

Bigger Is Not Always Better for Overwintering Young-of-Year Steelhead

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Abstract.—Many fishes occur across broad ranges of latitude and elevation, where winter temperatures can vary from mild to harsh. We conducted a laboratory experiment with three sizes of age-0 steelhead *Oncorhynchus mykiss* to examine growth, condition, and energy reserves under low rations at three levels of water temperature typical of this species' distribution during winter. At the end of the 111-d experiment, all three starting sizes of age-0 steelhead (small, 2–3 g; medium, 3–4 g; large, 4–5 g) held in 3°C water had lower total lipid weight than those held in 6°C and 9°C water. Large fish had higher total lipid weight than small fish at the onset of the experiment and retained higher amounts at the end. However, large fish had either the lowest percentage increases or the highest percentage decreases in fork length, biomass, condition factor, total lipid weight, and percent lipids within all thermal treatments. The magnitude of the differences between small and large fish was highest in the warmest (9°C) water. We used bioenergetics simulations of juvenile steelhead growth to examine fish response to initial size, winter temperature, and food availability. Relatively warm water temperatures in winter, coupled with limited food availability, may present more of a physiological challenge to larger age-0 steelhead than to smaller fish. Our results suggest that achievement of large size before the start of a steelhead's first winter can have a cost under episodic conditions found across the wide ranges of latitude and elevation within this species' distribution.

Overwinter survival of young-of-year fishes has been recognized as a limiting factor in stream salmonids, including brook trout *Salvelinus fontinalis* (Hunt 1969), brown trout *Salmo trutta* (Elliott 1989), and steelhead *Oncorhynchus mykiss* (anadromous rainbow trout; Ward and Slaney 1993; Wentworth and LaBar 1994; but see Seelbach [1987]). Survival during cold winters has been directly related to the size achieved before winter in a number of salmonids (Quinn and Peterson 1996; Hunt 1969) and nonsalmonids (Oliver et al. 1979; Toney and Coble 1979, 1980; Miranda and Hubbard 1994). Growth can be limited by food availability (Johnson and Evans 1990; Railsback and Rose 1999), cohort density (Wentworth and LaBar 1994; Dunham and Vinyard 1997; Jenkins et al. 1999), habitat complexity (Cunjak 1996; Meyer and Griffith 1997; Maki-Petays et al. 1999), and stream geomorphology (Kaeding and Osmundson 1988; Rodenhouse et al. 1997). Even when food is abundant during their first winter, young-of-year fish may be unable to assimilate it (Cunjak et al. 1987). A size-dependent overwinter survival relationship appears especially strong for populations at the northernmost (Shuter and Post 1990;

Shindler 1999) or most upstream (Thompson et al. 1991) portions of their ranges.

Although attainment of a large size before a cold winter can be beneficial for the young-of-year of many fish species, severely cold winter conditions may occur only occasionally for populations that rear in warmer climates, such as those at low to moderate elevations or those at the southern limits of the species' ranges. Larger fish have lower basal metabolism than their smaller cohorts, which enables the larger fish to endure longer periods of limited food intake or starvation during cold winters (Cargnelli and Gross 1997; Berg and Bremset 1998). However, unusually warm winters induce an increased metabolic rate and an increased energy requirement, which may shift the survival advantage to small fish within a young-of-year cohort (Schultz and Conover 1999). Because lipid reserves are often related to the size and survival of an individual fish (Thompson et al. 1991; Miranda and Hubbard 1994; Sogard and Olla 2000), it is important to understand what factors affect a fish's ability to store or spend lipid reserves.

The severity of winters within the steelhead's West Coast distribution generally increases from south to north and from west to east (Seelbach 1987). Climate and its variability with latitude and elevation can explain much of a species' distri-

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bution (Conover and Present 1990; Flebbe 1994; McMichael and Pearsons 1998; Dunham et al. 1999). On the west coast of North America, steelhead range from a latitude of 34°N in southern California to 49°N in southeast Alaska (Busby et al. 1996). Within these latitudes, steelhead spawn and rear in low-elevation streams of coastal ranges to high-elevation streams that drain inland mountain ranges, including the Cascades and the Rocky Mountains. At six midelevation (287–585 m) stream sites within the Wind River watershed (Cascade Mountains, southeastern Washington), located in the midlatitude (46°N) of the steelhead distribution, continuously recording thermographs recorded mean monthly temperatures between 3°C and 6°C during the 1997–1998 winter (authors' unpublished data). In more southerly latitudes at low elevations, daily winter temperatures may often exceed 10°C (e.g., the Sacramento River; Domagalski et al. 2000). We used this temperature information in designing a laboratory experiment to help us understand the importance of winter conditions and their effect on juvenile steelhead growth and lipid reserves during their first winter.

The objective of our laboratory experiment was to measure overwinter changes in body size, condition, and energy stores of young-of-year steelhead and to relate these changes both to the sizes that the steelhead attained before winter and to the water temperatures that they experienced during winter. The experiment was conducted under controlled conditions with water temperatures of 3, 6, and 9°C, which broadly represent water temperatures expected within the distributional range of North American steelhead.

Methods

We conducted a laboratory experiment to test for the effects of fish size and winter water temperature on growth, condition, lipid content, and survival of juvenile steelhead. We obtained age-0 Skamania-stock steelhead (mean weight, 0.35 g) from Skamania State Hatchery (Washington) in February 1997. In April 1997, the fry were allocated to three 2-m-diameter tanks and fed differing rations to achieve three size-classes of fish for use in the experiment: small (2–3 g), medium (3–4 g), and large (4–5 g).

