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Rainbow trout performance in food-limited environments: implications for future assessment and management

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We evaluated the performance of rainbow trout in food-limited lake and hatchery environments using whole-body water content as a proxy for fish energy reserves and lipid content. Relative abundance of rainbow trout stocked in an oligotrophic lake from 2002 to 2006 decreased by 88% in 145 days. Whole-body water content of rainbow trout increased following stocking in the lake and similar increases in water content were observed in fish from a food-deprived hatchery treatment. Water content in the fed hatchery fish was significantly lower than water content observed in stocked lake fish. Traditional metrics of body condition (i.e., Fulton's *K* and relative weight) based on length–weight relationships were insufficient to detect the observed changes in whole-body water content for all lake and hatchery treatments. We conclude that depletion of energy reserves contributed to poor survival and low angling returns of stocked rainbow trout in the study lake.

Keywords: body condition; *Oncorhynchus mykiss*; starvation; water content; Fulton *K*; energy reserves

Introduction

Recreational fisheries for rainbow trout (*Oncorhynchus mykiss*) have been established, enhanced, and maintained by stocking programs in lake and river systems throughout North America for decades (Baird et al. 2006; Swales 2006). Stocked rainbow trout may exhibit poor survival, growth, and return to anglers in lakes and streams due to a number of factors (Kerr and Lasenby 2000). Differences in post-stocking survival and growth of rainbow trout have been attributed to strain (Hudy and Berry 1983; Babey and Berry 1989), age and size at stocking (Wiley et al. 1993; Baird et al. 2006), predation (Matkowski 1989), movements (Shetter 1947; Baird et al. 2006), disease (Dick et al. 1987; Menezies et al. 1990), competition (Hubert and Guenther 1992; Hubert and Chamberlain 1996), and productivity of stocked waters (Donald and Anderson 1982; Gipson and Hubert 1991; Hume and Tsumura 1992). Despite the potential for poor survival and return to anglers,

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rainbow trout stocking is a common management practice throughout North America, therefore it is important to improve our understanding of factors that influence growth and survival of stocked rainbow trout.

Food limitation is a mechanism commonly used to explain poor growth and survival of stocked rainbow trout in oligotrophic environments inhabited by competitors (Hudy and Berry 1983; Gipson and Hubert 1991; Hubert and Chamberlain 1996) and starvation of stocked trout in food-limited environments is frequently inferred from measures of body condition (Reimers 1963; Ersbak and Haase 1983; Haddix and Budy 2005). Body condition indices used to assess the energy reserves of fish have substantial limitations because water typically replaces lost lipids in fish with little or no changes in weight (Gardiner and Geddes 1980). In addition, age, sex, and reproductive status further confound length–weight relationships (Cone 1989; Jonas et al. 1996; Trudel et al. 2005). Water content is inversely related to the energy reserves and lipid content in fishes and serves as a proxy for these metrics in somatic tissue (Gardiner and Geddes 1980; Steinhart and Wurtsbaugh 2003; Pothoven et al. 2006). Thus, water content is a more sensitive measure of fish energy reserves than body condition indices (Hartman and Brandt 1995; Steinhart and Wurtsbaugh 2003; Peters et al. 2007).

We evaluated energy reserve depletion as a potential factor contributing to the observed poor survival and angling returns of stocked rainbow in a hyper-oligotrophic Adirondack lake. Angler surveys conducted annually from 1964–2005 in our study lake showed consistent rainbow trout catch rates of 0.5 (±0.04 SE) fish per trip throughout this 42-year period (unpublished data). Anglers were generally dissatisfied with these returns, and several management approaches were implemented during this period in an attempt to increase stocked rainbow trout survival and angler catches.

