

Interacting effects of water temperature and swimming activity on body composition and mortality of fasted juvenile rainbow trout

Darin G. Simpkins, Wayne A. Hubert, Carlos Martinez del Rio, and Daniel C. Rule

Abstract: We assessed changes in proximate body composition, wet mass, and the occurrence of mortality among sedentary and actively swimming (15 cm/s) juvenile rainbow trout (*Oncorhynchus mykiss*) (120–142 mm total length) that were held at 4.0, 7.5, or 15.0 °C and fasted for 140 days. Warmer water temperatures and swimming activity accentuated declines in lipid mass, but they did not similarly affect lean mass and wet mass. Swimming fish conserved lean mass independent of water temperature. Because lean mass exceeded lipid mass, wet mass was not affected substantially by decreases in lipid mass. Consequently, wet mass did not accurately reflect the effects that water temperature and swimming activity had on mortality of fasted rainbow trout. Rather, lipid mass was more accurate in predicting death from starvation. Juvenile rainbow trout survived long periods without food, and fish that died of starvation appeared to have similar body composition. It appears that the ability of fish to endure periods without food depends on the degree to which lipid mass and lean mass can be utilized as energy sources.

Résumé : Nous avons mesuré les changements dans la composition générale du corps, la masse humide et la fréquence de la mortalité chez de jeunes truites arc-en-ciel (*Oncorhynchus mykiss*) (120–142 mm de longueur totale) sédentaires et actives (nage de 15 cm/s), gardées à 4,0, 7,5 et 15,0 °C et soumises à un jeûne de 140 jour. La température accrue de l'eau et l'activité de nage accentuent le déclin de la masse lipidique, mais n'ont pas le même effet sur la masse maigre et la masse humide. Les poissons qui nagent conservent leur masse maigre, quelle que soit la température de l'eau. Comme la masse maigre est plus grande que la masse lipidique, la masse humide n'est pas affectée de façon significative par le déclin de la masse lipidique. En conséquence, la masse humide ne reflète pas de façon précise les effets de la température de l'eau et de l'activité de nage sur la mortalité de truites arc-en-ciel soumises au jeûne. C'est plutôt la masse lipidique qui prédit le plus exactement la mort par carence alimentaire. Les jeunes truites arc-en-ciel survivent longtemps sans nourriture et les poissons qui meurent de manque de nourriture paraissent tous posséder la même composition corporelle. Il semble que la capacité des poissons à survivre à des périodes sans alimentation dépende de la possibilité d'utilisation de la masse lipidique et de la masse maigre comme sources d'énergie.

[Traduit par la Rédaction]

Introduction

Water temperature affects physiological processes in many ectothermic animals including trout (see Hazel 1993; Houlihan et al. 1993). Studies of the effects of water temperature on physiological processes in trout have focused on respiratory responses and changes in growth associated with variation in water temperature (Fry 1971; Stewart et al. 1983; Selong et al. 2001). Respiratory data are used to estimate metabolic rates and can be used to identify types of energy reserves that are being catabolized (Adams and Breck

1990; Cech 1990; Lauff and Wood 1996a). Metabolic experiments suggest that rates of decline in body composition and wet mass in fasted trout (*Oncorhynchus* spp., *Salmo* spp., and *Salvelinus* spp.) increase with increasing water temperature (Stewart et al. 1983; Railsback and Rose 1999). So, the ability of trout to endure periods without food should decrease with increasing water temperature. Nevertheless, little information is available as to how differences in water temperature affect body composition and survival of fasted trout.

Laboratory studies examining body composition and mor-

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D.G. Simpkins^{1,2} and W.A. Hubert. U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit,³ University of Wyoming, Laramie, WY 82071-3166, U.S.A.

C. Martinez del Rio. Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166, U.S.A.

D.C. Rule. Department of Animal Science, University of Wyoming, Laramie, WY 82071-3684, U.S.A.

¹Corresponding author (e-mail: simpkins@cnr.colostate.edu).

²Present address: Colorado Cooperative Fish and Wildlife Research Unit, 201 Wagar Building, Colorado State University, Fort Collins, CO 80523-1484, U.S.A.

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tality of fasting trout have been conducted in static water, thereby minimizing energetic demands on fish (Elliot 1976; Toney and Coble 1980). Elevated metabolic costs associated with residence in water currents may increase the rate at which energy reserves are used and decrease the ability for trout to endure periods without food (Stewart 1980; Lauff and Wood 1996b; Hurst and Conover 2001). However, the metabolic costs associated with holding a position against currents have not been examined in detail (but see Stewart 1980; Facey and Grossman 1990). Little is known about the effects of swimming activity on body composition and survival of fasted trout.

