

Effect of Swimming Activity on Relative Weight and Body Composition of Juvenile Rainbow Trout

DARIN G. SIMPKINS*¹ AND WAYNE A. HUBERT

U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit,²
University of Wyoming, Laramie, Wyoming 82071-3166, USA

CARLOS MARTINEZ DEL RIO

Department of Zoology and Physiology, University of Wyoming,
Laramie, Wyoming 82071-3166, USA

DANIEL C. RULE

Department of Animal Science, University of Wyoming,
Laramie, Wyoming 82071-3166, USA

Abstract.—Fisheries managers often assess body condition using relative weight (W_r) because it provides a comparative measure of fish plumpness among individuals and populations. However, it is not known whether the morphological information that W_r summarizes reflects physiological measures, such as relative lipid reserves, in rainbow trout *Oncorhynchus mykiss*. The purpose of this study was to determine whether swimming activity affects either the W_r or proximate body composition of juvenile (total length, 170–260 mm) rainbow trout. When rainbow trout from a hatchery were fed ad libitum for 147 d, inactive (no current) and active (15 cm/s current velocity) fish did not differ in W_r . However, inactive rainbow trout maintained relatively constant lipid levels, whereas active fish declined in lipid content. Relative weight may provide a comparable measure of body form, but it is not an accurate index of lipid content between active and inactive rainbow trout fed an excess ration. For assessing the physiological condition of rainbow trout, measurement of proximate body composition appears to be more accurate than indices based on length and weight.

Fisheries surveys frequently include the collection of length and weight data to describe various characteristics of fish populations, such as growth, length structure, and body condition. Assessments of body condition are important to biologists who manage fish populations, and various body condition indices have been developed to aid in these

assessments. Condition indices measure the “plumpness” of fish and have been used to assess the effects of environmental variation on fish populations, such as changes in habitat and prey availability (Austen et al. 1994; Filbert and Hawkins 1995; Lio et al. 1995; Simpkins and Hubert 2000). Condition indices have frequently been used as monitoring tools and to assess the status of fish populations for management purposes (Gabelhouse 1991; Johnson et al. 1992; Marwitz and Hubert 1995; Weiland and Hayward 1997).

Debate has centered on methodological and statistical issues of using body condition indices (see Bolger and Connolly 1989; Cone 1989; Springer et al. 1990). From these discussions, relative weight (W_r) has become the most accepted index for assessing body condition (Murphy et al. 1990; Ney 1999). Relative weight compares the weight of an individual fish to a standard weight derived from a standard length–weight relationship for the species and the measured total length of the fish. A characteristic of W_r is that it provides a comparative measure of fish plumpness (Murphy et al. 1990). However, little is known whether the morphological information that W_r summarizes reflects possible physiological differences among fish, such as lipid or protein reserves.

The assumption in the use of W_r is that the weight of an individual fish reflects its physiological condition (Gutreuter and Childress 1990; Murphy et al. 1990). Physiological condition of fish has often been described in terms of reserve nutrients, particularly lipids, present in the body (Love 1970; Gershanovich et al. 1984; Mommsen 1998). Physiological condition determines the ability of fish to compete for foraging and spawning sites, maintain and repair tissues, and cope

* Corresponding author: darinsimpkins@hotmail.com

¹ Present address: Colorado Cooperative Fish and Wildlife Research Unit, 201 Wagar Building, Colorado State University, Fort Collins, Colorado 80523-1484, USA.

² The Unit is jointly supported by the University of Wyoming, Wyoming Game and Fish Department, U.S. Geological Survey, and Wildlife Management Institute.

