/null deviance, Zuur et al. 2009) and the significance of the model fit compared with a null model using a likelihood ratio test. We examined differences between the LT50s of static and fluctuating treatments using the procedures of Payton et al. (2003). A Welch two-sample *t*-test was used to compare mean percent survival of eggs and alevins to 14 d at a particular static temperature with mean percent survival of eggs and alevins when the same temperature was the midpoint of a fluctuation. Percent data were arcsine-transformed before *t*-test analyses. All analyses were conducted using program R version 2.12.2 (R: 2.12.2 [GNU General Public License]).

RESULTS

Apache Trout eggs were unable to survive the 27°C treatment and experienced 100% mortality by the second day of the test (Figure 1). In the 24°C treatment, there was >90% mortality by day 2 and 99% mortality by day 6. After just 3 d in the 21°C treatment there was >65% mortality, and by the end of the 14-d test there was 85.9% mortality (Table 1). The 18°C treatment had a mean of 63.3% mortality of eggs and larvae. The 15°C temperature treatment had the lowest egg and larvae mortality of 24.0% and exhibited a steady rate of mortality over the test period. The

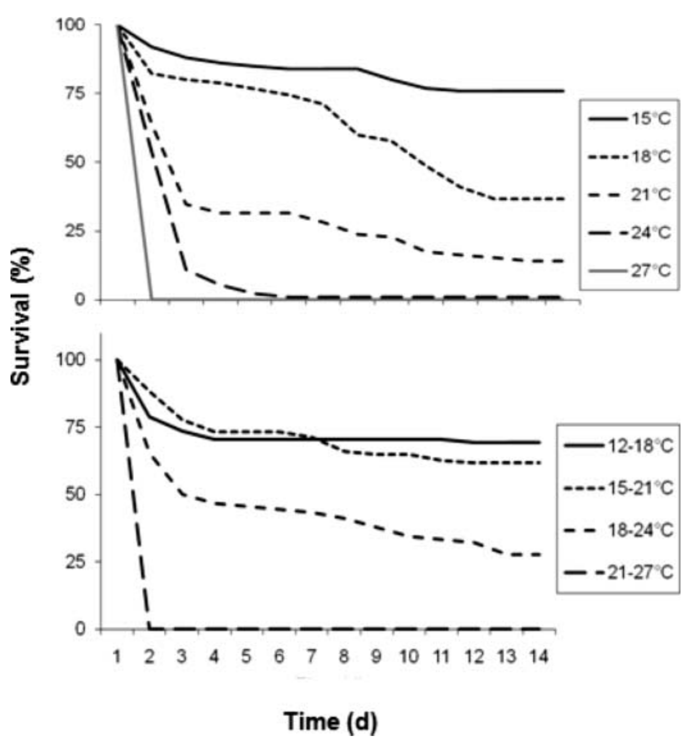

FIGURE 1. Mean survival (%) of Apache Trout during a 14-d exposure to five static temperatures: 15, 18, 21, 24, and 27°C (top panel) and four fluctuating temperatures: 15 ± 3, 18 ± 3, 21 ± 3, and 24 ± 3°C (bottom panel). No eggs or alevins survived past the first day of the 27 ± 3°C treatment, so data were not plotted.

TABLE 1. Mortality (%) of Apache Trout eggs and larvae at five static temperatures: 15, 18, 21, 24, and 27°C.

	Mortality (%)				
Replicates	15°C	18°C	21°C	24°C	27°C
1	14.7	76.7	90.0	100	100
2	32.4	80.0	75.0	100	100
3	25.0	33.3	93.3	96.7	100
Mean (SD)	24.0 (8.5)	63.3 (26.3)	86.1 (9.8)	98.9 (1.9)	100 (0.0)

LT50 for the static temperature treatments calculated using the logistic model was 17.1°C (SE, 0.27). Likelihood ratio R^2 of the model was 0.87, and was highly significant ($P < 0.001$; Figure 2). Probit analysis obtained almost identical results (LT50 = 17.1°C [SE, 0.27]); likelihood ratio $R^2 = 0.88$; likelihood ratio test: $P < 0.001$). Intercept and temperature parameters on both models were highly significant ($P < 0.001$; Figure 2).