Before the experiment (12–13 November 1997), we measured the fork lengths and determined the biomass of all fish. Fish of the same size-class were sorted into six half-filled 113.6-L circular treatment tanks. Each tank was stocked with 50 fish, resulting in densities ranging from 2.20 to 3.96 g/

L in each tank. The 18 treatment tanks were systematically dispersed throughout a room. Three additional tanks were used to hold marked fish for replacing those that died during the experiment, in order to maintain 50 fish in each treatment tank. To simulate light conditions encountered in the wild, fish were exposed to a 10 h light : 14 h dark photoperiod with 0.5-h transition periods adjusted with an automated light intensity system.

Fish were held at a relatively constant ambient water temperature (about 6°C) for 6 d before water temperatures were adjusted to treatment levels over a period of 48 h. Two tanks (replicates) per size-class of fish were exposed to one of three water temperatures: 3°C, 6°C (ambient), and 9°C. These water temperatures were maintained with little variation (coefficients of variation < 1%) throughout the course of the experiment, in spite of three power outages (one on day 41 and two on day 54) of less than 4 h each. During the power outages, water temperatures in the 9°C tanks adjusted to ambient inflow water temperatures and then readjusted to treatment temperatures when power was restored.

We used two constraints in determining the amount of food to provide fish during our experiment: First, we assumed that the amount of food available to young-of-year steelhead in the wild would be relatively low and constant through the winter. Second, we designed the food regime across all treatments so that *expected* growth would be zero. This second constraint was implemented to allow us to test the basic hypothesis that variations in size and/or temperature would produce changes in *observed* growth. Without adjusting the feeding regime based on this zero-growth constraint, observed changes in growth would have been confounded with food levels, making it more difficult to distinguish the effects of the primary treatments, temperature and size.

The mass of food provided to fish in each treatment was determined by first estimating the expected growth of fish under various rations with a bioenergetics model. During experimental design, we used the model of Hanson et al. (1997) and the best available model parameters for rainbow trout (Rand et al. 1993; S. Railsback, Lang, Railsback, and Associates, personal communication), although this parameter set was subsequently improved (Railsback and Rose 1999). For our fish size-groups and temperatures, preliminary model results suggested that providing a 1% ration would produce zero growth during the experiment. We set the target ration for medium-sized fish in the

TABLE 1.—Mean percent ration ([weight of total feed/biomass of all fish in tank] \times 100) for three size-classes of juvenile steelhead held at three water temperatures. Because grams of feed supplied to individual fish tanks were held constant throughout the experiment (111 d), the change in ration was because of fish growth. The proportions of maximum consumption (*P*-values; Hanson et al. 1997; Railsback and Rose 1999) were obtained from a bioenergetics model incorporating the starting and ending sizes of fish in each treatment (see text).

Fish size-class	Temperature		
	3°C	6°C	9°C
Start of experiment			
Small (2–3 g)	0.8 (1.0)	1.1 (1.4)	1.4 (1.7)
Medium (3–4 g)	0.7 (1.2)	1.0 (1.8)	1.3 (2.3)
Large (4–5 g)	0.7 (1.6)	0.9 (2.0)	1.2 (2.7)
End of experiment			
Small	0.7	0.8	1.1
Medium	0.6	0.8	1.1
Large	0.7	0.8	1.0
Model <i>P</i> -value			
Small	0.203	0.164	0.141
Medium	0.207	0.159	0.139
Large	0.201	0.164	0.137

6°C treatment to 1%, and adjusted rations slightly up or down in other treatment groups so that expected growth was zero for the projected duration of the experiment (120 d). The actual duration of the experiment was 111 d (21 November 1997 through 12 March 1998). Fish were fed dry commercial food (Abernathy Diet, 4/64-in crumble) two times per week throughout the course of the experiment. The total mass of food provided to each tank was kept constant throughout the experiment (Table 1).

Fish that were dead or dying (unable to maintain equilibrium) were removed daily during the experiment. At the end of the experiment, fork length and biomass data on each fish were collected, and all fish were held at -70°C until lipid analyses were performed.

Lipid analysis.—We analyzed the lipid content of fish to obtain as an index of energy stores (Sutton et al. 2000), which can become depleted when metabolic demand exceeds adequate food intake (Berg and Bremset 1998; Sogard and Olla 2000). Lipid analyses were conducted on pretreatment fish ($N = 30$ from each of the three size-groups) and on posttreatment fish ($N = 16$ –23 from each of the 18 treatment tanks). Lipid content for individual fish was assessed by a modified version of Bligh and Dyer (1959), with chloroform and methanol used for extraction. For our calculations of percent lipids of individual fish, we used total lipid weight and fresh wet weight, following Sut-

ton et al. (2000). Also based on Sutton et al. (2000), we derived a residualized fat weight index from the residuals of a fitted linear regression. An index value was derived independently for pretreatment fish ($N = 90$) and for posttreatment fish ($N = 350$), with \log_{10} transformed fork length as the independent variable and \log_{10} transformed total lipid weight as the dependent variable. Sutton et al. (2000) found this residual index to be more appropriate than Fulton's condition factor *K*, which has rather stringent assumptions (e.g., that the slope of the weight–length relation is 3.0) that are rarely met (Cone 1989). Dry weight was also determined, but analyses of this variable did not differ substantially from those of fresh wet weight. To allow comparisons to other studies, we derived an equation by linear regression to convert wet weight to dry weight.

Statistical analysis.—To test for the contributing effects of fish size and water temperature on the dependent variables of length, biomass, condition factor, lipid weight, and percent lipids, we ran two-way analysis of variance (ANOVA) tests on tank averages (Snedecor and Cochran 1980). With \log_{10} transformed data for total lipid weight as a covariate, we used analysis of covariance (ANCOVA) to test whether Sutton et al.'s (2000) residualized fat weight index varied with fish size and water temperature. To relate fresh weight to dry weight, we used ANCOVA to simultaneously test significance of categorical and continuous variables. When ANOVA and ANCOVA tests indicated significant effects ($\alpha = 0.05$), we performed Tukey's *W* studentized range procedure (Tukey's test) as a multiple comparison approach to provide differentiation of multiple levels within a main effect (Ott 1977). We used the same tests to analyze of the percentage changes in the dependent variables from the beginning to the end of the experiment. Prior to ANOVA or ANCOVA testing, data were tested and found to be in compliance with the normality assumptions, based on the Shapiro–Wilk *W* and normal probability plots.