The metabolic costs associated with variation in both water temperature and swimming activity have received attention (see Jobling 1993; Elliot 1994; Brett 1995), but few studies have assessed changes in body composition of fasted trout. Our purpose was to examine the effects of water temperature and swimming activity on body composition during fasting by juvenile rainbow trout (*Oncorhynchus mykiss*). Our objectives were to (i) determine the effects of water temperature on rates of change in measures of body composition, (ii) assess differences in body composition between actively swimming and sedentary fish, and (iii) define possible interactive effects of water temperature and swimming activity on body composition and fasting endurance of juvenile rainbow trout. Based on metabolic experiments (Stewart et al. 1983; Lauff and Wood 1996a, 1996b; Railsback and Rose 1999), we hypothesized that warmer water temperatures and swimming activity would cause measures of body composition and wet mass of juvenile rainbow trout to change over time at faster rates than in fish held in cooler water temperatures and that were sedentary. Furthermore, we hypothesized that the increased use of energy reserves associated with increased water temperatures and swimming activity would result in lower ability of trout to endure periods without food.

Methods

Juvenile rainbow trout (120–142 mm total length, 19–30 g total mass) were obtained from the Wyoming Game and Fish Department's Como Bluffs Fish Hatchery and transported to the University of Wyoming's Red Buttes Environmental Research Laboratory near Laramie. One hundred fish were marked with individually coded soft visual-implant tags (Northwest Technologies, Inc., Shaw Island, Wash.) and haphazardly placed in each of five 240-L circular tanks (height 0.85 m, radius 0.30 m) that received a continuous flow (10 L/min) of aerated well water that remained at 7.5 °C. An automated timer and fluorescent lights were used to produce a 12 h light : 12 h dark photoperiod. Fish were allowed to acclimate for 21 days during which they were fed an excess ration of pelleted trout food (Nelson and Son's, Inc., Murray, Utah). Twelve fish from each tank were randomly selected, sedated with MS 222 (3-aminobenzoic acid ethyl ester methanesulfonate), individually identified, weighed to the nearest gram, measured to the nearest millimetre total length, euthanized with a quick blow to the head, and frozen. We deprived the remaining fish of food and used three water temperatures and two levels of swimming activity as experimental treatments to affect body composition.

Over 48 h, water temperature was decreased to 4 °C for two treatments and increased to 15 °C for another treatment. Water temperature for the other two treatments remained at 7.5 °C. Fish in the 4 and 7.5 °C treatments were held either in a current (measurements with a flowmeter averaged 15 cm/s) produced by circulating water pumps (model 2U; March Manufacturing, Inc., Glenview, Ill.) or in standing water. Fish in the 15 °C treatment were held only in standing water. Fish in a 15 °C treatment with flowing water were lost owing to a mechanical failure.

Six fish were randomly selected from each tank, sedated, individually identified, weighed, measured, euthanized, and frozen to assess proximate body composition every 14 days after the acclimation period. Analysis of proximate body composition was conducted similar to Simpkins et al. (2003) with the exception of fatty acid content, which followed the protocol of Bolte et al. (2002). Total lipid was expressed as a proportion of dry mass. Lean mass was determined as the difference between dry mass and lipid mass.

We used analysis of variance to test for differences in means of initial lengths, masses, and proximate body components among treatments. Data collected from fish that were sampled prior to initiation of experimental treatments were used to account for allometric variation in measurements from fasted fish following the procedure in Simpkins et al. (2003). We assessed changes over time in residuals of proximate body composition and wet mass using a general linear model (GLM) (Neter et al. 1996) as described in Simpkins et al. (2003). We conducted statistical analyses on residuals, but we report changes in response variables over time for fish of average length (residual + aTL^b where a is the intercept, TL is total length, and b is the slope) to facilitate interpretation. Statistical computations were performed using JMP 4.0.4 (SAS Institute Inc. 2001). Significance was determined at $P < 0.05$ and data are presented throughout as means \pm SE.