Received February 22, 2002; accepted June 6, 2002

with stress caused by environmental change (Brown and Murphy 1991). Changes in endogenous energy reserves are associated with metabolic processes that either store or deplete lipid or protein (Wedemeyer et al. 1990; Navarro and Gutiérrez 1995). Rose (1989) found that W_r could be used to assess body composition of immature walleyes *Stizostedion vitreum* during feeding experiments. Brown and Murphy (1991) observed that W_r was correlated with body composition of juvenile striped bass *Morone saxatilis* and palmetto bass (striped bass \times white bass *M. chrysops*) that were fed different rations. Studying adult white crappie *Pomoxis annularis*, Neumann and Murphy (1992) found that seasonal variation in W_r corresponded to changes in percent whole body lipid. Jonas et al. (1996) found significant relationships between seasonal changes in W_r and energy density of age-0 and age-1 muskellunge *Esox masquinongy* but suggested that W_r was not a robust indicator of seasonal changes in energy density.

Allocation of consumed energy can differ among active and sedentary fish (Warren and Davis 1967; Adams and Breck 1990). Fish that swim actively tend to partition more consumed energy into metabolic processes and less into storage than do fish that are relatively sedentary (Kitchell 1983; Mommsen 1998). Consequently, at similar feeding rates, actively swimming fish should have lower lipid reserves than fish that are inactive (Busacker et al. 1990; Moyes and West 1995; Mommsen 1998). Relative weight is thought to serve as a surrogate for estimating proximate body composition (Blackwell et al. 2000). So, actively swimming fish should have lower W_r values than fish that are relatively sedentary if they are eating similar amounts. However, research on lipid reserves of fish has been limited to monitoring rates of depletion associated with periods of starvation and spawning migrations (Idler and Bitners 1959; Jöbling 1980; Black and Love 1986). Little attention has been devoted to studying the effects of swimming activity on the allocation of consumed energy into protein and lipid reserves (Moyes and West 1995; Mommsen 1998). To our knowledge, no studies have evaluated whether W_r and measures of proximate body composition are different between actively swimming and sedentary populations of fed fish.

The purpose of this study was to determine whether swimming activity affects the W_r and proximate body composition of juvenile (169–233 mm total length [TL]) rainbow trout *Oncorhynchus mykiss*. Our objectives were to describe the changes

in W_r and measures of proximate body composition (i.e., whole body estimates of lipid, water, and protein) and evaluate differences in W_r and measures of proximate body composition between actively swimming and sedentary juvenile rainbow trout held under controlled laboratory conditions.

Methods

Juvenile rainbow trout (130–150 mm TL; 35–45 g total weight) 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, Wyoming. Seventy-five fish were marked with soft visual-implant tags (Northwest Marine Technologies, Inc.) and placed in each of two 240-L circular tanks (height = 0.85 m; radius = 0.30 m) that received a continuous flow (10 L/min) of aerated well water maintained at 7.5°C. An automated timer and fluorescent lights were used to produce a photoperiod of 12 h light: 12 h dark. Fish were allowed to acclimate for 21 d and were fed an excess ration of Silver Cup pelleted trout chow (Nelson and Sons, Inc.).

After the acclimation period, rainbow trout were sedated with MS-222 (3-aminobenzoic acid ethyl ester methanesulfonate), individually identified, weighed to the nearest gram, and measured to the nearest millimeter TL. Two experimental treatments were used to affect W_r and proximate body composition. Fish continued to receive an excess ration of trout chow but were held either in a current (approximately 15 cm/s) produced by circulating water pumps (March Manufacturing, Inc., Model 2U) or in standing water.

All of the rainbow trout from each tank were sedated, individually identified, weighed, and measured every 21 d. Six fish were randomly selected from each treatment and killed to allow assessment of proximate body composition on each sampling date. The dead fish were quartered and dried at 60°C to constant mass (approximately 48 h). Whole body water content was determined as the difference between wet and dry tissue weight. Dry tissues of individual fish were homogenized and stored in air-tight plastic containers at -20°C away from light. Total lipid content of dry tissue was assessed by quantifying total fatty acid concentration. Duplicate 200-mg samples of dried tissue were subjected to direct transesterification with boron trifluoride in methanol to obtain fatty acid methyl esters (Rule 1997). Fatty acid methyl esters were quantified by gas-liquid chromatography (Hewlett-Packard 5890) as described by

TABLE 1.—Mean length, weight, and relative weight (W_r) did not differ significantly ($P < 0.05$) between sedentary and actively swimming juvenile rainbow trout at the onset (day 0) or conclusion (day 147) of the experiment.