We had an unaccountable loss of fish from a number of the 18 experimental tanks. When the experiment ended, 6 of the 18 tanks had a full complement of 50 fish, 9 tanks had 46–49 fish, and 3 tanks had fewer than 45 fish. Some fish may have escaped through openings in the central drain stem, either by entering small pores at the bottom ends of the drain stems or by jumping up and into the top ends of the 2-in-diameter stems. Because decreases in density could affect the amount of food available to the remaining individuals, we

conducted two analyses to check for sensitivity of results to density. Results from an ANOVA of data from all tanks were compared with results based on a subset of data derived by eliminating the three tanks containing fewer than 40 fish. Because significance of the results ($\alpha = 0.05$) did not differ between these tests for each dependent variable (fork length, biomass, condition factor, total lipids, percent lipids), we present only the results for the analysis with all tanks included.

Bioenergetics simulations.—We conducted bioenergetics simulations to demonstrate the growth response during winter for juvenile steelhead of various sizes. Simulations were conducted with the program of Hanson et al. (1997) and based on the parameters of Railsback and Rose (1999). All simulations were run for 111 d, the actual length of the laboratory experiments. We used energy density values of 5,306 J/g for prey (Abernathy diet; Ann Gannam, U.S. Fish and Wildlife Service, personal communication) and 5,900 J/g for juvenile steelhead (following Railsback and Rose [1999]).

In the first simulation, we modeled the response surface of growth for 2–6-g juvenile steelhead at temperatures from 3°C to 9°C. We calibrated the feeding response in this simulation with the laboratory results by first computing the proportion of maximum consumption (P -value) from each of the nine treatments (Table 1). The P -values for intermediate sizes and temperatures were linearly interpolated from the experimentally determined P -values. For the second simulation, we used model results to demonstrate how fish growth responded when all fish were feeding at 17% of maximum consumption (i.e., P -value = 0.17), which was the average of the experimentally derived P -values (Table 1). This second simulation also helped to test whether the adjustments we made to our feeding regime to achieve zero growth might have biased our results.

To explore the role of food availability, which we did not test in the laboratory, we varied P -values in simulations from low (0.05) to high (0.30) for 2.5-g and 5.0-g fish and included two temperatures (3°C and 9°C). We again used energy density values of 5,306 J/g for prey and 5,900 J/g for juvenile steelhead. The range of P -values that we used incorporated the average P -value (0.17) predicted from our laboratory experiments. Although P -values in field studies might be generally higher than the values we simulated (e.g., Railsback and Rose 1999), the energy of the food used in our experiment was high relative to natural foods.

Results

Mean length and biomass increased for all size-groups of fish under each thermal treatment in our experiment (Table 2). Percentage changes in length and biomass were directly related to water temperature (Tukey's test, $P < 0.05$; Table 3). Within a thermal treatment, the hierarchy of mean length and biomass values at the beginning of the experiment (large fish > medium fish > small fish) was maintained at the end of the experiment (Tukey's test, $P < 0.05$).

Within each thermal treatment, small fish had higher percentage increases in length and biomass than large fish (Tukey's test, $P < 0.05$), but the growth of small and large fish was not always distinct from that of medium fish (Figure 1A; Table 3). Within each initial size-group, fish held in 9°C water had higher percentage increases in length and biomass than fish held in 6°C water, which in turn had higher percentage increases in length and biomass than fish held in 3°C water (Tukey's test, $P < 0.05$; Table 3).

At the beginning of the experiment, the condition factor and Sutton et al.'s (2000) residualized fat weight index were higher for large fish than for small fish. Because the condition factor of small fish tended to increase whereas that of large fish either increased slightly (at 3°C) or decreased (at 6°C and 9°C) over the duration of the experiment, a difference in condition factor between large and small fish was not evident at the end of the experiment (Table 3). This result persisted in spite of gains in biomass by both groups (Figure 1B), indicating that biomass gains were not enough to compensate for growth in length (Figure 1A). At the end of the experiment, fish held in 9°C water had the lowest condition factor and the highest percentage decrease in condition factor relative to fish held in 6°C and 3°C water (Figure 1C), but fish held in 6°C and 3°C water had similar condition factors (Table 3).

Because of a significant interaction between fish size-class and water temperature ($P = 0.032$) in our ANCOVA of residualized fat weight index data, separate tests for each size-class and each water temperature were conducted. These tests indicated that small fish were in poorer condition than large fish in the 3°C water but in better condition than large fish in 9°C water (each ANCOVA and each Tukey's test, $P < 0.05$). Additional tests indicated that small fish were in best condition in 6°C water, but were in better condition at 9°C than at 3°C ($P < 0.05$). In contrast, large fish were in

TABLE 2.—Mean length, biomass (fresh wet weight), condition factor (Fulton’s *K*), lipid weight, and percent lipids (based on fresh wet weight) of three size-classes of juvenile steelhead at the start and end of a 111-d experiment with three thermal treatments. Standard deviations (parentheses) are for single samples from the beginning of the experiment or the means of two replicates from the end of the experiment. The term “all remaining” refers to all experimental fish that were alive at the end of the experiment ($N = 30\text{--}50$ within each of two replicates); the acronym RS refers to random samples of fish from each of two replicate tanks ($N = 16\text{--}23$ per replicate).