No eggs survived through the first day in the 27 ± 3°C treatment. Eggs in the 24 ± 3°C treatment experienced 100% mortality by the second day (Figure 1). In the 21 ± 3°C treatment, there was 72.2% egg and larvae mortality over the test period and only 50% survival after the first 2 d (Table 2). In the 18 ± 3°C treatment eggs and larvae exhibited 37.8% mean mortality. In the 15 ± 3°C treatment there was a mean mortality of 31.9% over 14 d, and mortality steadily declined until day 4 after which no mortality was seen. The LT50 for the fluctuating ±3°C treatments calculated using the logistic model was 17.9°C (SE, 0.30). The likelihood ratio R^2 of the model was 0.68 and was highly significant ($P < 0.001$; Figure 2). Again, probit analysis obtained almost identical results (LT50 = 17.9°C [SE, 0.30]; likelihood ratio $R^2 = 0.70$; likelihood ratio test: $P < 0.001$). Intercept and temperature parameters on both models were highly significant ($P < 0.001$; Figure 2).

For both static- and fluctuating-temperature treatments, survival was highest at the lowest temperature tested (i.e., 15°C; Figure 2). Differences between the LT50s for static and fluctuating temperatures were slight (0.8°C) but significant ($P < 0.05$). However, we found no significant differences in mean survival when comparing the midpoints of the fluctuations with the corresponding static temperatures ($P > 0.05$) for all midpoint comparisons. For 15°C midpoints there was no significant difference in mean percent survival ($t = -0.3018$, df = 2.542, $P = 0.786$), no significant difference for 18°C midpoints ($t = 1.5283$, df = 3.015, $P = 0.223$), no significant difference for 21°C midpoints ($t = 0.710$, df = 2.617, $P = 0.536$), and no significant difference for 24°C midpoints ($t = -1.000$, df = 2.000, $P = 0.423$).

DISCUSSION

Developing embryos, newly hatched larvae (alevins), and juveniles are the most sensitive stages to environmental stressors in the life history of fishes and have been recommended