Domestic yearling and 2-year-old rainbow trout were stocked in early to mid-June during two distinct time periods. High densities (20–50 fish per ha) of yearlings (150–230 mm) were stocked from 1964 to 1993 and low densities (1–5 fish per ha) of 2-year-old fish (250–410 mm) were stocked from 1994 to 2005. The stocking of larger 2-year-old fish beginning in 1994 was aimed at reducing suspected predation by lake trout and loons on smaller yearlings. Other lake management practices included maintenance of an outlet barrier from 1999 to 2006 to prevent emigration of stocked fish and approximately 9000 kg of lime has been applied to the lake surface every 2 years since 1990 to reduce acidity and maintain lake pH above 6.0. Although these management actions, which were implemented to reduce predation, emigration, and lake acidity, were expected to improve survival and angler catch of stocked rainbow trout in First Bisby Lake, they were unsuccessful. Voluntary angling surveys revealed that angler catch rates were not different when stocking yearling (1964–1993; 0.6 fish/trip) or 2-year-old fish (1994–2005; 0.5 fish/trip) and showed no consistent trend during the past 42 years (unpublished data). Consequently, we explored an alternative explanation that food limitation in First Bisby Lake may have led to loss of lipids, depletion of energy reserves and eventual mortality of stocked rainbow trout.

The performance of stocked rainbow trout in the lake environment was evaluated and compared to their performance in fed and food-deprived environments in a hatchery, in which water content and body condition indices (Fulton's *K* and relative weight) were compared as metrics of rainbow trout performance across treatments. We provide experimental evidence that energy reserve depletion contributed to the low observed survival and return to anglers of stocked rainbow trout in our study lake. Further, we provide justification for the use of energy reserve metrics (i.e., water content), rather than body condition indices, for assessing fish health.

Methods

Study site

First Bisby Lake is a 62.3 ha lake located on private land within the Adirondack Park in New York State (43°36′14.15″ N, 74°56′01.85″ W). The lake is hyper-oligotrophic with low levels of chlorophyll *a*, total *P*, and total dissolved solids and high water clarity (Table 1). First Bisby Lake historically and currently supports cold-water fisheries for salmonids. Catchable-size rainbow trout have been stocked in First Bisby Lake since 1964 to supplement the recreational fishery. Native lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*), white sucker (*Catostomus commersoni*), creek chub (*Semotilus atromaculatus*), central mudminnow (*Umbra limi*), non-native smallmouth bass (*Micropterus dolomieu*), and stocked Atlantic salmon (*Salmo salar*) also inhabit the lake.

We designed a series of experiments to evaluate survival and changes in water content (as a proxy for energy reserves) of stocked 2-year-old rainbow trout in First Bisby Lake (2002–2006) and in a controlled hatchery environment (2005 and 2006). Water content was less expensive and easier to measure than lipid content, while still serving as a reliable proxy for energy levels. We assumed that the strong inverse relationship between lipids and water content in salmonids in other studies (Gardiner and Geddes 1980; Steinhart and Wurtsbaugh 2003; Pothoven et al. 2006) would be similar for the rainbow trout in this study. Domestic-strain rainbow trout used during this study were purchased from two commercial hatcheries in New York. Rainbow trout were stocked into First Bisby Lake or held at the Little Moose Field Station hatchery near Old Forge, New York.

Lake experiment

Two-year-old domestic-strain rainbow trout were stocked in First Bisby Lake in May of each year from 2002 through 2005 (Table 2). Rainbow trout were given unique fin clips every year to identify individuals from each stocking event ($n = 4$).

Table 1. Morphometry and chemical measures of biological productivity for First Bisby Lake (2002–2005).

Parameter	Sample size (n)	Measurement (mean ± SE)
Surface area (ha)	–	62.3
Mean depth (m)	–	11.6
Maximum depth (m)	–	30.8
Chlorophyll *a* (μg/L)	30	0.7 ± 0.05
pH	75	6.4 ± 0.01
Total phosphorous (μg/L)	30	3.3 ± 0.05
Total dissolved solids (mg/L)	18	23.6 ± 0.44
Secchi depth (m)	24	8.5 ± 0.04

Table 2. Spring and fall 2-year-old rainbow trout stocking information for First Bisby Lake (2002–2005).