Thermal treatment	Fish size-class	Data set	Fork length (mm)	Biomass (wet weight [g])	Condition factor	Lipid weight (g)	Percent lipids
Start of experiment							
Pretreatment	Small	All ($N = 30$)	64 (3.3)	2.4 (0.32)	0.90 (0.052)	0.07 (0.021)	3.0 (0.80)
	Medium	All ($N = 30$)	70 (2.3)	3.3 (0.33)	0.93 (0.041)	0.13 (0.034)	4.1 (0.97)
	Large	All ($N = 30$)	76 (1.9)	4.2 (0.30)	0.95 (0.042)	0.24 (0.042)	5.7 (0.80)
End of experiment							
3°C	Small	All remaining	68 (0.2)	2.9 (0.07)	0.92 (0.016)	0.12 (0.012)	4.1 (0.34)
		RS	67 (0.1)	2.8 (0.07)	0.92 (0.019)		
	Medium	All remaining	74 (0.6)	3.9 (0.14)	0.95 (0.013)	0.18 (0.002)	4.4 (0.02)
		RS	74 (0.3)	4.0 (0.09)	0.97 (0.010)		
	Large	All remaining	79 (0.1)	4.7 (0.04)	0.94 (0.003)	0.23 (0.005)	4.8 (0.05)
		RS	79 (0.0)	4.8 (0.05)	0.96 (0.010)		
6°C	Small	All remaining	73 (0.2)	3.6 (0.02)	0.94 (0.001)	0.19 (0.002)	5.0 (0.01)
		RS	73 (0.1)	3.7 (0.01)	0.95 (0.004)		
	Medium	All remaining	78 (0.8)	4.3 (0.11)	0.92 (0.004)	0.18 (0.003)	4.1 (0.22)
		RS	78 (1.6)	4.3 (0.27)	0.91 (0.002)		
	Large	All remaining	84 (0.5)	5.5 (0.22)	0.92 (0.019)	0.26 (0.036)	4.7 (0.33)
		RS	84 (1.0)	5.6 (0.38)	0.93 (0.028)		
9°C	Small	All remaining	76 (<0.1)	4.0 (0.01)	0.89 (0.004)	0.18 (0.007)	4.5 (0.23)
		RS	76 (0.5)	3.9 (0.06)	0.89 (<0.001)		
	Medium	All remaining	82 (1.3)	5.0 (0.02)	0.90 (0.022)	0.23 (0.018)	4.7 (0.27)
		RS	82 (1.5)	4.9 (0.08)	0.90 (0.033)		
	Large	All remaining	87 (1.1)	5.9 (0.24)	0.88 (0.001)	0.24 (0.014)	4.0 (0.20)
		RS	88 (1.8)	6.0 (0.31)	0.88 (0.012)		

TABLE 3.—Results of Tukey’s multiple comparison tests ($P < 0.05$) using mean values of length, biomass (fresh wet weight), condition factor (Fulton’s *K*), lipid weight, and percent lipids (fresh wet weight) and the percentage increase (PI) of these values from the start to the end of a 111-d experiment. Lowercase letters indicate significant main factors within a two-way ANOVA test ($P < 0.05$) that was followed by Tukey’s test. Within groups, z denotes the highest value and x the lowest, and numbers indicate the relative ranks of the variables; a common letter indicates no significant difference regardless of the number (e.g., z1 and z2 are not significantly different). Each size group had 30 observations at the beginning of the experiment. At the end of the experiment, the mean values obtained from a random sample of each of two replicates ($N = 16\text{--}23$) were used in statistical tests.

Size of fish	Thermal treatment	Fork length		Biomass (wet weight [g])		Condition factor		Weight of lipids		Percent lipids	
		Mean	PI	Mean	PI	Mean	PI	Mean	PI	Mean	PI
		Start of experiment									
Small		x		x		y		x		x	
Medium		y		y		z2		y		y	
Large		z		z		z1		z		z	
End of experiment											
Small	All	x	z1	x	z		z1	x			
Medium	All	y	z2, y1	y	y1	NS ^a	z2, y1	y	SI ^b	SI	SI
Large	All	z	y2	z	y2		y2	z			
All	3°C	x	x	y	x	z1	z1	y			
	6°C	y	y	z2	y	z2	z2	z2	SI ^c	SI	SI ^c
	9°C	z	z	z1	z	y	y	z1			

^a No significant difference detected for this main effect.
^b SI = significant interaction between size-class of fish and thermal treatment.
^c Percentage change significantly higher for small fish than for large fish.