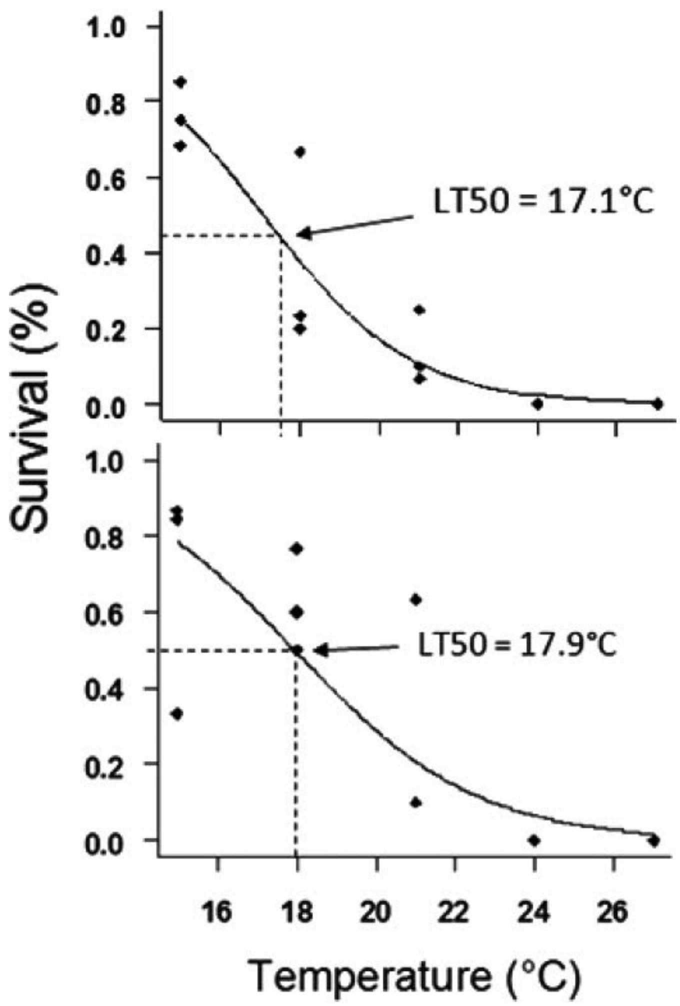

FIGURE 2. The LT50 of Apache Trout eggs and alevins after a 14-d exposure to five static temperatures: 15, 18, 21, 24, and 27°C (top panel); and five fluctuating temperatures: 15 ± 3, 18 ± 3, 21 ± 3, 24 ± 3, and 27 ± 3°C (bottom panel). Both models were fit by logistic regression, and the LT50 is the temperature at which 50% of the eggs hatch and survive. Parameter estimates for the static temperature model were: likelihood ratio $R^2 = 0.87$, intercept (SE) = 9.2066 (0.9563), Z-value = −9.627, $P < 0.001$; and temperature (SE) = −0.5390 (0.0533), Z-value = −10.112, $P < 0.001$. Parameter estimates for the fluctuating temperature model were: likelihood ratio $R^2 = 0.68$, intercept (SE) = 7.8593 (0.7889), Z-value = 9.963, $P < 0.001$; and temperature (SE) = −0.4382 (0.0416), Z-value = −10.532, $P < 0.001$.

TABLE 2. Mortality (%) of Apache Trout eggs and Larva at five fluctuating temperatures: 15 ± 3, 18 ± 3, 21 ± 3, 24 ± 3, and 27 ± 3°C.

	Mortality (%)				
Replicates	15 ± 3°C	18 ± 3°C	21 ± 3°C	24 ± 3°C	27 ± 3°C
1	13.3	50.0	90.0	100	100
2	15.6	40.0	90.0	100	100
3	66.7[a]	23.3	36.7	100	100
Mean (SD)	31.9 (30.2)	37.8 (13.5)	72.2 (30.8)	100 (0.0)	100 (0.0)

[a]*Saprolegnia* infection pronounced.

as the life stages to test in toxicology tests (McKim 1977). The egg incubation period is particularly sensitive to temperature and requires a specific accumulation of degree-days for proper hatching and emergence timing (Alderdice and Velsen 1978; Crisp 1981; Beacham and Murray 1990). Egg survival is contingent on the environment in which they are spawned, because they are not able to escape to more favorable conditions if temperatures are unsuitable. While Apache Trout in later life stages (i.e., fry to adult) are able to survive in water up to 22°C (Lee and Rinne 1980; Recsetar 2011), this experiment suggests that over 50% of Apache Trout eggs perish when incubation temperatures rise above 17–18°C. Therefore, stream temperatures approaching or exceeding 17°C would be unsuitable for Apache Trout eyed eggs and alevins.

The 14-d LT50 for Apache Trout eggs and alevins was 17.1°C under static temperatures, and 17.9°C (midpoint) under the ± 3°C diel fluctuating temperatures (Figure 2). Mean survival at static temperatures and equivalent midpoints of the fluctuating temperatures was not different. Yet, LT50s were slightly but significantly different. Midpoint of a fluctuating temperature may be the most important measure to evaluate stream temperature suitability for Apache Trout eyed eggs and alevins, at least within the ranges of temperature fluctuations we used. However, perhaps small fluctuations provide a thermal refuge to give eggs a slightly higher thermal tolerance.