Date stocked	Number stocked	Mean length (mm)	Fin clips
15 May 2002	350	378	No mark
23 May 2003	350	334	Adipose
21 May 2004	350	280	Right pelvic
16 May 2005	350	362	Left pelvic
25 October 2005	100	285	No mark

Stocked rainbow trout were captured by nighttime boat electrofishing the entire lake perimeter within a 6–7 h period. Single-pass nighttime boat electrofishing was conducted every spring (late May) and fall (late-September) from 2002 to 2006 to assess relative abundance of fish from each year class stocked. Post-stocking catch per unit effort (CPUE, number of fish captured per hour) was used as a measure of relative abundance and was calculated for all sampling events ($n = 10$). Comparisons of post-stocking CPUE for the first spring, first fall, second spring, and second fall after stocking were made by calculating the mean CPUE for each sampling period (spring 1, fall 1, spring 2, and fall 2) for the four stocked cohorts. Mixed-model analyses (cohort as a random effect and sampling period as a fixed effect using the PROC_MIX procedure) were conducted using SAS (SAS Institute Inc.) and *post-hoc* comparisons (Tukey's honestly significant difference test) was used to test for differences in CPUE over each of the four sampling periods.

Rainbow trout water content (%) was determined by drying whole fish for 10 days at 60°C (Gardiner and Geddes 1980). Water content, Fulton's K and relative weight of five rainbow trout were measured prior to stocking in May 2005.

Fulton's K was calculated according to Anderson and Neumann (1996) as

$$\left[W/L^3\right] \times 10^6 \tag{1}$$

where $W =$ weight (g) and $L =$ length (mm).

Relative weight was calculated according to Simpkins and Hubert (1996) as

$$\log_{10} W = -4.898 + 2.99(\log_{10} L) \tag{2}$$

where $W =$ weight (g) and $L =$ length (mm).

Prior to stocking on 16 May 2005, rainbow trout ($n = 5$) were collected from the hatchery group of fish to be stocked in First Bisby Lake. These rainbow trout were measured and weighed (wet and dry) to determine the body condition of fish at stocking. Following stocking in May 2005, rainbow trout were collected from First Bisby Lake at intervals of 62 days ($n = 4$; angling), 137 days ($n = 2$; trap net), and 162 days ($n = 1$; trap net). Water content, Fulton's K, and relative weight were calculated for all fish collected. One-way analysis of variance (ANOVA) and *post-hoc* comparisons (Tukey's honestly significant difference test) were used to examine differences in water content and body condition indices through time for 2-year-old fish stocked in May 2005. The first two sampling events (16 May pre-stocking; and 17 July angling) were considered separately. The last two sampling events (30 September and 25 October trap netting) were combined for analysis due to low sample size ($n = 2$ and 1, respectively) and the proximity of the sampling dates. All rainbow trout were measured and weighed (wet) immediately upon capture from First Bisby Lake.

Concurrent hatchery and lake food-resource manipulation experiment

Response of adult rainbow trout to varying levels of food availability was evaluated through concurrent treatments of fish in hatchery and lake environments. 2-year-old rainbow trout were held in the Little Moose Field Station fish hatchery starting on 19 October 2005 after being delivered from Morrisville State University Hatchery. Five of these fish were measured and weighed (wet and dry) to determine the body condition of fish at the initiation of the hatchery experiment. Each remaining fish was individually marked with a Floy FD-94 T-Bar Anchor tag (Floy Tag and Manufacturing Co., Seattle, Washington, USA), and fish were randomly selected for one of two treatments, a fed group and a food-deprived group. The fed treatment consisted of two groups of five fish each in 1.2 m diameter tanks (580 L) and one group of five fish in a 3.0 m diameter tank (3350 L). The food-deprived treatment consisted of one group of five fish in a 1.2 m diameter tank and one group of five fish in a 3.0 m diameter tank. The fed treatment groups were given 3-mm diameter floating pellets (Zeigler Brothers, Inc.). Fish were fed 200 g/tank at 8:00 am and 4:00 pm daily. Food-deprived treatments were not fed, but zooplankton was present in the hatchery water delivered from the water source (Little Moose Lake, Herkimer County, NY). Zooplankton was delivered to the tanks at rates of 1.8–3.7 g/day dry weight (1.2 m tanks) and 3.7–7.3 g/day dry weight (3.0 m tanks). The experiment was terminated on 17 February 2006, and all fish were processed to determine water content, Fulton's *K*, and relative weight as previously described.