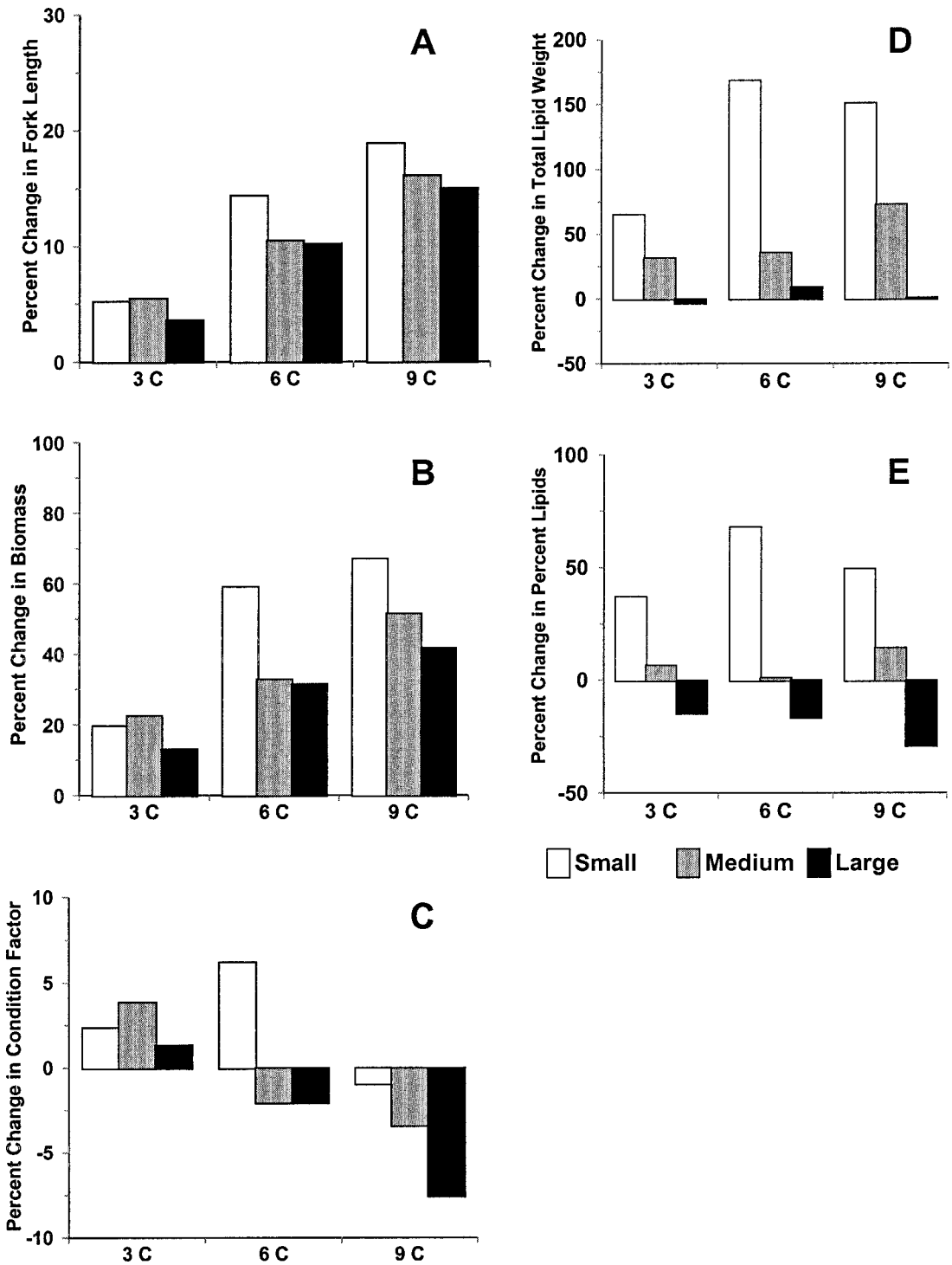


FIGURE 1.—Percentage change in (A) fork length, (B) biomass, (C) condition factor, (D) total lipid weight, and (E) percent lipids for three sizes of juvenile steelhead held at three water temperatures (3, 6, or 9°C) over the 111-d experiment.

best condition at 3°C and poorest condition at 9°C ($P < 0.05$). Results from analyses of the condition factor and residualized fat weight index were largely corroborative, but the residualized fat weight index allowed greater separation of treatment effects.

Mean weight of total lipids and mean percent lipids varied directly with size-class of fish at the beginning of the experiment, but by the end of the experiment this pattern was evident only for mean weight of total lipids (Table 3). Within all size-groups of fish, mean weight of total lipids was consistently lower in the 3°C treatment than in the 6°C or 9°C treatments (Tukey's test, $P < 0.05$), but no difference was found between the 6°C and 9°C treatments (Tukey's test, $P > 0.05$). Interactions between the two main effects, fish size-class and thermal treatment, were significant for all other comparisons of mean weight of total lipids and mean percent lipids (ANOVA, $P < 0.05$). The size-group with the lowest values of percent lipids varied directly with water temperature: small fish in 3°C water, medium fish in 6°C water, and large fish in 9°C water (Table 2). Percentage changes in mean weight of total lipids (Figure 1D) and in mean percent lipids (Figure 1E) were decidedly different between small and large fish (Tukey's test, $P < 0.05$), with high positive changes ($>35\%$) in small fish for all thermal treatments and low positive ($<10\%$) to high negative changes in large fish. As with percentage change in condition factor (Figure 1C), the highest percentage decrease in percent lipids (-29%) was in large fish held at the highest temperature (9°C).

When we combined all sizes of juvenile steelhead and regressed percent lipids against fork length, a distinct difference in pattern emerged between fish held in 3°C water and those held in 9°C water. In addition to a difference in fork length of fish held at these two water temperatures (t -test, $P < 0.001$), the slope of the relationship between percent lipids and fork length was positive for fish held in 3°C water (Figure 2A) but negative for fish held in 9°C water (Figure 2B). Percent lipids were lowest for the small fish held in 3°C water but were lowest for the large fish in 9°C water.

For all size-classes and treatments combined, dry weight was highly related to fresh wet weight, but the relationship was significantly different between the start and end of the experiment (ANCOVA, $P < 0.001$). Fresh wet weight explained 98% of the variation in dry weight at the beginning of the experiment (linear regression slope = 0.252, y -intercept = -0.131 , $P < 0.001$) and 96% at the

end of the experiment (linear regression slope = 0.272, y -intercept = -0.044 , $P < 0.001$). At least part of this difference may be explained by a higher percentage increase in water weight for large fish relative to small fish by the end of the experiment (Tukey's test, $P < 0.05$), but mean values for water weight and the percentage change in water weight were not significantly different among fish held at the three temperatures (Tukey's test, $P > 0.05$). The results of dry weight analyses were very similar to those of analyses involving fresh wet weight (see Table 3), except that the percentage increase in dry weight was distinctly different among the three size-groups, with small fish having the largest increase and large fish having the smallest increase (Tukey's test, $P < 0.05$).

Although an unexplained loss of fish from some experimental tanks prevented us from calculating survival estimates, observed mortality was low. Three or fewer fish were found dead in 15 of the 18 tanks during the experiment. The three tanks with higher observed mortality included two tanks of small fish held at 6°C water temperature and one tank of small fish held at 9°C. Although these higher losses were exclusively in tanks with small fish, the number found dead was related neither to the size-class of fish (one-way ANOVA, $P = 0.449$) nor to thermal treatment ($P = 0.074$). As with mortalities, the number of fish that were unaccountably lost was related neither to size-class of fish ($P = 0.791$) nor to thermal treatment ($P = 0.449$).