Results

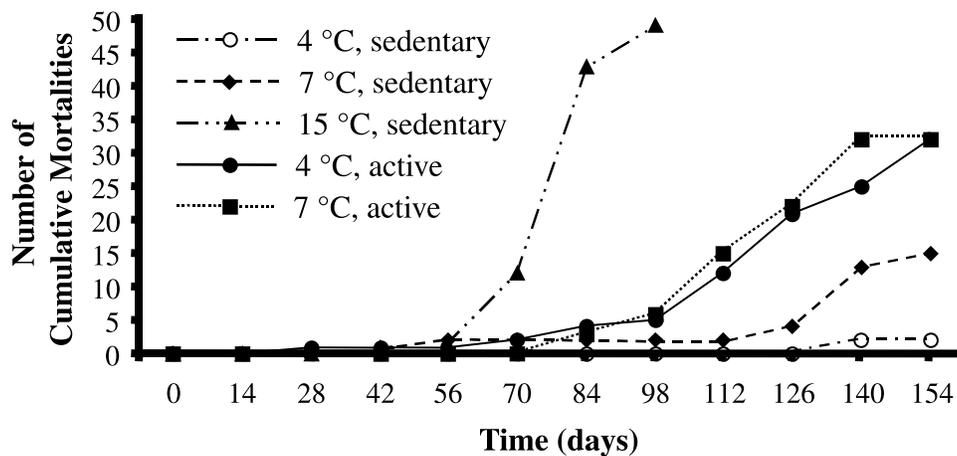
Fish did not differ significantly in mean total length (132 ± 0.7 mm), mean wet mass (22 ± 0.4 g), or measures of proximate body composition among treatments at the onset of the experiment. Lipid mass, water mass, lean mass, and wet mass increased allometrically with body length (see Table 1). Consequently, residuals of these measures were calculated for fasted fish, and changes over time in these measures are presented for fish of average initial length. Percent lipid and percent water were not significantly related to total length, so statistical computations were performed using observed values. All sedentary fish in the 4 °C treatment that were sampled over 140 days were included in the analyses. However, analyses were performed for active fish in the 4 °C treatment up to 112 days, sedentary fish in the 7.5 °C treatment up to 126 days, active fish in the 7.5 °C treatment up to 98 days, and sedentary fish in the 15 °C treatment up to 70 days because the number of cumulative mortalities exceeded 30% of the remaining population thereafter (Fig. 1).

Trends in lipid measures over time did not differ significantly from a linear model in any treatment, but rates of change differed among treatments in both lipid mass ($F_{[1,289]} = 6.44$, $P < 0.05$) and percent lipid ($F_{[1,289]} = 5.11$,

Table 1. Relationships between total length (TL) and measures of body composition of juvenile rainbow trout (*Oncorhynchus mykiss*) prior to treatment initiation ($Y = aTL^b$, range = 120–142 mm total length) used to account for allometric variation in measures collected from fasted fish.

Response variable	Intercept			Slope			r^2
	a	SE	P	b	SE	P	
Lipid mass (g)	1.13×10^{-7}	1.17×10^{-8}	<0.001	3.35	0.27	<0.001	0.76
Lipid (%)	114.38	25.89	<0.001	-0.33	0.23	0.28	0.02
Water mass (g)	9.70×10^{-6}	5.27×10^{-7}	<0.001	2.94	0.15	<0.001	0.96
Water (%)	65.86	11.81	<0.001	0.03	0.04	<0.001	0.86
Lean mass (g)	3.83×10^{-8}	2.95×10^{-9}	<0.001	3.75	0.23	<0.001	0.86
Wet mass (g)	1.41×10^{-6}	8.07×10^{-7}	<0.001	3.37	0.17	<0.001	0.96

Fig. 1. Cumulative mortalities of sedentary (no current) and actively swimming (15 cm/s current velocity) juvenile rainbow trout (*Oncorhynchus mykiss*) (132 mm mean total length) that were fasting and residing in different water temperatures.



$P < 0.05$) (Fig. 2, Table 2). Mean lipid mass decreased more rapidly over time for fish in warmer water than for fish in cooler water among sedentary ($F_{[1,177]} = 46.45$, $P < 0.001$) and active treatments ($F_{[1,106]} = 7.07$, $P < 0.01$). Similarly, the rate of decline in mean percent lipid differed significantly among sedentary ($F_{[1,177]} = 25.40$, $P < 0.001$) and active treatments ($F_{[1,106]} = 7.46$, $P < 0.01$) (Fig. 2). Mean lipid mass decreased at rates that differed significantly between sedentary and active fish in 4 °C water ($F_{[1,129]} = 8.29$, $P < 0.005$) and sedentary and active fish in 7.5 °C water ($F_{[1,113]} = 18.18$, $P < 0.001$) (Table 2). Declines in lipid mass over time were greater for active fish than sedentary fish in both treatments. The rate of change in percent lipid did not differ significantly between sedentary and active fish in 4 °C water ($F_{[1,129]} = 1.84$, $P = 0.18$) (Fig. 2a) but differed significantly between sedentary and active fish in 7.5 °C water ($F_{[1,113]} = 12.46$, $P < 0.001$) (Fig. 2c). Active fish in 7.5 °C water exhibited greater losses in percent lipid per day than sedentary fish (Fig. 2c).

