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Temperature requirements of rainbow trout and brown trout in relation to flows between O'Shaughnessy Dam and Early Intake on the Tuolumne River, California

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Executive Summary

The US Fish and Wildlife Service has proposed a flow regime for the 12.1 mile reach of the Tuolumne River between O'Shaughnessy Dam and Early Intake that is designed to optomize conditions for trout in 4 mile stretch from Preston Falls to Early Intake. Maintaining healthy wild trout populations in this reach is regarded particularly important because it is the most accessible portion of the regulated reach and the most heavily fished as a consequence. Therefore a flow regime has been recommended that keeps temperatures below 20 C at almost all times. In addition, USFWS has suggested that increasing winter flows in the river could increase temperatures and therefore increase trout production by increasing the development rates of embryos and the growth rates ofjuvenile and adult fish. The purpose of this paper is to examine the role of temperature in maintaining the fish communities of this reach of river. To do this, we reviewed the literature on the temperature requirements of the various life history stages of rainbow trout and brown trout, focussing especially on rainbow trout because it is native to the river, as well as those of other fishes native to this reach of river.

A 1976 USFWS survey of the reach showed that brown trout dominated the fish community above Preston Falls but that below the falls rainbow trout dominated and Sacramento sucker, California roach, and riffle sculpin were present as well. Overall, trout were most abundant in the Tuolumne Gorge reach and least abundant in reach between the gorge and the dam.

The literature suggests that the temperatures of 25-26 C are invariably lethal to rainbow trout and temperatures of 26-27 C are invariably lethal to brown trout. Lower temperatures can be lethal if the fish had been acclimated to cold water. For suckers and roach, absolute lethal temperatures seem to be 35-37 C. Optimal growth for rainbow trout occurs at 15-17 C and for brown trout at 12-19 C, under constant temperatures. Studies on rainbow trout indicate that fastest growth occurs at fluctuating temperatures, where daytime temperatures approach, but do not exceed, 20 C. Temperatures selected by trout when given a choice vary considerably but: 12-20 C for adult rainbow trout; 13-19 C for adult brown trout both species of trout seem to prefer water between 13 C and 20 C and often select temperatures that would seem suboptimal for growth. California roach and Sacramento suckers seem to have temperature preferences of around 25-26 C.

Optimal temperatures for incubation of embryos in the gravel range from 4 to 15 C for rainbow trout and 2 to 14 C for brown trout, although time to hatching is shortest at the higher temperatures. Development temperatures for embryos of roach and sucker are probably optimal at 12-18 C but optimal temperatures for larval growth presumably considerably higher.

It appears that rainbow trout have a competitive and reproductive advantage over brown trout at higher temperatures and vice versa. This may explain why rainbow trout become progressively more abundant in a downstream direction from the dam.

The flow regime proposed by USFWS most likely would increase the trout populations in the reach of the Tuolume River between Preston Falls and Early Intake by reducing the number of summer days in which water temperatures would be stressful to both species of trout We predict, however, the flow regime, with its reduced temperatures, would have several biological consequences:
(1) The Early Intake section should switch from being dominated by native rainbow trout to being dominated by exotic brown trout. Brown trout dominance would become even stronger in the upper sections. (2) Sacramento sucker and California roach should decrease in abundance. (3) Catchable trout numbers should decrease in uppermost sections of the reach because the cold temperatures will decrease growth rates and, perhaps, survival rates of juveniles. This would essentially mean that average total numbers of catchable trout will not change much in the entire reach, but more of the trout would be present in the lowermost section. In short, the improved fishery in the lowermost section would come at the expense of a reduced fishery in the uppermost section and at the expense of the native rainbow trout-nongame fish community which would be replaced with a community largely dominated by brown trout.

There seems to be little justification for increasing flows in the winter to improve development rates of embryos and growth rates of fry. Temperatures for this purpose are close to optimal in most years in the lowermost sections for rainbow trout and in the other sections for brown trout (except for being on cold side of the range in January and February).