Bioenergetics Simulations

Based on the starting and ending weights observed in our laboratory experiments and the temperatures we tested, we found that P -values varied somewhat by temperature but varied little across size-classes within a temperature treatment (Table 1). Average P -values were 0.204 at 3°C, 0.162 at 6°C, and 0.139 at 9°C. The overall average P -value was 0.168 ($N = 9$).

When the model was calibrated to the P -values from the laboratory experiments, the results suggested a dynamic relationship among temperature, fish size, and growth (Figure 3A). Percentage growth varied from 10% (5-g fish at 3°C) to 76% (2-g fish at 9°C). At 3°C, growth varied from 10% for 5-g fish to 23% for 2-g fish. At 9°C, growth varied from 36% for 5-g fish to 76% for 2-g fish. Growth of small fish responded more to changes in temperature than did growth of large fish.

For all sizes and temperatures, the variation in growth predicted with a constant P -value of 0.170

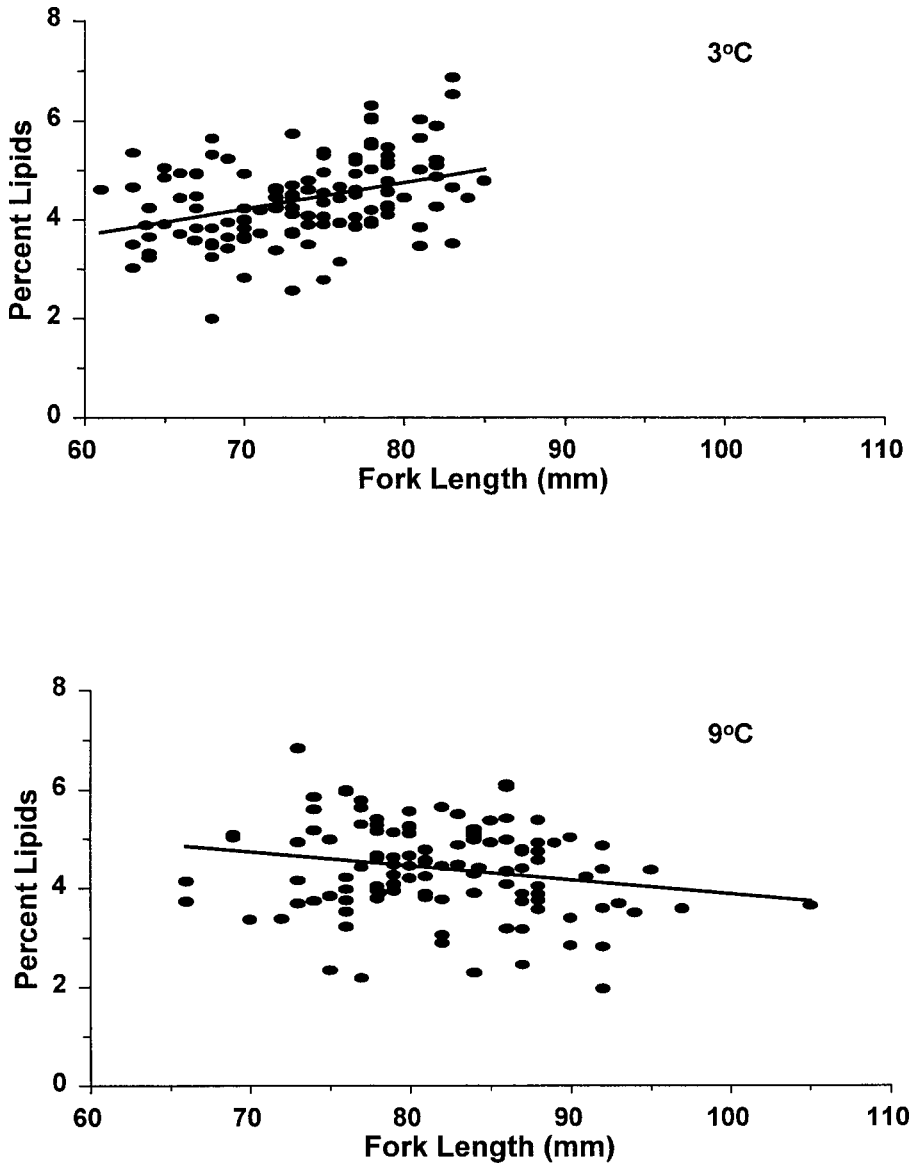


FIGURE 2.—Relationship between percent lipid content (based on wet weight) and fork length for juvenile steelhead (three size-classes combined) held at water temperatures of 3°C ($N = 122$; upper panel) and 9°C ($N = 115$; lower panel) over a 111-d period. Lines are linear regressions for each treatment (3°C: slope = 0.053, y -intercept = 0.522, $r^2 = 0.135$, $P < 0.001$; 9°C: slope = -0.029 , y -intercept = 6.747, $r^2 = 0.046$, $P = 0.021$).

(Figure 3B) was larger than the variation observed in our laboratory experiments (Figure 3A). With the 0.17 P -value at 3°C, fish between 3 and 5 g were predicted to lose weight (1–5%) by the end of the simulation period, whereas 2-g fish were predicted to gain 2% mass. At 9°C, 2-g fish were predicted to grow to 5.1 g (154%), whereas 5-g fish were predicted to attain 9.6 g (93%). Import-

tantly, the general relationship of faster growth of small fish compared to large fish across the simulated temperatures was retained in the simulation with a constant P -value, suggesting that our laboratory results were not an artifact of the adjustments made in our feeding regime.