A concurrent lake experiment was initiated on 25 October 2005 when 2-year-old domestic-strain rainbow trout from the same lot as the hatchery experiment fish were stocked in First Bisby Lake (Table 2). This stocked group of rainbow trout was sampled by boat electrofishing 217 days later in May 2006 ($n = 6$). All fish were processed to determine water content, Fulton's *K*, and relative weight.

Mixed-model analyses (tank as a random effect and feeding treatment as a fixed effect using the PROC_MIX procedure) were conducted using SAS (SAS Institute Inc.) to test for treatment effects on rainbow trout water content, Fulton's *K*, and relative weight. Fish length was included as a fixed effect but was never significant and was therefore excluded from the final models. One-way ANOVA and *post-hoc* comparisons (Tukey's honestly significant difference test) were used to examine differences in body condition indices for fish among the initial, tank fed, tank food-deprived, and lake stocked groups in the food manipulation experiment.

Results

Lake assessment

There was a significant negative effect of time since stocking on the boat electrofishing CPUE of rainbow trout stocked in May from 2002 to 2006 ($F_{3,9} = 7.70$, $p < 0.01$; Figure 1). Based on Tukey's *post-hoc* comparisons, mean CPUE in the spring in which fish were stocked (spring 1) was significantly larger than in all other sampling periods (fall 1, $p = 0.02$; spring 2, $p < 0.02$; fall 2, $p = 0.01$).

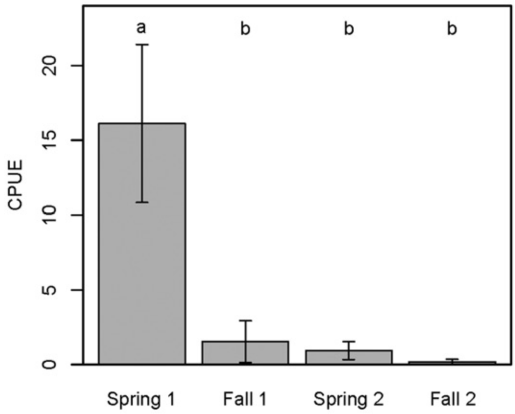

Figure 1. Mean boat electrofishing CPUE (number of fish captured per hour) for each of four sampling periods for the four stocked cohorts of rainbow trout in First Bisby Lake, 2002–2006. The four sampling periods included Spring 1 (first spring after stocking), Fall 1 (first fall after stocking), Spring 2 (second spring after stocking), and Fall 2 (second fall after stocking). Error bars represent one standard error from the mean. Significant differences were found between seasons not sharing a common letter.

No differences were detected between mean CPUE in the other sampling periods (all p values > 0.98). An 88% reduction in boat electrofishing catch rates was observed from spring stocking to the first fall after stocking (approximately 145 days). The low catch rates were sustained through the following spring and fall seasons indicating that the most substantial loss of stocked rainbow trout occurred soon after stocking during the summer months. Angler mortality ranged from 0.6–5.4% of the rainbow trout stocked from 2002 to 2006 based on angler surveys.

Water content of rainbow trout stocked in spring 2005 increased significantly between May and October 2005 (ANOVA: $F_{2,9} = 5.21$, $p = 0.03$; Figure 2). Water content of fish sampled within the lake ranged from a low of 69.0% at the time of stocking (16 May) to a high of 78.0% 137 days after stocking (30 September). Based on Tukey's *post-hoc* comparisons, there was no difference in mean water content between fish at the time of stocking and 62 days post-stocking ($p = 0.10$), a significant difference between fish at the time of stocking and 137–162 days post-stocking ($p = 0.04$), and no difference between the 62 and 137–162 days post-stocking groups ($p = 0.70$). No differences were detected in mean Fulton's K (ANOVA: $F_{2,9} = 1.64$, $p = 0.25$, Figure 2) or mean relative weight (ANOVA: $F_{2,9} = 1.73$, $p = 0.23$, Figure 2) between values at the time of stocking and values for any post-stocking sampling event.