Introduction

The 12.1 mile reach of the upper Tuolumne River between O'Shaughnessy Dam (Hetch-Hetchy Reservoir) and Early Intake has its flows regulated by the City of San Francisco, as part of the water supply system for the city. As part of the licensing procedure to permit the city to use the diverted water for power production, the US Fish and Wildlife conducted an instream flow study (Aceituno 1992). The weighted usable area curves generated by this study indicated that "flows as low as 80 cfs would provide at least 90 percent of the maximum predicted adult trout habitat" and "flows as low as 20 to 30 cfs would provide at least 90 percent of the maximum habitat area predicted for juvenile rainbow and brown trout (Aceituno 1992, p. 24)". The USFWS draft report concludes, however, that these flows would result in temperatures in the lower four miles of the reach that would be high enough at times to be stressful, and perhaps lethal, to trout. Maintaining healthy wild trout populations in this reach is regarded particularly important because it is the most accessible portion of the regulated reach and the most heavily fished as a consequence. Therefore a flow regime has been recommended that keeps temperatures in this 4 mile reach below 20 C at almost all times. In addition, M. Aceituno (pers. comm.) has suggested that increasing winter flows in the river could increase temperatures and therefore increase trout production by increasing the development rates of embryos and the growth rates ofjuvenile and adult fish.

The purpose of this paper is to examine the role of temperature in maintaining the fish communities of the O'Shaughnessy-Early Intake (OEI) stretch of river. To do this, we reviewed the literature on the temperature requirements of the various life history stages of rainbow trout and brown trout, focussing especially on rainbow trout because it is native to the river. We also examined the limited information available on the temperature requirements of other fishes native to this reach of river because we feel that one goal of the flow regime should be to maintain as much of the native biodiversity as possible.

Background: fish communities

The most detailed survey of the fishes of the OEI area was USFWS (1976) which indicated there were five distinct habitat reaches: (1) O'Shaughnessy Dam to Poopenaut Valley, (2) Poopenaut Valley, (3) the Tuolumne Gorge, (4) mouth of the gorge to Preston Falls, and (5) Preston Falls to Early Intake. In comparing these five reaches, the study shows the following:

1. Brown trout (not native) predominate in the uppermost reach (83% of the catchable size [175+ mm] trout in 1976) but become proportionally less abundant in a downstream direction. Rainbow trout predominate (55% of catchable-size trout) in the lowermost reach.

2. In 1976, Trout densities were highest in the Gorge (925 catchable-size trout per mile), followed by the above falls reach (762 catchable trout per mile), the below falls reach (600), the dam reach (553), and the Poopenaut Valley (451). Presumably, this general situation still exists, although densities are likely to vary considerably from year to year due to natural factors.

3. Preston Falls serves as a natural barrier to the upstream distribution of native freshwater fishes, except trout. Other species found in the reach below the falls are Sacramento sucker (Catostomus occidentalis), California roach (Lavinia symmetricus), and riffle sculpin (Cottus gulosus). The USFWS study did not measure the abundance of these fishes, but observations by P. Moyle made in 1986 indicated that they were present only in low numbers. The combination these three species with rainbow trout is a fairly typical assemblage of native fishes in larger middle elevation streams on the west side of the Sierras.

Background: Tuolumne River temperatures

There are two USGS gaging stations in the O'Shaugnessy-Early Intake reach that record flows and temperatures. One station is immediately below the dam, the other is above Early Intake. The temperature recorders were installed in both places in 1987. Below the dam, temperatures are typically between 5 and 9 C in January through June and they gradually become higher through September, reaching daily maxima of 12-14 C. The water warms considerably by the time it reaches Early Intake and shows considerable year to year variation in temperature regime. The temperature has a negative relationship with the amount of water being released (more water, cooler temperatures) and a positive relationship with air temperature. During June-September, daily minimum temperatures always remain below 19 C (usually below 16 C) although daily maxima can reach 22-23 C during times of low releases from the dam. The highest temperatures on record were during May 28- June 4, 1992, when temperatures reached 23-24 C during the day but only dropped to 19-20 C at night.

Background: importance of temperature to fish

Environmental temperature exerts a dominating influence over the lives of animals. This is decidedly pronounced in poikilothermic ("cold-blooded") organisms such as fishes whose gills act as counter current heat exchangers with their surroundings. Fish are under more strict limitations than terrestrial vertebrates due to the high heat capacity of their environment. As a result, temperature regulation is largely limited to behavioral responses to thermal gradients, as radiative and evaporative heat exchange are not possible (Beitinger and Fitzpatrick 1979).