At the coldest temperature tested (3°C), the response of both small and large simulated fish to

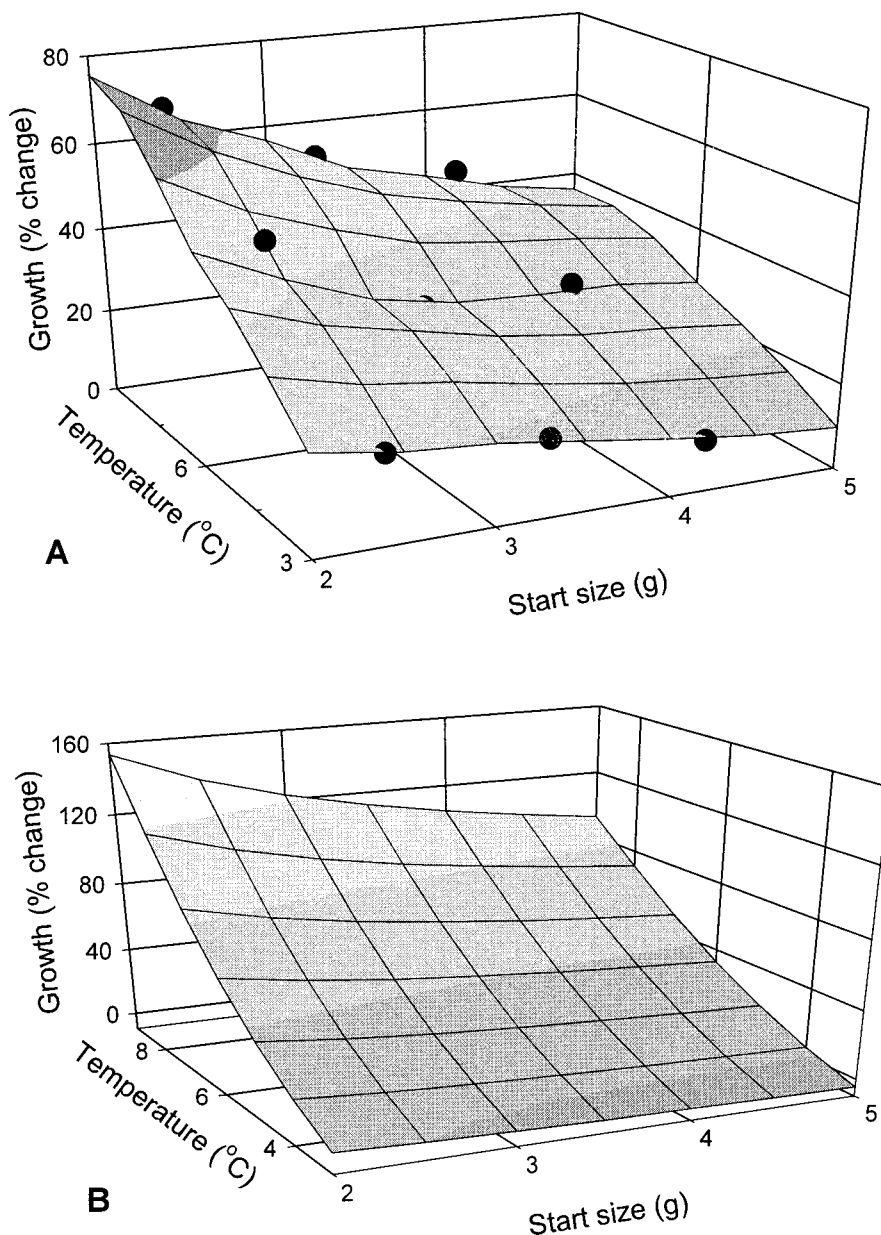


FIGURE 3.—Growth of juvenile steelhead predicted by bioenergetics simulations based on (A) P -values fit to laboratory experiments (black circles indicate laboratory results) and (B) P -values held constant at 0.170.

changes in food availability were similar, and the maximum difference in size at the end of the winter was predicted to be only about 3.5 g when the P -value was 0.30 (Figure 4). At the higher temperature, the simulated difference in sizes of small and large fish was only 1.2 g when prey availability was low (P -value = 0.05); however, the difference was 8.5 g when prey availability was high (P -value = 0.30; Figure 4).

Discussion

Our laboratory results suggest that cold winters could decrease the energy stores of small young-of-year fish by the end of winter and that exceptionally mild winters could deplete the energy stores of large young-of-year fish. For all three sizes of age-0 steelhead that we tested in the laboratory, those held in the coldest water (3°C) had

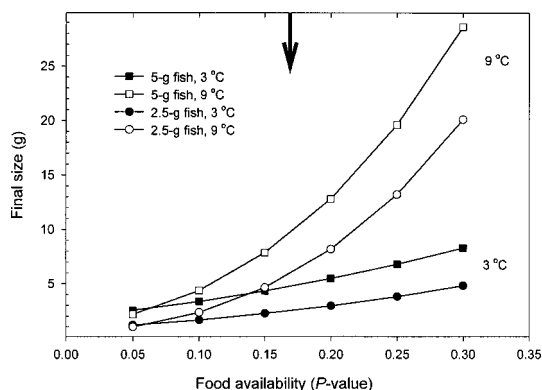


FIGURE 4.—Size predicted at the end of a winter period for small (2.5-g initial size) and large (5-g initial size) juvenile steelhead as a function of food availability (P -value) and temperature. Size was predicted with a bioenergetics model simulating fish growth over a 111-d period and was configured to match our laboratory experiments (see text). The vertical arrow is the average P -value for laboratory experiments.

lower total lipid weights than those held in 6°C or 9°C water. Condition factor and percent lipids did not differ among size-groups, but small fish consistently had less total lipid weight than large fish of the same cohort at all water temperatures. Low lipid content implies low energy reserves (Reshnikov et al. 1970; Sutton et al. 2000), which for many fish species decreases the ability to survive severe or prolonged winter conditions (Cunjak and Power 1987; Johnson and Evans 1990; Sogard and Olla 2000). With limited food available to fish held in cold water (3°C), total lipid weight and percent lipids increased for small fish but decreased for large fish. However, these large fish still retained higher total lipid weight than small fish at the end of the experiment. This pattern corresponds with that noted by Berg and Bremset (1998) in Atlantic salmon *Salmo salar* and brown trout exposed to winter conditions: larger fish had a higher rate of decline in energy stores than smaller fish, although smaller fish had less to lose because they had lower energy stores initially.