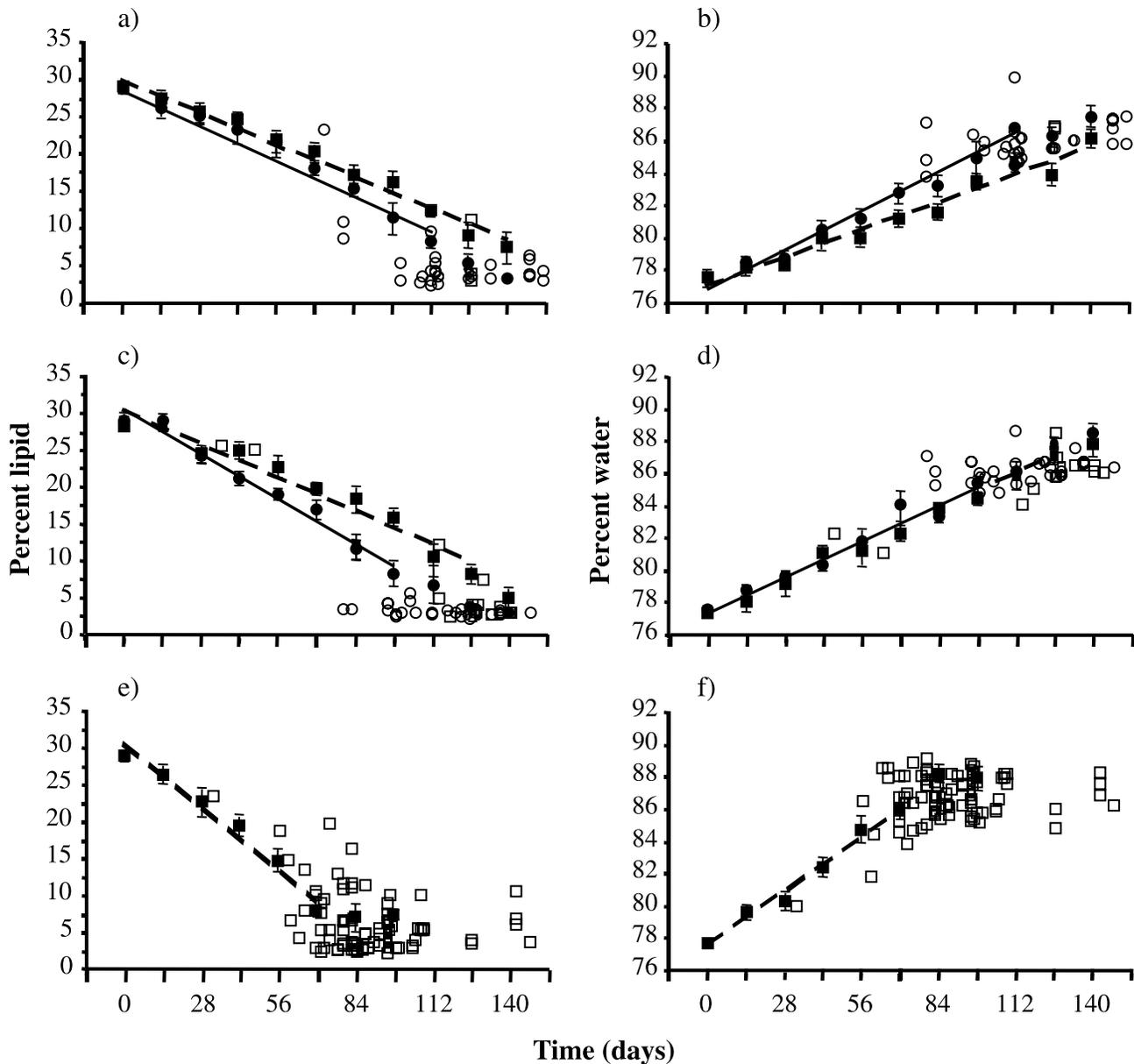
Changes in measures of water content over time did not differ significantly from a linear pattern for any treatment; however, slopes differed significantly among treatments for both water mass ($F_{[1,289]} = 6.31$, $P < 0.05$) and percent water ($F_{[1,289]} = 6.78$, $P < 0.01$) (Fig. 2, Table 2). The rate of change in mean water mass differed significantly among water temperatures for sedentary fish ($F_{[1,177]} = 10.03$, $P < 0.005$) but not for active fish ($F_{[1,106]} = 1.02$, $P = 0.31$). Mean percent water increased with time at significantly

faster rates for sedentary fish in warmer water than sedentary fish in cooler water ($F_{[1,177]} = 58.66$, $P < 0.001$), but rates were not different among water temperatures for active fish ($F_{[1,106]} = 1.02$, $P = 0.31$). The rate of change in water mass differed between sedentary and active fish in 4 °C water ($F_{[1,129]} = 4.97$, $P < 0.05$) (Table 2). Water mass declined more rapidly in active fish than in sedentary fish at 4 °C, but rates were not different at 7.5 °C ($F_{[1,113]} = 0.07$, $P = 0.79$). The rate of increase in percent water was enhanced by swimming activity for fish in 4 °C water ($F_{[1,129]} = 12.55$; $P < 0.001$) (Fig. 2b) but not for fish in 7.5 °C water ($F_{[1,113]} = 0.15$, $P = 0.70$) (Fig. 2d).