Measure	Day 0			Day 147		
	Mean	SE	Range	Mean	SE	Range
Sedentary						
Length (mm)	169	0.8	152–182	233	2.5	208–257
Weight (g)	49	0.7	36–63	142	4.9	88–182
W_r	94	0.6	83–109	103	1.1	88–113
Active						
Length (mm)	170	0.7	158–183	228	1.7	198–245
Weight (g)	49	0.7	37–61	132	3.0	101–171
W_r	94	0.7	79–114	103	1.1	94–124

Rule (1997). Nitrogen content of dry tissue was determined by using a CHNS analyzer (Fisons Instrument EA 1108) with 5–10-mg samples; results were converted to total crude protein (percent crude protein = percent nitrogen \times 6.25). Total lipid and crude protein were expressed as dry-weight percentages.

Relative weight (W_r ; Wege and Anderson 1978) was calculated as

$$W_r = (W/W_s) \times 100,$$

where W was the wet weight (g) of the individual fish and W_s was the length-specific standard weight. The lotic W_s equation for rainbow trout ($\log_{10} W_s = -5.023 + 3.024 \log_{10} TL$) was from Simpkins and Hubert (1996).

Two-sample t -tests were used to test for differences in the distributions of initial lengths, weights, and W_r values between treatments. This test was also used to evaluate differences in final measurements between treatments. Simple linear regression was used to evaluate relationships between dependent variables (W_r , percent total body water, percent lipid, and percent protein) and duration of swimming activity or inactivity by rainbow trout. A t -test was used to test for differences in intercepts of the relationships between treatments (Zar 1996). Coefficients of determination, residual plots, and an F lack-of-fit test were used to evaluate the suitability of applying linear models to assess trends in W_r and measures of proximate body composition over time (Neter et al. 1996). For relationships where initial estimates (i.e., intercepts) were not significantly different, the general linear model (GLM; Neter et al. 1996) was used to evaluate whether slopes of the relationships between dependent variables and time differed among treatments. The GLM took the form:

$$Y = \beta_0 + \beta_1 X_1 X_2 + \varepsilon_r$$

where Y was the dependent variable of interest, X_1 was a nominal variable equal to 0 if fish were inactive and 1 if fish were active, and X_2 was a continuous variable equal to the time (duration) of treatment (d). The value of β_0 was a derived constant equal to the common intercept of the relationship between the dependent variable and time. Statistical computations were performed by using SuperANOVA (Abacus Concepts 1991). Significance was determined at $P < 0.05$ for all tests.

Results

No significant differences were observed in the length ($t_{148} = 0.60$; $P = 0.55$), weight ($t_{148} = 0.41$; $P = 0.41$), or W_r ($t_{148} = 0.78$; $P = 0.43$) of fish among treatments at the onset of the experiment (Table 1). Relative weight significantly increased over time for both sedentary ($t_{429} = 11.13$; $P < 0.001$; $r^2 = 0.23$) and active ($t_{468} = 8.74$; $P < 0.001$; $r^2 = 0.14$) fish, and relationships did not significantly differ from a linear pattern for active ($F_{6,462} = 2.01$; $P = 0.06$) or inactive ($F_{6,423} = 1.87$; $P = 0.08$) fish. Moreover, rates of change in W_r were not significantly different between active and inactive treatments ($F_{1,899} = 1.29$; $P = 0.26$; $\beta_1 = 0.065 \pm 0.001$; $r^2 = 0.19$; Figure 1). By the end of the experiment, active and sedentary fish did not differ significantly in mean length ($t_{63} = 1.83$; $P = 0.07$), weight ($t_{63} = 1.73$; $P = 0.09$), or W_r ($t_{63} = 0.46$; $P = 0.65$; Table 1).