Apache Trout eggs survived best at the lowest temperatures we tested (i.e., 15°C), and mortality increased as mean water temperatures rose above 15°C. We did not test survival at temperatures lower than 15°C although based on information from hatcheries in Arizona currently propagating Apache Trout (AZGFD, unpublished data), temperatures from 8°C to 11°C do not appear to limit hatch rates or alevin survival. In comparison, a closely related species, Rainbow Trout, experienced less than 15% mortality at incubation temperatures between 4°C and 9°C and between 10.5°C and 15°C (Velsen 1987). Based on our data and trends of LT50 curves for other species (Selong et al. 2001; Widmer et al. 2006a; Carveth et al. 2007), Apache Trout should experience equal or better survival in temperatures below 15°C than in those above.

Our data suggest hatchery and stream upper temperatures should be below 15°C during the hatching period to ensure highest hatch success and alevin survival. Furthermore, if spring stream temperatures increase to 17°C in Apache Trout incubation areas, substantial mortality of Apache Trout eggs will occur. Spring stream temperature data should be analyzed, in addition to stream temperature data taken at summer low-flow conditions, to identify potential stocking locations and to help inform managers to better protect wild trout populations.

Our study had limitations and offered avenues for future research. Because some eyed eggs began to hatch prior to experimentation, we could only test posthatch survival of a combination of eyed eggs and alevins and could not evaluate the percentage of eggs hatching or effects of elevated water temperatures on early egg development. Early life stage fish embryos are more sensitive to extreme temperatures than are those in later stages of development (e.g., Combs 1965; Kelley 1968; Hokanson et al. 1973; Wagner et al. 2006). Hokanson et al. (1973) found the upper thermal tolerance limit of Brook Trout *Salvelinus fontinalis* eyed eggs was 1°C higher than for earlier developmental stages. An estimate of the upper thermal tolerance of the earlier life stages of Apache Trout embryos is needed, and biologists applying the thermal tolerance information presented in our study to earlier embryonic life stages of Apache Trout may overestimate their upper thermal tolerance.

Saprolegnia was present in low levels during experiments and accumulated on eggs within a day of mortality. We removed dead eggs and alevins diligently, but sometimes they would stick to incubator sides and we were unable to remove them without interfering with the experiment. Although present in small amounts in all treatments, *Saprolegnia* was particularly pronounced in one replicate of the 15 ± 3°C treatment in which eggs exhibited 67% mortality (Table 2). Stress induced by changes in temperature as well as lower water temperatures makes fish more vulnerable to saprolegniasis (Willoughby 1994; Bruno and Wood 1999), which could have accounted for the higher mortality seen in some of the replicates. To test the effects of presence of outliers on the LT50s, we ran the logistic regression with and without these influential data points. The effect of removing any outliers on the LT50 was slight. Static treatment LT50s with and without outliers ranged from 16.72°C to 17.12°C, while fluctuating treatment LT50s ranged from 17.91°C to 19.00°C. Presence of these outliers did not affect the overall conclusions of our experiments.

We were only able to test the effects of a $\pm 3°C$ fluctuation, although larger fluctuations ($\pm 6°C$) during Apache Trout spawning periods are common (e.g., West Fork Black River, Trout Unlimited, unpublished data). Therefore, wider fluctuations in stream temperatures may demonstrate additional effects. Further study of the effects of wider fluctuations especially concentrating on temperatures near to the 17–18°C LT50 would be beneficial.

Future studies could incorporate in situ measurements of egg survival and spawning distribution of Apache Trout related to thermal regimes and water quality. Containers holding known numbers of fertilized eggs have been buried in streams to evaluate egg survival under a variety of environmental conditions including a range of temperatures and dissolved oxygen concentrations (e.g., Pauwels and Haines 1994; Rubin and Glimsäter 1996). Comparison of instream measurements of survival with those obtained in the laboratory would useful to corroborate findings of this study.

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REFERENCES

Alderdice, D. F., and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of Chinook Salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada 35:69–75.

Baird, H. B., C. C. Krueger, and D. C. Josephson. 2002. Differences in incubation period and survival of embryos among Brook Trout strains. North American Journal of Aquaculture 64:233–241.

Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific Salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927–945.