Declines in mean lean mass did not differ significantly from a linear pattern, but rates differed among treatments ($F_{[1,289]} = 8.64$, $P < 0.005$) (Fig. 3, Table 2). The rate of loss in lean mass among sedentary fish increased with warmer water temperatures ($F_{[1,177]} = 21.87$, $P < 0.001$) but did not differ between temperatures for fish that were swimming ($F_{[1,106]} = 0.45$, $P = 0.50$). Fish in 4 °C water lost lean mass at rates that differed between active and sedentary treatments ($F_{[1,129]} = 10.52$, $P < 0.005$), with active fish declining in lean mass more rapidly than sedentary fish (Fig. 3a, Table 2). However, the rate did not differ significantly between sedentary and active treatments at 7.5 °C ($F_{[1,113]} = 0.09$, $P = 0.77$) (Fig. 3c).

Mean wet mass linearly declined over time in all treatments, but rates differed among treatments ($F_{[1,289]} = 9.63$, $P < 0.005$) (Fig. 3, Table 2). Slopes differed among water

Fig. 2. Changes in percent lipid (a, c, e) and percent water (b, d, f) over time among sedentary (no current) (solid squares, broken line) and actively swimming (15 cm/s current velocity) (solid circles, solid line) juvenile rainbow trout (132 mm mean total length) that were fasting and residing in different water temperatures (a and b at 4 °C, c and d at 7.5 °C, and e and f at 15 °C). Sedentary mortalities are represented by open squares and active mortalities by open circles. Percent lipid is expressed as a proportion of dry mass. Bars represent standard errors.



temperatures for sedentary fish ($F_{[1,177]} = 21.57$, $P < 0.001$), with warmer water causing more rapid declines in wet mass. However, rates of decline did not differ significantly among temperatures for fish that were swimming ($F_{[1,106]} = 0.35$, $P = 0.55$). Wet mass declined at rates that were accentuated when fish were swimming at 4 °C ($F_{[1,129]} = 9.54$, $P < 0.005$) (Fig. 3b) but were not significantly affected by swimming activity for fish at 7.5 °C ($F_{[1,113]} = 0.06$, $P = 0.80$) (Fig. 3d).

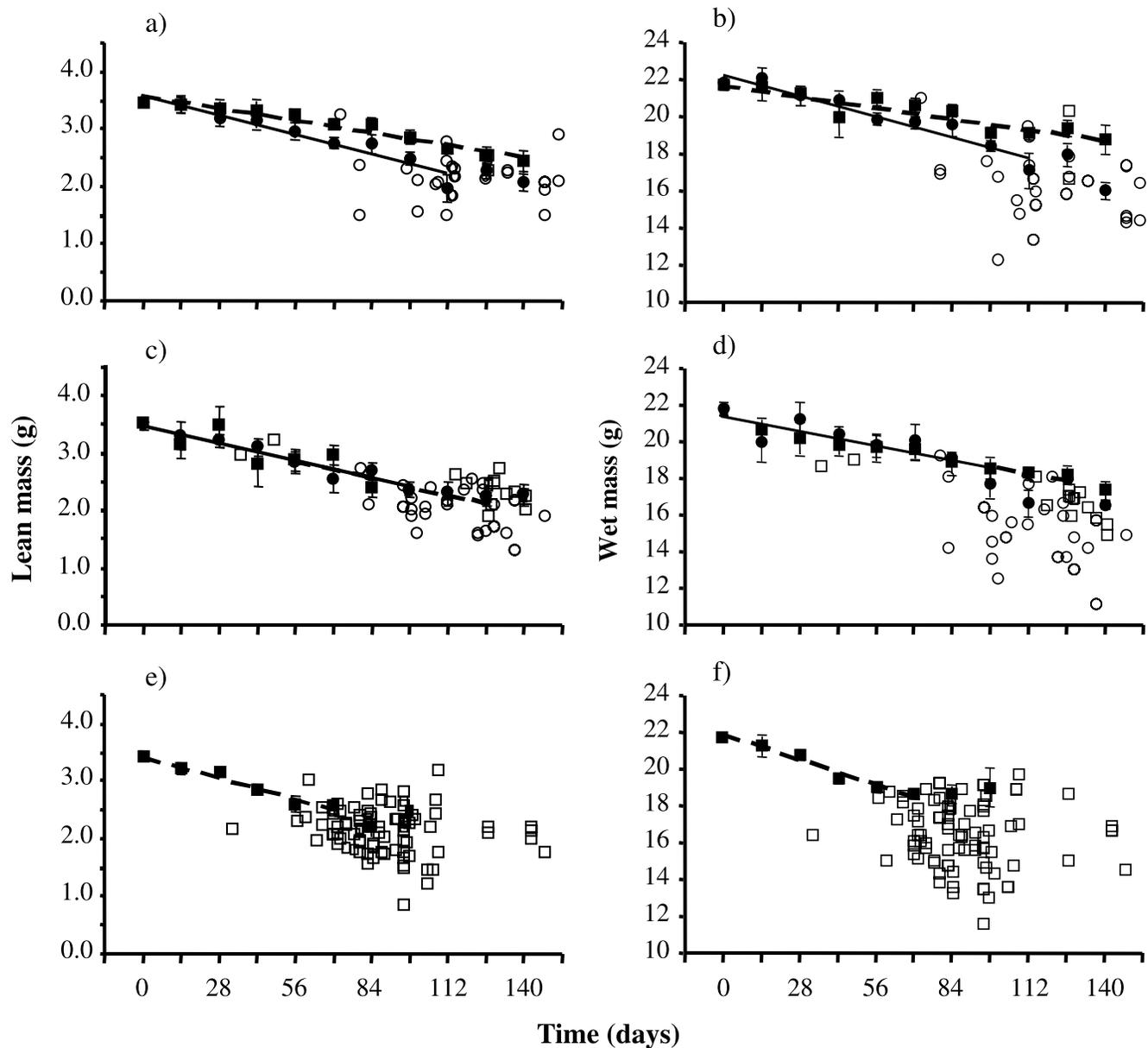
During our experiment, a total of 136 fish died of starvation. Two sedentary fish and 32 active fish died in 4 °C treatments, 15 sedentary fish and 33 active fish died in 7.5 °C