The fish sizes and water temperatures that we tested were broad enough to encompass a graded response to a range in water temperatures that would be expected to occur during winter within the distributional range of North American steelhead. Recovery efforts for steelhead in basins where rearing areas are characterized by wide climatic heterogeneity might best be located across a range of streams to account for variable winter conditions and rates of survival. If climate regime

shifts or global warming (Beamish et al. 1999) increase the frequency of mild winters, such changes would likely influence overwinter conditions for steelhead across much of their range, which would likely affect long-term recovery plans for a life history form that has already become widely depleted (Nehlsen et al. 1991; Busby et al. 1996).

Our results have some implications for understanding the range of life history characteristics in steelhead in regions where temperatures and other conditions vary greatly. Our study shows that lipid levels in steelhead parr can vary with the severity of winter and the size of fish in fall. Thorpe et al. (1998) developed a predictive model of life history variation for Atlantic salmon, and concluded that individual Atlantic salmon have two developmental switches, one occurring in November for reproduction and one in April for emigration. These developmental conversions are dependent on the rate of change in lipid levels and growth during an "assessment period" in fall or spring. Because depletion of lipid reserves can vary greatly in cold versus warm winters, it would be highly advantageous for salmonids to be able to respond to early climatic cues that may foretell the potential severity of an approaching winter. If the cues are not perceived, or if the cues are not sufficient, then inappropriate developmental conversions could lead to increased mortality and decreased reproductive success.

Large size at the start of winter for young-of-year fish may not always be the best strategy to achieve high overwinter survival for species that occur across a wide range of latitudes and elevations. Subpopulations of such species will encounter considerable variability in winter conditions, both spatially and temporally, making it unlikely that large size will always result in the highest overwinter survival (Schultz and Conover 1999). For walleye pollock *Theragra chalcogramma*, Sogard and Olla (2000) suggested that overwintering capabilities could be compromised when conditions of warmer-than-normal winters and depleted prey abundance prevail. Similarly, young-of-year steelhead that grow to a large size before winter may not have a survival advantage if food is limited during relatively warm winters, creating high metabolic demands and depletion of energy stores.

The bioenergetics simulations provided a detailed description of the growth of various sizes of young-of-year juvenile steelhead held at 3–9°C. Fish in our laboratory tanks were feeding at slight-

ly different percentages of maximum consumption, based on the *P*-value fits we observed, with somewhat higher *P*-values at the low temperature compared to the high temperature. Because food was completely consumed during each feeding period, the observed *P*-values were likely limited by the fact that we provided a constant amount of food per tank during the experiment. In field situations, the amount of food during both summer and winter months is thought to limit steelhead and trout growth in a variety of natural systems (Beauchamp 1990; Railsback and Rose 1999). Fish were fed a fairly low ration throughout the experiment (<1.5%), and the ration declined during the experimental period due to the growth of fish. Based on our preliminary growth estimates, we did not expect such good growth during the experiment, and therefore we did not plan to vary the amount of food provided to each tank. Although ration declined, the decline was fairly minor (0.1–0.4%) and consistent across treatments (Table 1). Although small fish were fed a slightly higher ration (but a lower total weight of food) than large fish during the course of the experiment, the absolute difference in percent ration was, at most, 0.2% at the start of the experiment and 0.1% at the end of the experiment. The bioenergetics simulations, in which all fish were feeding at the same proportion of maximum consumption, suggested the same growth response. For these reasons, we do not believe that our feeding regime affected our overall conclusions.

The relatively good growth of juvenile steelhead at the temperatures we tested was somewhat surprising but is generally consistent with the field observations and modeling of Railsback and Rose (1999). The growth of rainbow trout during fall through spring at two sites on the North Fork and Middle Fork of the Tule River in northern California ranged from 0.37% to 0.78% body weight per day (Railsback and Rose 1999). Their data were collected over a longer seasonal period (273 d) than our winter experiments (111 d), so some of the growth that they observed likely occurred during warm fall and spring periods, rather than solely during winter. Our results, however, suggest that growth during cold winter months is possible, assuming food levels are sufficient. Railsback and Rose (1999) concluded that growth rates were higher and more temperature-dependent during fall through spring than during summer. They suggested that future studies and evaluations should consider nonsummer periods. Our results also sug-

gest that winter temperatures can be very important to fish growth.

Railsback and Rose (1999) did an extensive analysis of temperature versus food consumption based largely on *P*-values estimated from observed starting and ending weights in field populations. Their fall-through-spring *P*-values ranged from about 0.30 to 0.45, whereas the *P*-values that we fit to our laboratory experiments ranged from about 0.14 to 0.21. The primary reason for this difference was probably the energy density of prey used in the two models: whereas Railsback and Rose (1999) used an average of 2,500 J/g, we used 5,306 J/g.

The results of our experiment suggest that juvenile steelhead growth and condition are susceptible to temperature during winter months, with differential responses for large versus small fishes. We did not examine ration during our experiment, which may also vary considerably at different sites and between years in natural systems (Filbert and Hawkins 1995; Railsback and Rose 1999). Filbert and Hawkins (1995), for example, found that winter food availability (overall drift density) for rainbow trout varied more than sevenfold between two sites in Utah. Beauchamp (1990) detected a two-fold variation in the ration size of rainbow trout in Lake Washington between 1984 and 1985. Future studies should consider the interactions between food availability, size in the fall, and temperature during the winter for juvenile steelhead. Such studies could be conducted in a laboratory situation, but analyses of field data collected in several streams over a series of years with variable temperatures would provide the best understanding of this complex interaction.

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