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

Bruno, D. W., and B. P. Wood. 1994. *Saprolegnia* and other *Oomycetes*. Pages 599–659 *in* P. T. K. Woo and D. W. Bruno, editors. Fish diseases and disorders, volume 3: viral, bacterial and fungal infections. CABI Publishing, Wallingford, UK.

Burgmer, T., H. Hillebrand, and M. Pfenninger. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151:93–103.

Carveth, C. J., A. M. Widmer, S. A. Bonar, and J. R. Simms. 2007. An examination of the effects of chronic static and fluctuating temperature on the growth and survival of Spikedace, *Meda fulgida,* with implications for management. Journal of Thermal Biology 32:102–108.

Chamberlin, T. W., R. D. Harr, and F. H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. Pages 181–205 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Combs, B. D. 1965. Effect of temperature on the development of salmon eggs. Progressive Fish-Culturist 27:134–137.

Cramer, K. L., and A. V. Maywright. 2008. Cold temperature tolerance and distribution of the brown recluse spider *Loxosceles reclusa* (Araneae, Sicariidae) in Illinois. Journal of Arachnology 36:136–139.

Crisp, D. T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11:361–368.

Crisp, D. T. 1988. Prediction, from temperature, of eyeing, hatching and 'swim-up' times for salmonid embryos. Freshwater Biology 19:41–48.

Deacon, J. E., P. B. Schumann, and E. L. Stuenkel. 1987. Thermal tolerances and preferences of fishes of the Virgin River system (Utah, Arizona, Nevada). Great Basin Naturalist 47:538–546.

Finney, D. J. 1971. Probit analysis, 3rd edition. Cambridge University Press, Cambridge, UK.

Geist, D. R., C. S. Abernethy, K. D. Hand, V. I. Cullinan, J. A. Chandler, and P. A. Groves. 2006. Survival, development, and growth of fall Chinook Salmon embryos, alevins, and fry exposed to variable thermal and dissolved oxygen regimes. Transactions of the American Fisheries Society 135:1462–1477.

Harper, K. C. 1976. On the biology of *Salmo apache* and its management implications. Master's thesis. University of Arizona, Tucson.

Harper, K. C. 1978. Biology of a southwestern salmonid, *Salmo apache* (Miller 1972). Pages 99–111 *in* J. R. Moring, editor. Proceedings of the wild trout–catchable trout symposium. Oregon Department of Fish and Wildlife, Research and Development Section, Eugene.

Hinshaw, J. M., and S. L. Thompson. 2000. Trout production: handling eggs and fry. Southern Regional Aquaculture Center, Publication 220 (revised), Stoneville, Mississippi.

Hoerling, M. P., and J. Eischeid. 2007. Past peak water in the Southwest. Southwest Hydrology 6(1):18–19, 35.

Hokanson, K. E. F., J. H. McCormick, B. R. Jones, and J. H. Tucker. 1973. Thermal requirements for maturation, spawning, and embryo survival of the Brook Trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 30:975–984.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.

Kelley, J. W. 1968. Effects of incubation temperature on survival of Largemouth Bass eggs. Progressive Fish-Culturist 30:159–163.

Kincaid, W. S. 1910. New methods of transporting eggs and fish. U.S. Bureau of Fisheries Bulletin 28:1037–1039.

Klimogianni, A., G. Koumoundouros, P. Kaspiris, and M. Kentouri. 2004. Effect of temperature on the egg and yolk-sac larval development of Common Pandora, *Pagellus erythrinus*. Marine Biology 145:1015–1022.

Koumoundouros, G., P. Divanach, L. Anezaki, and M. Kentouri. 2001. Temperature-induced ontogenetic plasticity in Sea Bass (*Dicentrarchus labrax*). Marine Biology 139:817–830.

Lee, R. M., and J. N. Rinne. 1980. Critical thermal maxima of five trout species in the southwestern United States. Transactions of the American Fisheries Society 109:632–635.

McKim, J. M. 1977. Evaluation of tests with early life stages of fish for predicting long-term toxicity. Journal of the Fisheries Research Board of Canada 34:1148–1154.