treatments, and 54 sedentary fish died in the 15 °C treatment. Fish that died averaged 0.1 ± 0.01 g of lipid, $6 \pm 2.3\%$ lipid, 14.1 ± 0.49 g of water, $86 \pm 0.3\%$ water, 2.2 ± 0.09 g lean mass, and 17 ± 0.6 g wet mass. Mortality occurred earlier and more frequently in warmer water than in cooler water and more frequently among active fish than among sedentary fish (Fig. 1). Additionally, mortality occurred more frequently among active fish in 4 °C water than among sedentary fish in 7.5 °C water. Fourteen days prior to the cumulative number of mortalities exceeding 30% of the remaining population for each treatment (or after 140 days for sedentary fish held in 4 °C water), fish of average length did

Table 2. Relationships between duration of fasting (days) and measures of body composition of juvenile rainbow trout (120–142 mm total length) at different water temperatures for sedentary and swimming (15 cm/s current velocity) fish.

Response variable	Sedentary										Active										
	Intercept					Slope					Intercept					Slope					
	N	β_0	SE	P	r^2	N	β_1	SE	P	r^2	N	β_0	SE	P	r^2	N	β_1	SE	P	r^2	
4 °C																					
Lipid mass (g)	75	1.4	0.03	<0.001	0.88	58	1.4	0.03	<0.001	0.88	58	1.4	0.03	<0.001	0.88	58	-0.011	0.0005	<0.001	0.88	
Lipid (%)	75	29.8	0.64	<0.001	0.83	58	29.4	0.63	<0.001	0.83	58	29.4	0.63	<0.001	0.82	58	-0.170	0.0105	<0.001	0.82	
Water mass (g)	75	16.9	0.17	<0.001	0.11	58	17.2	0.18	<0.001	0.11	58	17.2	0.18	<0.001	0.31	58	-0.015	0.0031	<0.001	0.31	
Water (%)	75	77.1	0.24	<0.001	0.85	58	77.1	0.30	<0.001	0.85	58	77.1	0.30	<0.001	0.82	58	0.080	0.0050	<0.001	0.82	
Lean mass (g)	75	3.5	0.06	<0.001	0.49	58	3.5	0.06	<0.001	0.49	58	3.5	0.06	<0.001	0.66	58	-0.011	0.0011	<0.001	0.66	
Wet mass (g)	75	21.7	0.23	<0.001	0.42	58	22.1	0.23	<0.001	0.42	58	22.1	0.23	<0.001	0.61	58	-0.037	0.0039	<0.001	0.61	
7.5 °C																					
Lipid mass (g)	65	1.4	0.03	<0.001	0.89	52	1.4	0.03	<0.001	0.89	52	1.4	0.03	<0.001	0.92	52	-0.013	0.0005	<0.001	0.92	
Lipid (%)	65	30.0	0.70	<0.001	0.80	52	30.1	0.57	<0.001	0.80	52	30.1	0.57	<0.001	0.89	52	-0.211	0.0105	<0.001	0.89	
Water mass (g)	65	16.9	0.22	<0.001	0.17	52	16.8	0.26	<0.001	0.17	52	16.8	0.26	<0.001	0.08	52	-0.010	0.0048	<0.001	0.08	
Water (%)	65	77.2	0.26	<0.001	0.88	52	77.5	0.27	<0.001	0.88	52	77.5	0.27	<0.001	0.84	52	0.080	0.0050	<0.001	0.84	
Lean mass (g)	65	3.4	0.07	<0.001	0.61	52	3.4	0.08	<0.001	0.61	52	3.4	0.08	<0.001	0.45	52	-0.010	0.0016	<0.001	0.45	
Wet mass (g)	65	21.7	0.28	<0.001	0.49	52	21.5	0.33	<0.001	0.49	52	21.5	0.33	<0.001	0.37	52	-0.033	0.0061	<0.001	0.37	
15 °C																					
Lipid mass (g)	41	1.4	0.03	<0.001	0.90	41	1.4	0.03	<0.001	0.90	41	1.4	0.03	<0.001	0.90	41	-0.016	0.0009	<0.001	0.90	
Lipid (%)	41	30.2	0.85	<0.001	0.82	41	30.2	0.85	<0.001	0.82	41	30.2	0.85	<0.001	0.82	41	-0.298	0.0220	<0.001	0.82	
Water mass (g)	41	17.0	0.18	<0.001	0.41	41	17.0	0.18	<0.001	0.41	41	17.0	0.18	<0.001	0.41	41	-0.024	0.0047	<0.001	0.41	
Water (%)	41	77.6	0.32	<0.001	0.84	41	77.6	0.32	<0.001	0.84	41	77.6	0.32	<0.001	0.84	41	0.119	0.0082	<0.001	0.84	
Lean mass (g)	41	3.4	0.07	<0.001	0.61	41	3.4	0.07	<0.001	0.61	41	3.4	0.07	<0.001	0.61	41	-0.015	0.0019	<0.001	0.61	
Wet mass (g)	41	21.8	0.21	<0.001	0.72	41	21.8	0.21	<0.001	0.72	41	21.8	0.21	<0.001	0.72	41	-0.054	0.0055	<0.001	0.72	