Beitinger and Fitzpatrick stated that temperature legislates control over fish more than any other single abiotic factor. The justification for this statement is multi-faceted. Temperature influences all aspects of a fish's life. Changes in water temperature effect water chemistry, the amount of dissolved oxygen, respiratory efficiency (Cech et al. 1990), swimming efficiency (Cech et al. 1990), metabolism (Cech et al. 1990, Crowder and Magnuson 1983, Moyle and Cech 1988, Moyle 1976), growth rates (Cech et al. 1990, Crowder and Magnuson 1983, Moyle and Cech 1988, Moyle 1976), and feeding behavior, (Cech et al. 1990, Crowder and Magnuson 1983, Moyle and Cech 1988, Moyle 1976). Environmental temperature also stimulates reproductive and developmental changes (Moyle and Cech 1988, Houston 1982, Moyle 1976), such as the initiation of spawning runs and the parr/smolt transformation in salmonids (Moyle 1976).

In light of this, the concern over thermal effects on fishes by environmental managers and water agencies around the nation is well founded. The literature on this subject is quite extensive, yet is often contradictory and confusing. What is presented here is a literature review of the effects of temperature on the life histories of rainbow trout (Onchorynchus mykiss) and brown trout (Salmo trutta), with emphasis on rainbow trout. Limited additional information is presented on Sacramento sucker (Catostomus occidentalis) and California roach (Lavinia symmetricus). This report will cover the interactions of environmental temperature with thermal maxima/minima, growth optima, preferenda, reproduction/ontogeny, and competition.

Temperature maxima and minima

The thermal limits of salmonids have been investigated following two distinct methodologies (Bjornn and Reiser 1991): critical thermal maxima (CTM), where fishes are exposed to rapid but continuous increases (1 degree C per minute) in temperature until a maximum threshold is reached, and the upper incipient lethal temperature (UILT), where fish are abruptly transferred between temperatures. The CTM values tend to be higher on average than the UILT values (Bjornn and Reiser 1991). These critical values tend to co-vary with two factors in fishes life history: the developmental stage of the fish, and the recent acclimation history of the fish (Bjornn and Reiser 1991, Raleigh et al. 1984, Houston 1982, Jobeling 1981, Cherry et al. 1975). The values generated for trout from laboratory studies have to be treated with a certain amount scepticism because the experiments typically rely on small numbers of juveniles of hatchery origin.

Development. Thermal tolerance during development has been directly studied very little, some inferences can be made from the literature for the two trout species. In both species, it appears that thermal tolerance increases during juvenile development and declines with the attainment of adulthood (Houston 1982). There exists no rigorous quantification of this observation and no satisfactory explanation for it either. Further reference will be made to the effects of temperature on ontogeny.

Acclimation history. Acclimation temperature is defined by Houston (1982) as the temperature to which an organism has been exposed prior to testing. There is a wealth of evidence showing that thermal maxima increase with increasing acclimation temperature (Table 1) (Bjornn and Reiser 1991, Raleigh et al. 1984, Stauffer et al 1984, Houston 1982, Spigarelli et al. 1983, Spigarelli and Thomas 1979, Hokanson et al. 1977, Cherry et al. 1975)

UILT for brown and rainbow trout are given in Table 2, as these values are more commonly found in the literature than are CTM values. Although individual salmonids may be able to survive higher temperatures for short periods of time, they enter a potentially life threatening situation when their ambient water temperature falls above 23-25°C (Bjornn and Reiser 1991).

Table 1: Acclimation Temp. and UILT for rainbow trout (O. mykiss)	
Acclimation temp. (°C)	UILT (°C)
6	24.6
12	25.9
18	26.7
24	26.0*

*value based on estimate from data

Table 2: Upper Incipient Lethal Temperature (UILT)	
Rainbow trout (O. mykiss)	25°C (Bjorn & Reiser 1991)
	25°C (Raleigh et al. 1984)
	25°C (Houston 1982)
	21-22°C (Houston 1982)
	25.8°C (Jobling 1981)*
	25.6°C (Hokanson et al. 1977)
Brown trout (S. trutta)	26.7°C (Bjorn & Reiser 1991)
	27.2°C (Raleigh et al. 1986)
	23°C (Houston 1982)
	24.1°C (Jobling 1981)
	26.4°C (Staley 1966)

*average of 5 values

Lower temperature limitations of trout are less well studied. The lower critical temperatures tend to vary with acclimation temperatures (Bjornn and Reiser 1991). Most fishes generally expire when temperatures reach 0°C to -0.1°C, although temperatures in the range of 1-4°C can be potentially life threatening depending on acclimation history and developmental stage (Bjornn and Reiser 1991, Raleigh et al. 1984). Low temperatures can also be harmful if over-wintering habitat becomes clogged with ice, freezes solid, or if heavy snow pack deprives the stream of oxygen (Bjornn and Reiser 1991, Raleigh et al. 1984).