Concurrent hatchery and lake food-resource manipulation experiment

The mean water content of rainbow trout at the start of the experiment (initial group, fall 2005) was 76.3%, and mean water content for the fed, food-deprived, and lake groups at the end of the experiment (spring 2006) was 73.0%, 79.3%, and 78.2%, respectively. Mixed model results revealed a significant effect of feeding treatment on water content ($F_{1,21} = 54.36$, $p < 0.01$). Based on Tukey's *post-hoc* comparisons, the mean water content of the initial group was greater than the final

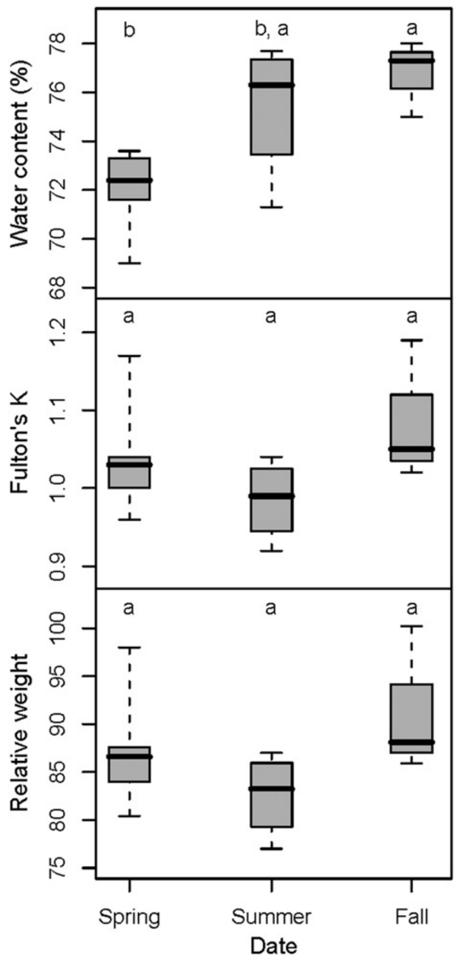

Figure 2. Water content (%), Fulton's *K*, and relative weight of rainbow trout sampled from First Bisby Lake from May to October 2005. Spring data represent values at time of stocking. Horizontal lines on the boxes represent the upper quartile, median, and lower quartile, and the whiskers extend to data extremes. Significant differences were found between dates not sharing a common letter.

value for the fed group ($p = 0.01$) and less than the final value for the food-deprived group ($p = 0.05$). Water content of the lake group was similar to the initial ($p = 0.38$) and food-deprived groups ($p = 0.73$) and greater than the fed group ($p < 0.01$; Figure 3). One rainbow trout died in each of the 1.2 m diameter and 3.0 m diameter food-deprived treatment tanks at 22 and 53 days, respectively. No fish died in the fed treatment tanks.

Fulton's *K* for the initial experimental group was 0.98, and Fulton's *K* for the fed, food-deprived, and lake groups at the end of the experiment were 1.14, 0.76, and 1.03, respectively. Mixed modeling revealed a significant effect of feeding treatment on Fulton's *K* ($F_{1,21} = 50.04$, $p < 0.01$). Based on Tukey's *post-hoc* comparisons, the mean Fulton's *K* for the food-deprived group was lower than the other three groups (fed, $p < 0.01$; initial, $p = 0.02$; lake, $p < 0.01$) and the initial, fed, and lake groups were similar (Figure 3).