Fig. 3. Changes in lean mass (*a, c, e*) and wet mass (*b, d, f*) over time among sedentary (no current) (solid squares, broken line) and actively swimming (15 cm/s current velocity) (solid circles, solid line) juvenile rainbow trout (132 mm mean total length) that were fasting and residing in different water temperatures (*a* and *b* at 4 °C, *c* and *d* at 7.5 °C, and *e* and *f* at 15 °C). Sedentary mortalities are represented by open squares and active mortalities by open circles. Bars represent standard errors.



not significantly differ in lipid mass ($F_{[4,22]} = 1.60$, $P = 0.21$), water mass ($F_{[4,22]} = 1.24$, $P = 0.32$), lean mass ($F_{[4,22]} = 2.11$, $P = 0.11$), or wet mass ($F_{[4,22]} = 1.30$, $P = 0.31$). Among fish in our treatments, mortality occurred after lipid mass declined to less than 0.2 ± 0.02 g, water mass declined to less than 15.5 ± 0.19 g, lean mass declined to less than 2.6 ± 0.07 g, and wet mass declined to less than 18.6 ± 0.25 g.

Discussion

The most evident change in body composition that occurred during fasting was in lipid content. Prior to death from starvation, both sedentary and actively swimming fish

lost on average 86% of their initial lipid mass. Water temperature substantially affected the rate of decline in lipid mass and percent lipid. As metabolic studies would suggest (Lauff and Wood 1996a, 1996b; Railsback and Rose 1999), higher water temperatures caused whole-body lipids to decline more rapidly. Similar findings have been reported for other fasted salmonids (Parker and Vandstone 1966; Brett et al. 1969; Elliot 1976). However, the extent of lipid loss in previous experiments was not as great as what we observed among juvenile rainbow trout, probably owing to the high metabolic rates of small fish.

Among sedentary rainbow trout, the effects of water temperature on rates of decline in lean mass generally conformed to our hypothesis that lean mass would decline more

rapidly in warmer water. However, water temperature did not affect the rate of decline in lean mass among actively swimming fish. Since fish were swimming against the same current velocity (15 cm/s), it is possible that they were conserving enough body proteins for the extent of muscular activity endured. Fasting sockeye salmon (*Oncorhynchus nerka*) have been found to conserve body proteins for muscular activity associated with spawning migrations (Idler and Bitners 1959; Mommsen et al. 1980).

We observed that water mass declined during fasting. The decline in water mass was probably due to the catabolism of energy stores that are associated with water (Olsson and Satlin 1968; Hill and Wyse 1989; Schmidt-Nielsen 1997). Higher water temperatures increased the rates of decline in water mass in sedentary fish but not in actively swimming rainbow trout. It is possible that the conservation of body proteins for activity by fasted fish may have resulted in the retention of associated water mass.