For Sacramento sucker and California roach the only temperature tolerance study available is that of Knight (1985), who found that the critical thermal maxima of these species also increased with temperature. For suckers, the CTM at 15 C was 30 C; at 20 C, 33 C; at 25 C and 30 C, 35.5 C. For roach, the CTM at 10 and 15 C was 30 C; at 20 C, 32 C; at 25 C, 35 C and at 30 C, 37 C. Obviously, suckers and roach can survive much higher temperatures than trout, which is not surprising considering they are often found in streams that have temperatures exceeding 32 C for short periods of time during the day.

Growth Optima

Environmental temperature is the principal abiotic factor influencing the growth of fishes (Houston 1982). Temperature optima for growth vary throughout the life stages of fishes (McCauley and Cassleman 1981), but are typically calculated for juvenile to adult stages (Table 3). As a principal controlling factor in the environment, temperature sets limits on rates of growth. It alters the metabolic level required for basic maintenance, thereby influencing the amount of calories available for growth. At high temperatures, more energy is needed for maintenance thus increasing the caloric intake necessary for a given growth rate. The highest growth rates therefore are generally obtained at intermediate temperatures (Houston 1982).

Houston (1982) suggested that there are qualitatively different growth limiting effects associated with increasing temperatures. At low temperatures, the rate of digestion limits growth. In the intermediate range, food conversion efficiency is limiting, while at high temperatures non-growth metabolism is often balanced by energy intake therefore reducing the net growth rate to zero.

The majority of studies concerned with optimizing temperature effects with growth rates are conducted under a constant temperature regime (Hokanson et al. 1977). It is generally assumed that a constant temperature environment will produce the same response as a fluctuating system with the same average temperature (Hokanson et al. 1977). This methodology is acceptable when designing temperature regimes for aquaculture systems, but fails to adequately model a natural system. Natural diurnal patterns produce temperature fluctuations in aquatic systems. Hokanson et al. (1977) tested the assumption that constant temperature systems have the same growth optima as fluctuating systems for rainbow trout. Their study examined growth at seven constant temperatures and growth under six sine wave regimes with a constant amplitude of 3.8°C. (Fig. 1) The results showed interesting trends (Fig. 2 & Table 3). Under constant temperature the optima occurred at 17.2°C, while under a fluctuating system the optima occurred at an average temperature of 15.5°C with daily highs and lows of 19.3°C and 11.7°C respectively. This growth maxima also correlated with an increase in biomass (Hokanson et al. 1977).

Table 3: Maximum Growth Rate	
Rainbow trout (O. mykiss)	16.8°C (McCauley et al.1981)
	16.9°C (Jobling 1981)
	15.5°C (Hokanson et al. 1977)*
Brown trout (S. trutta)	12-19°C (Raleigh et al. 1984)
	12.6°C (Jobling 1981)
	7-19°C (Moyle 1976)

*average under diurnal environmental fluctuations.

It is believed that these fluctuations in temperature allow the fish to feed at high efficiency during the day while the period of colder temperature allows them a metabolic rest when their food conversion efficiency is higher.

Hokanson et al. (1977) also noticed that temperatures near or at the trout's thermal limit (23°C) increased mortality sharply under the fluctuating regime, indicating the fish were acclimated to a lower temperature. This would indicate that fluctuations that approach the physiological maxima are more harmful than currently estimated from constant temperature studies (Hokanson et al. 1977).

Seasonal changes in temperature do not prompt marked variation in adult growth rate, the estimated rates under a seasonal regime approximate those under conditions of mean seasonal temperature (Houston 1982).

Preferenda

Temperature preference is based on the observation that a fish when given a choice, will spend most of their time within a narrow range of temperatures, characteristic of the species, named the final temperature preferendum (Bjornn and Reiser 1991, Houston 1982, Jobeling 1981, Beitenger and Fitzpatrick 1979). Table 4 provides a compiled list of adult preferenda for rainbow and brown trout. The final preferendum appears to be independent of acclimation temperature and tends to vary with developmental stage (Houston 1982 Jobeling 1981). (table 5) In rainbow trout, younger trout tend to have higher preferenda than older fish (Jobeling 1981).