Estimates of initial percent lipid content did not differ significantly between active and inactive fish ($t_{83} = 0.99$; $P = 0.32$; $\beta_0 = 16.27 \pm 0.04$), and relationships between percent lipid and time did not significantly differ from a linear pattern for active ($F_{5,36} = 0.26$; $P = 0.93$) or inactive ($F_{5,35} = 1.36$; $P = 0.26$) fish. However, slopes of the

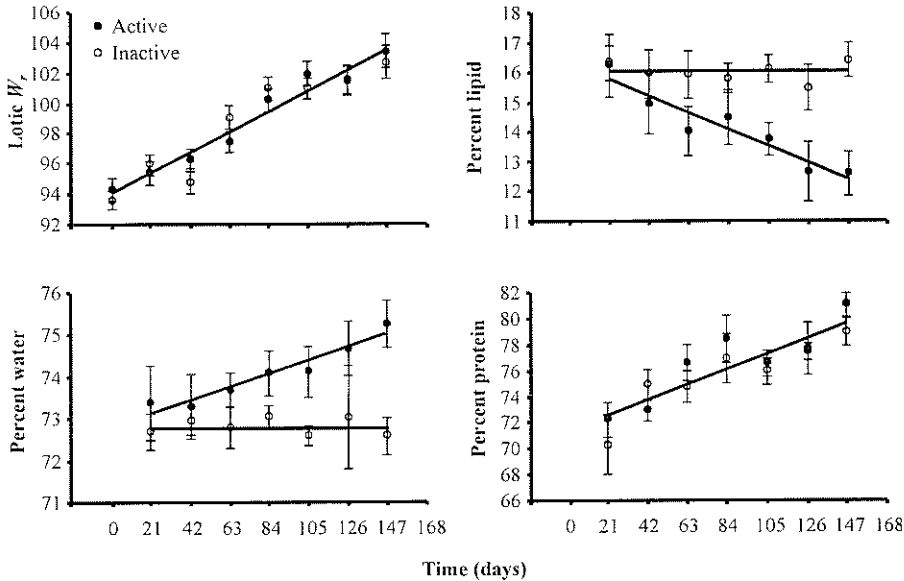


FIGURE 1.—Mean lotic relative weight (W_p) and mean percent protein did not differ among actively swimming (15 cm/s) and inactive juvenile rainbow trout (169–233 mm TL), but percent lipid decreased and percent water increased in the bodies of active fish over 147 d of being fed ad libitum. Total lipid and crude protein are expressed as percent of dry body weight; bars represent standard errors.

relationships between percent lipid and time were significantly different between treatments ($F_{1,84} = 5.33$; $P < 0.05$). Percent crude lipid did not change significantly over time for inactive fish ($t_{40} = 0.37$; $P = 0.72$) but did decrease significantly in active fish ($t_{41} = 3.49$; $P < 0.005$; $\beta_1 = -0.027 \pm 0.001$; $r^2 = 0.23$; Figure 1).

The estimated initial percent water content in fish was not significantly different between active and inactive treatments ($t_{83} = 1.22$; $P = 0.23$; $\beta_0 = 72.48 \pm 0.29$), and relationships between percent water and time did not differ significantly from a linear model for active ($F_{5,36} = 0.31$; $P = 0.90$) or inactive ($F_{5,35} = 0.50$; $P = 0.77$) fish. However, the slopes of the relationships between percent total body water and time were significantly different between treatments ($F_{1,84} = 6.12$; $P < 0.05$). Percent total body water did not change significantly over time for inactive fish ($t_{40} = 0.68$; $P = 0.50$) but did increase significantly for active fish ($t_{41} = 2.92$; $P < 0.01$; $\beta_1 = -0.015 \pm 0.001$; $r^2 = 0.19$; Figure 1).