Pauwels, S. J., and T. A. Haines. 1994. Survival, hatching, and emergence success of Atlantic Salmon eggs planted in three Maine streams. North American Journal of Fisheries Management 14:125–130.

Payton, M. E., M. H. Greenstone, and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? Journal of Insect Science [online serial] 3:34.

Platts, W. S. 1991. Livestock grazing. Pages 389–423 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Polo, A., M. Yúfera, and E. Pascual. 1991. Effects of temperature on egg and larval development of *Sparus aurata* L. Aquaculture 92:367–375.

Recsetar, M. S. 2011. Thermal tolerance of Apache Trout at various life stages. Master's thesis. University of Arizona, Tucson.

Rubin, J. F., and C. Glimsäter. 1996. Egg-to-fry survival of the Sea Trout in some streams of Gotland. Journal of Fish Biology 48:585–606.

Scherr, M. A., D. E. Wooster, and S. Rao. 2010. Effects of temperature on growth rate and behavior of *Epeorus albertae* (Ephemeroptera: Heptageniidae) nymphs. Environmental Entomology 39:2017–2024.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of Bull Trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. 2007. Climate change 2007: the physical science basis—contribution of working group I to the fourth assessment report of the IPCC (Intergovernmental Panel on Climate Change). Cambridge University Press, Cambridge, UK.

Stonecypher, R. W., Jr., W. A. Hubert, and W. A. Gern. 1994. Effect of reduced incubation temperatures on survival of trout embryos. Progressive Fish-Culturist 56:180–184.

Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. Limnology and Oceanography 23:461–477.

Teletchea, F., and P. Fontaine. 2010. Comparison of early life-stage strategies in temperate freshwater fish species: trade-offs are directed towards first feeding of larvae in spring and early summer. Journal of Fish Biology 77: 257–278.

Trimble, S. W. 1994. Erosional effects of cattle on streambanks in Tennessee, U.S.A. Earth Surface Processes and Landforms 19:451–464.

USFWS (U.S. Fish and Wildlife Service). 2009. Apache Trout recovery plan, 2nd revision. USFWS, Region 2, Albuquerque, New Mexico.

Velsen, F. P. J. 1987. Temperature and incubation in Pacific Salmon and Rainbow Trout: compilation of data on median hatching time, mortality and embryonic staging. Canadian Data Report of Fisheries and Aquatic Sciences 626.

Wagner, E. J., R. E. Arndt, and R. Roubidoux. 2006. The effect of temperature changes and transport on Cutthroat Trout eggs soon after fertilization. North American Journal of Aquaculture 68:235–239.

Wang, Y. L., R. K. Buodington, and S. I. Doroshov. 1987. Influence of temperature on yolk utilization by the White Sturgeon, *Acipenser transmontanus*. Journal of Fish Biology 30:263–271.

Wedekind, C., and C. Küng. 2010. Shift of spawning season and effects of climate warming on developmental stages of a grayling (Salmonidae). Conservation Biology 24:1418–1423.

Widmer, A. M., C. J. Carveth, S. A. Bonar, and J. R. Simms. 2006a. Upper temperature tolerance of Loach Minnow under acute, chronic, and fluctuating thermal regimes. Transactions of the American Fisheries Society 135:755–762.

Widmer, A. M., C. J. Carveth, J. W. Keffler, and S. A. Bonar. 2006b. Design of a computerized, temperature-controlled, recirculating aquaria system. Aquacultural Engineering 35:152–160.

Williams, J. E., and J. M. Carter. 2009. Managing native trout past peak water. Southwest Hydrology 8(2):26–27, 34.

Willoughby, L. G. 1994. Fungi and fish diseases. Pisces Press, Stirling, Scotland.

Zale, A. V. 1984. Applied aspects of the thermal biology, ecology, and life history of the Blue Tilapia, Tilapia aurea (*Pisces*: Cichlidae). Doctoral dissertation. University of Florida, Gainesville.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.