Table 5: Adult Preferred Temperature	
Rainbow trout (O. mykiss)	16-18.2°C (Baltz et al. 1987)
	12-19.3°C (Raleigh et al. 1984)
	14.7°C (Stauffer et al. 1984)
	20.3°C (McCauley 1981)
	13-15°C (Spigarelli 1979)
Brown trout (S. trutta)	17.6°C (Spigarelli et al. 1983)
	17.6°C (McCauley 1981)
	13-19°C (Moyle 1976)

Table 6: Fry/Juvenile Preferred Temperature	
Rainbow trout (O. mykiss)	13-19°C (Raleigh et al. 1984)
	14.3°C (Peterson et al. 1979)
	14-19°C (Spigarelli 1979)
Brown trout (S. trutta)	17.4°C (Spigarelli et al. 1983)

This data indicates that both species of trout prefer water between 13 C and 20 C and often select temperatures that would seem suboptimal for growth. Knight (1985) found that California roach have an acute final temperature preferendum of 25-26 C. The final temperature preferendum for Sacramento sucker was not determined but the limited data presented by Knight (1985) indicates it is probably also around 26 C.

According to Beitinger and Fitzpatrick (1979), the final temperature preferendum chosen by fish in laboratory experiments implies three asumptions: 1. The final preferendum is species specific. 2. When possible, fishes will occur at their final preferendum. 3. The final preferendum is the result of an optimization of one or more key life-history parameters. In the literature, the first two of these hypotheses are generally met (Beitinger and Fitzpatrick 1979). The last hypothesis has proven more difficult to quantify.

From the previous discussion of growth optima, a simple comparison reveals that rainbow and brown trout are apparently not regulating their behavior to maximize growth rate, as might be expected. However dispersion in a heterogenous environment can be influenced by other environmental variables such as season, diet, swimming efficiency, oxygen, diet, predator avoidance, and diel patterns (Stauffer et al. 1984). Crowder and Magnuson (1983) hypothesized, based on optimal foraging theory, that fishes foraging in a heterogenous environment are balancing a complex energy budget and are optimizing both food intake and temperature. Their analysis suggests that optimal temperatures for growth will be depressed by one or two degrees below preferred temperatures given a patchy distribution of food resources. This is likely to be the situation in a natural environment, and reflects the disparity between preferred and growth optimizing temperatures in the published literature. Thermal preferenda is therefore likely to be highly correlated with food availability.

Reproduction/ontogeny

Reproductive processes in temperate stream fishes exhibit some dependency on environmental temperature (Bjornn and Reiser 1991, Houston 1982). Often developmental thermal requirements are tightly correlated with the natural seasonal variations in temperature (Houston 1982). When favorable thermal conditions are present for reproductively active fish, normal gonadal development will occur. However, if the ambient temperatures are too high or low, too gamete maturation will be arrested and spawning may not take place (Houston 1982). This may lead to a complete loss of one year's reproductive effort. For trout which, on average, exhibit only 1-4 spawning seasons, the loss of one spawning season can have profound effects on each fish's lifetime reproductive success.

Spawning initiation and timing likely evolved as a response to multiple stimuli, including water temperature (Bjornn and Reiser 1991). Spawning temperature has been correlated to gamete thermal tolerance (Bjornn and Reiser 1991). Rainbow trout spawn during intervals of changing water temperature, with absolute temperature and rate of change in temperature both being important (Houston 1982, MacCrimmon and Gordon 1981). Spawning is often stimulated by the presence of freshets or storm flows (Bjornn and Reiser 1991, MacCrimmon and Gordon 1981). These events increase stream volume and temperature which may act as a signal that ambient water temperatures are on the increase. The warmer temperatures are necessary for normal embryo development to occur, which would be retarded in cold water. There may also be an evolutionary/survival advantage to early spawning if it results in an extended growing season.

Water temperature also affects the rate of embryo and alevin development during the incubation period (Bjornn and Reiser 1991). There exist species specific upper and lower temperature thresholds for successful development (Table 7).