Initial percent protein estimates were not significantly different between active and inactive treatments ($t_{83} = 1.14$; $P = 0.26$; $\beta_0 = 71.39 \pm 0.07$). Percent protein increased significantly over time for both active ($t_{41} = 4.74$; $P < 0.001$; $r^2 = 0.35$) and inactive ($t_{40} = 2.49$; $P < 0.05$; $r^2 =$

0.13) fish, and the relationships did not differ significantly from a linear model for active ($F_{5,36} = 2.21$; $P = 0.07$) or inactive ($F_{5,35} = 1.72$; $P = 0.16$) fish. The rate of change in percent protein did not differ between active and inactive treatments ($F_{1,84} = 0.84$; $P = 0.36$; $\beta_1 = 0.056 \pm 0.002$; $r^2 = 0.25$; Figure 1).

Discussion

Juvenile rainbow trout that were actively swimming differed from sedentary fish in proximate body composition. Fish that were swimming at 15 cm/s had substantially lower lipid reserves and higher water content than sedentary fish after 147 d (Figure 1). Despite differences in proximate body composition between actively swimming and sedentary fish, swimming activity did not affect W_p . Fish were equally plump in both treatments but differed significantly in lipid reserves. Consequently, our results do not support the hypothesis that W_p serves as a surrogate for proximate body composition as a measure of fish health (Blackwell et al. 2000).

Swimming activity substantially influenced the allocation of consumed energy in juvenile rainbow trout. Fish that were sedentary maintained relatively constant lipid levels, whereas fish that were swimming decreased in lipid content. These results

suggest that active fish allocated more consumed energy to metabolic demands and less to storage than did inactive fish. Percent protein increased similarly among active and inactive fish, suggesting that both active and inactive fish consumed enough energy for the synthesis of muscle tissue. Despite differences in lipid content, mean TL and mean weight were not substantially different between active and inactive fish at the end of the experiment.

Concern has developed regarding the use of indices computed from measurements of length and weight to assess changes in body condition because assessments based on these indices do not account for the replacement of proximate body constituents by water (Navarro and Gutiérrez 1995; Mommsen 1998). Inverse relationships have been found between percent lipid and percent water content in sockeye salmon *O. nerka* (Idler and Bitners 1959; Brett et al. 1969), brown trout *Salmo trutta* (Elliot 1976), striped bass, palmetto bass (Brown and Murphy 1991), and several other species (Love 1970). Idler and Bitners (1959) found that the percent water content of sockeye salmon increased during the spawning migration, but the sum of percent water and percent lipid remained constant such that total body weight did not change. Similarly, we found that percent water increased as percent lipid decreased in actively swimming juvenile rainbow trout. However, we interpret these data cautiously because the percentages of water, lipid, and protein sum to 100% (Anderson and Neumann 1996). A decrease in the mass of one constituent would result in a corresponding increase in the percentage of another constituent with a constant mass. It is likely that W_r for rainbow trout was not sensitive enough to account for a 4% decline in lipid content. However, Brown and Murphy (1991) found that W_r was more strongly related to percent lipid in striped bass and palmetto bass over a wider range of fat content (20–30%).

A possible shortcoming of W_r is that statistical properties rather than physiological measures have been used to evaluate the suitability of the condition index (Murphy et al. 1990; Hyatt and Hubert 2001). The suitability of samples from fish populations for inclusion when developing W_r equations have been based on statistical properties of relationships between length and weight. Slopes, intercepts, and coefficients of determination for relationships between length and weight vary because of small sample sizes, narrow ranges of length and weights of fish within samples from

populations, and differences in morphology of sampled fish in populations used in developing W_r equations (Murphy et al. 1990; Pope et al. 1995; Kruse and Hubert 1997). A more sensitive basis for evaluating samples to include when developing body condition indices may be the use of relationships between length and measures of proximate body composition. Anderson and Neumann (1996) suggested that the ratio of lipid to protein should be similar across lengths, when assessments of body condition remain relatively constant. Therefore, a change in lipid content could be reflected by a change in body condition.