Wet mass declined over time for fasted fish in all of our treatments, but the extent to which wet mass declined prior to death from starvation was substantially less than observed for lipid mass and lean mass. As we hypothesized, warmer water temperatures caused wet mass to decline at faster rates than cooler temperatures. Brett et al. (1969) also observed that water temperature affected the rate of decline in wet mass of juvenile sockeye salmon that were sedentary. However, we observed that water temperature did not affect wet mass in fasted rainbow trout that were actively swimming.

The effects of water temperature on the ability of rainbow trout to endure periods without food generally supported our hypothesis. Fish in warmer water catabolized more energy reserves and died of starvation sooner and more frequently than fish in cooler water. Similar observations have been made for other fishes (Johnson and Evans 1996; Sogard and Olla 2000).

Lipid mass and percent lipids were substantially affected by swimming activity. Swimming activity caused lipids to decline at faster rates than observed in sedentary fish, which supported our hypotheses. Similarly, Simpkins et al. (2003) observed that swimming activity caused lipid levels to be lower in juvenile rainbow trout that were fasting, but they did not observe differences in the rate of lipid catabolism between sedentary and swimming fish.

Lean mass declined more rapidly in active fish than in sedentary fish at 4.0 °C but not at 7.5 °C. The swimming ability of trout decreases with decreasing water temperatures (Brett 1967; Griffiths and Alderdice 1972). If fish residing in 4.0 °C water had difficulty swimming, it is possible that by forcing them to swim against a low-velocity current, protein degradation was accentuated. Continuous low-level swimming has been observed to increase protein turnover and degradation in fed (Houlihan and Laurent 1987) and fasted (Simpkins et al. 2003) rainbow trout, but the effects of swimming activity and water temperature on protein degradation in fasted trout have not been studied.

Swimming activity affected the rates of decline in water mass and percent water in fish residing at 4.0 °C but not those at 7.5 °C. Since fish in 7.5 °C treatments did not differ in lean mass, water mass associated with body proteins may have been retained. Changes in wet mass associated with swimming activity generally supported our hypothesis for

fasted rainbow trout residing at 4.0 °C. Swimming activity accentuated the rates at which fish in 4.0 °C water lost wet mass. However, wet mass of fish in 7.5 °C water was not affected by swimming activity. Since lipid reserves weigh less than protein stores (Schmidt-Nielsen 1997), the lack of difference in wet mass among 7.5 °C treatments may have been due to sedentary and active fish utilizing protein reserves in lean mass at similar rates (Simpkins et al. 2003).

The ability of juvenile rainbow trout to endure periods without food was affected by swimming activity, which supported our hypothesis and previous findings (Simpkins et al. 2003). Mortality occurred more frequently in active fish than in sedentary fish at both water temperatures. Swimming activity has been found to accentuate mortality rates of fasted fishes in other experiments (Sogard and Olla 2000).

It appears that a limit exists as to the amount of structural lipids that must be retained in fasted fish before essential membrane functions are compromised and survival is questionable (Navarro and Gutiérrez 1995). We observed only two mortalities among sedentary rainbow trout in 4.0 °C water that were fasted for 140 days, despite that fish lost 86% of their initial lipid mass. Toney and Coble (1980) observed no mortalities among sedentary brook trout (*Salvelinus fontinalis*) that were fasted over 120 days, even though lipid levels declined 34%. Similarly, Simpkins et al. (2003) found no mortalities among larger (168 mm) rainbow trout that lost 80%–90% of their initial lipid content over 147 days of fasting. However, we found that warmer water temperatures and swimming activity caused lipid mass in juvenile rainbow trout to decline more rapidly, resulting in more frequent mortality. Juvenile rainbow trout that died had less than 6% lipid (less than 0.2 g) remaining in their bodies, and previous studies have found thresholds to be about 3% (Simpkins et al. 2003). Thus, the limit to which lipid can be used during fasting in juvenile rainbow trout may be 3%–6%. Similar thresholds in percent lipid have been reported for other species (Newsome and Leduc 1975; Thompson et al. 1991; Miranda and Hubbard 1994; Griffiths and Kirkwood 1995; Schultz et al. 1998; Sogard and Olla 2000).

The interactive effects of water temperature and swimming activity on lean mass and wet mass are not as clear as their effects on lipid mass. It appeared that water temperature did not affect lean mass and wet mass in active fish as it had in sedentary fish, and swimming activity did not appear to affect lean mass and wet mass in fish at 7.5 °C as it did at 4.0 °C. Apparently, juvenile rainbow trout were catabolizing lean mass tissues differently during fasting, depending on whether they resided in cold or warm water and whether they were sedentary or swimming.

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