Table 7: Incubation Temperature Optima	
Rainbow trout (O. mykiss)	7-12°C (Raleigh et al. 1984)
	8-15°C (Moyle 1976)
	4.4-15.5°C (McAfee 1966)
Brown trout (S. trutta)	2-13°C (Raleigh et al. 1986)
	6-10°C (Moyle 1976)
	1.6-12.8°C (Staley 1966)

As a general trend, higher temperatures (within limits) produce faster rates of development (Tables 8 & 9) (Bjornn and Reiser 1991, Raleigh et al. 1986, Raleigh et al. 1984, Houston 1982, Moyle 1976, McAffee 1966, Staley 1966). Early development provides an advantage, as early emergence creates a protracted growing season. This in turn allows the fish to compete more successfully outside and within the species. What all this indicates is that for rainbow trout, successful incubation (high survival rates to hatching) of the embryos in the gravel can occur between 4 and 15 C, although optimal temperatures are probably at the upper end of this range. For brown trout, successful incubation temperatures are slightly lower, 2-13 C, which may explain in part their greater abundance below O'Shaugnessy Dam.

Table 8: Incubation Period for Rainbow Trout Eggs vs. Temp.*	
Water Temp. (°C)	Average Hatching Time (days)
4.4	80
7.2	48
10.0	31
12.8	24
15.5	19

*adapted from McAfee (1966)

Table 9: Incubation Period for Brown Trout Eggs vs. Temp.*	
Water Temp. (°C)	Average Hatching Time (days)
1.9	148
3.6	118
4.7	97
6.1	77
7.8	60
10.0	41
11.1	35
12.2	---

*adapted from Staley (1966)

Both California roach and Sacramento suckers spawn in the spring, when temperatures are 12-18 C, and scatter their eggs in gravel riffles. Incubation takes 3-4 weeks and the tiny larvae generally concentrate in the shallow backwaters of the rivers where day-time temperatures are warm and predators are few.

Competition

The literature on specific competitive effects between rainbow and brown trout is sparse. The two species are known to share similar food habits and habitat preferences and therefore are expected by classical ecological theory to exhibit interspecific competition via niche shifts (Gatz et al. 1987). This is observed in nature as brown trout successfully out compete rainbow trout during most life history stages. The typical situation is one in which a few large brown trout dominate stream reaches. Brown trout are very aggressive and will force displacement of rainbows to sub-optimal habitat (Gatz et al. 1987, Moyle 1976).

There is no data regarding the effect temperature plays in this competition. Yet with the data presented in Tables 1-9 some tentative inferences may be drawn. Brown trout tend to prefer and grow better at lower temperatures than rainbow trout. Brown trout also exhibit lower incubation optima. In regards to UILTs brown trout appear to have similar or slightly higher tolerances than rainbow trout. With this in mind it would appear that rainbows may have a competitive advantage over brown trout at higher temperatures and vice versa. This hypothesis has not been tested but may explain the relative abundances of the two species in the different sections of the regulated reach of the Tuolumne River.

Conclusions

The flow regime proposed by USFWS most likely would increase the trout populations in the reach of the Tuolume River between Preston Falls and Early Intake by reducing the number of summer days in which water temperatures would be stressful to both species of trout. This would presumably increase growth rates of adults and juvenile trout and survival rates of juveniles (because they would reach larger sizes more quickly, reducing the number of predators on them). Whether or not this increase in trout numbers would be reflected in an improved fishery depends on many nonbiological factors, such as fishing regulations and fishing intensity. We predict, however, the flow regime, with its reduced temperatures, is likely to have the following biological consequences:

1. The Early Intake section should switch from being dominated by native rainbow trout to being dominated by exotic brown trout. Brown trout dominance would become even stronger in the upper sections.

2. Sacramento sucker and California roach numbers should decrease and the two native species might even be eliminated from the section. They are presumably on the upper edge of their natural range which is determined in part by thermal regime; populations are rarely found in streams that consistently stay below 20 C in the summer. Riffle sculpins would probably increase in numbers or stay at about the same densities as a result of the reduced temperatures.

3. Catchable trout numbers should decrease in uppermost sections of the reach because the colder summer and fall temperatures will decrease growth rates and, perhaps, survival rates of juveniles. This may mean that average total numbers of catchable trout will not change much in the entire reach, but more of the trout would be present in the lowermost section.

In short, the improved fishery in the lowermost section would come at the expense of a reduced fishery in the upper sections and at the expense of the native rainbow trout-nongame fish community which would be replaced with a community largely dominated by brown trout. Whether or not this replacement is desirable is a matter for debate.

It is also worth noting that there seems to be little justification for increasing flows in the winter to improve development rates of embryos and growth rates of fry. Temperatures for this purpose are close to optimal in most years in the lowermost sections for rainbow trout and in the other sections for brown trout (except for being on cold side of the range in January and February).

Literature Cited

to be completed