We conclude that activity had a measurable effect on the lipid content of juvenile rainbow trout but that W_r failed to identify differences. Relative weight may provide a comparable measure of body form, but it is not an accurate index of lipid content between active and inactive rainbow trout fed an excess ration. Further research is needed to evaluate relationships between W_r and body composition of rainbow trout in lotic or lentic habitats that differ in food availability. Nevertheless, measurement of proximate body composition appears to be more accurate than indices based on length and weight when assessing physiological condition of rainbow trout.

Acknowledgments

We thank L. Hebdon, C. Kruse, S. Mullner, M. Dare, H. Lease, J. Kaltenbach, and C. Murrieta for assistance collecting data. This project was funded by the Wyoming Game and Fish Department and a grant from the National Science Foundation.

References

- Abacus Concepts. 1991. SuperANOVA, the accessible general linear modeling package, version 1.11. Abacus Concepts, Berkeley, California.
- Adams, S. M., and J. E. Breck. 1990. Bioenergetics. Pages 389–415 in C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Austen, D. J., D. L. Scarnecchia, and E. P. Bergersen. 1994. Usefulness of structural and condition indices in management of high-mountain stream salmonid populations. North American Journal of Fisheries Management 14:681–691.
- Black, D., and R. M. Love. 1986. The sequential mobilization and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. Journal of Comparative Physiology 156B:469–479.

- Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. *Reviews in Fisheries Science* 8:1–44.
- Bolger, T., and P. L. Connolly. 1989. The selection of suitable indices in the measurement and analysis of fish condition. *Journal of Fish Biology* 34:171–182.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363–2394.
- Brown, M. L., and B. R. Murphy. 1991. Relationships of relative weight (W_r) to proximate body composition of juvenile striped bass and hybrid striped bass. *Transactions of the American Fisheries Society* 120:509–518.
- Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–388 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Cone, R. S. 1989. The need to reconsider the use of condition indices in fisheries science. *Transactions of the American Fisheries Society* 118:510–514.
- Elliot, B. J. M. 1976. Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. *Journal of Animal Ecology* 45:273–289.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* 124:824–835.
- Gabelhouse, D. W. 1991. Seasonal changes in body condition of white crappies and relations to length and growth in Melvern Reservoir, Kansas. *North American Journal of Fisheries Management* 11:50–56.
- Gershanovich, A. D., N. M. Markevich, and Z. T. Dergaleva. 1984. Using the condition factor in ichthyological research. *Journal of Ichthyology* 24:78–90.
- Gutreuter, S., and W. M. Childress. 1990. Evaluation of condition indices for estimation of growth of largemouth bass and white crappie. *North American Journal of Fisheries Management* 10:434–441.
- Hyatt, M. W., and W. A. Hubert. 2001. Statistical properties of relative weight distributions of four salmonid species and their sampling implications. *North American Journal of Fisheries Management* 21:666–670.
- Idler, D. R., and I. Bitners. 1959. Biochemical studies on sockeye salmon during spawning migration. *Journal of the Fisheries Research Board of Canada* 17:235–241.
- Jöbling, M. 1980. Effects of starvation on proximate chemical composition and energy utilization of plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 17:325–334.
- Johnson, S. L., F. J. Rahel, and W. A. Hubert. 1992. Factors affecting the size structure of brook trout populations in beaver ponds in Wyoming. *North American Journal of Fisheries Management* 12:118–124.
- Jonas, J. L., C. E. Kraft, and T. L. Margenau. 1996. Assessment of seasonal changes in energy density and condition in age-0 and age-1 muskellunge. *Transactions of the American Fisheries Society* 125:203–210.
- Kitchell, J. F. 1983. Energetics. Pages 312–338 in P. Webb and D. Weihs, editors. *Fish biomechanics*. Praeger, New York.
- Kruse, C. G., and W. A. Hubert. 1997. Proposed standard weight (W_s) equations for interior cutthroat trout. *North American Journal of Fisheries Management* 17:784–790.
- Lio, H., C. L. Pierce, D. H. Wahl, J. B. Rasmussen, and W. C. Leggett. 1995. Relative weight (W_r) as a field assessment tool: relationships with growth, prey biomass, and environmental conditions. *Transactions of the American Fisheries Society* 124:387–400.
- Love, R. M. 1970. *The chemical biology of fishes*, volume 1. Academic Press, New York.
- Marwitz, T. D., and W. A. Hubert. 1995. Descriptions of walleye stocks in high elevation reservoirs, Wyoming. *Prairie Naturalist* 27:101–114.
- Mommsen, T. P. 1998. Growth and metabolism. Pages 65–97 in D. H. Evans, editor. *The physiology of fishes*, 2nd edition. CRC Press, New York.
- Moyes, C. D., and T. G. West. 1995. Exercise metabolism of fish. Pages 367–392 in P. W. Hochachika and T. P. Mommsen, editors. *Biochemistry and molecular biology of fishes*, volume 4. *Metabolic biochemistry*. Elsevier, Amsterdam.
- Murphy, B. R., M. L. Brown, and T. A. Springer. 1990. Evaluation of the relative weight (W_r) index, with new applications to walleye. *North American Journal of Fisheries Management* 10:85–97.
- Navarro, I., and J. Gutiérrez. 1995. Fasting and starvation. Pages 393–434 in P. W. Hochachika and T. P. Mommsen, editors. *Biochemistry and molecular biology of fishes*, volume 4. *Metabolic biochemistry*. Elsevier, Amsterdam.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*, 4th edition. McGraw-Hill, Chicago.
- Neumann, R. M., and B. R. Murphy. 1992. Seasonal relationships of relative weight to body composition in white crappie, *Pomoxis annularis* Rafinesque. *Aquaculture and Fisheries Management* 23:243–251.
- Ney, J. J. 1999. Practical use of biological statistics. Pages 167–191 in C. C. Kohler and W. A. Hubert, editors. *Inland fisheries management in North America*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Pope, K. L., M. L. Brown, and D. W. Willis. 1995. Proposed revision of the standard weight (W_s) equation for redear sunfish. *Journal of Freshwater Ecology* 10:129–134.
- Rose, C. J. 1989. Relationship between relative weight (W_r) and body composition in immature walleye. Master's thesis. Texas A&M University, College Station.
- Rule, D. C. 1997. Direct transesterification of total fatty acids of adipose tissue and of freeze-dried muscle

- and liver with boron-trifluoride in methanol. *Meat Science* 46:23-32.
- Simpkins, D. G., and W. A. Hubert. 1996. Proposed revision of the standard-weight equation for rainbow trout. *Journal of Freshwater Ecology* 11:319-325.
- Simpkins, D. G., and W. A. Hubert. 2000. Drifting invertebrates, stomach contents, and body conditions of juvenile rainbow trout from fall through winter in a Wyoming tailwater. *Transactions of the American Fisheries Society* 129:1176-1184.
- Springer, T. A., B. R. Murphy, S. Gutreuter, R. O. Anderson, L. E. Miranda, D. C. Jackson, and R. S. Conc. 1990. Properties of relative weight and other condition indices. *Transactions of the American Fisheries Society* 119:1048-1058.
- Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. Pages 175-214 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford, UK.
- Wedemeyer, G. A., B. A. Barton, and D. J. McLeay. 1990. Stress and acclimation. Pages 451-490 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Wegc, G. J., and R. O. Anderson. 1978. Relative weight (W_r): a new index of condition for largemouth bass. Pages 79-91 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.
- Weiland, M. A., and R. S. Hayward. 1997. Cause for the decline of large rainbow trout in a tailwater fishery: too much putting or too much taking? *Transactions of the American Fisheries Society* 126:758-773.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd edition. Prentice-Hall, Upper Saddle River, New Jersey.