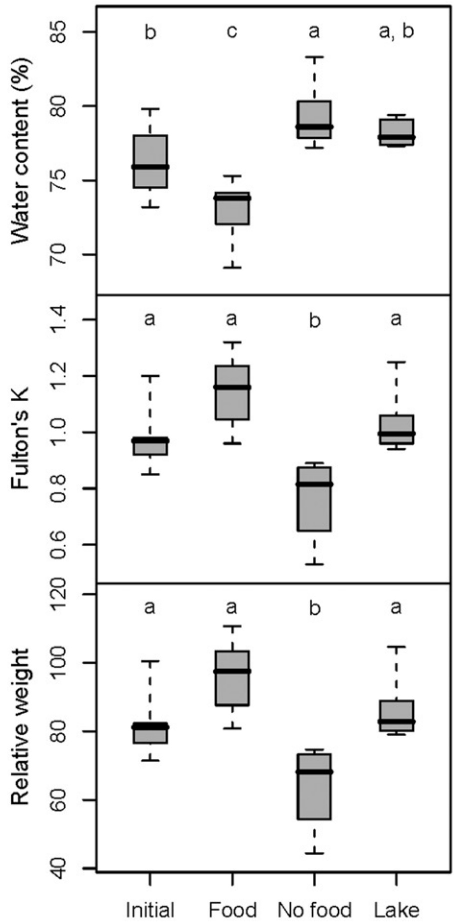

Figure 3. Water content (%), Fulton's *K*, and relative weight for rainbow trout from the initial group, fed group, food-deprived group, and lake group treatments in the food-resource manipulation experiment. Horizontal lines on the boxes represent the upper quartile, median, and lower quartile, and the whiskers extend to data extremes. Significant differences were found between treatments not sharing a common letter.

Relative weight for the initial experimental group was 82.4, and relative weight for the fed, food-deprived, and lake groups at the end of the experiment were 96.0, 63.8, and 86.4, respectively. Mixed model analysis revealed a significant effect of feeding treatment on relative weight ($F_{1,21} = 50.36$, $p < 0.01$). Based on Tukey's *post-hoc* comparisons, the mean relative weight for the food-deprived group was lower than the other three groups (fed, $p < 0.01$; initial, $p = 0.02$; lake, $p < 0.01$) and the initial, fed, and lake groups were similar (Figure 3).

Discussion

Our study results provide experimental evidence that energy reserve depletion is a plausible contributing factor to poor survival and angling returns of rainbow trout in First Bisby Lake and similar low-productivity lakes. In addition, we provide confirmatory evidence that body condition indices (e.g., Fulton's *K* and relative weight) should be used with caution or coupled with measures of energy reserves (e.g., water content) that have a more direct relationship to lipid content when assessing fish condition and performance in field studies.

First Bisby Lake is food limited due to low productivity and the presence of competing fish species; factors that have been implicated in poor survival and growth of rainbow trout in other lake environments (Donald and Anderson 1982; Hume and Tsumura 1992; Hubert and Chamberlain 1996). Our study revealed that water content increases in rainbow trout in food-limited lake and hatchery environments were indicative of energy reserve depletion due to rapid and sustained lipid loss. Other studies have reported similar linkages between lipid content and energy reserve depletion in salmonid species (Niva 1999; Steinhart and Wurtsbaugh 2003; Peters et al. 2007). Further, rainbow trout mortality was observed in each of the food-deprived hatchery treatments in this study. The low sample size of recaptured rainbow trout in First Bisby Lake following stocking is reflective of the large decline (88%) in the relative abundance 145 days after stocking as measured by boat electrofishing surveys. Despite low sample size and statistical power, we detected differences between initial rainbow trout water content and that of rainbow trout following stocking. This is indicative of large and consistent differences in water content. Consequently, energy reserve depletion is likely an important contributing factor to the low observed survival and angling returns of stocked rainbow trout in hyper-oligotrophic First Bisby Lake.

Body water content levels exceeding 78% correspond to low lipid levels and high mortality of salmonids, including rainbow trout (Babey and Berry 1989), brown trout (Berg and Bremset 1998), kokanee salmon (Steinhart and Wurstbaugh 2003), Chinook salmon (Peters et al. 2007), and Atlantic salmon (Gardiner and Geddes 1980). Salmonids and other fishes with low lipid levels and high water content experience reduced survival during both warm (Hudy and Berry 1983; Babey and Berry 1989) and cold (Hutchings et al. 1999; Madenjian et al. 2000; Biro et al. 2004) water periods. In our study, rainbow trout body water content rapidly approached or exceeded 78% when fish were stocked preceding warm (spring) or coldwater (fall) periods or deprived of food under hatchery conditions. Year-round food limitations in First Bisby Lake likely supplant other factors, such as size and strain of stocked rainbow trout, which might otherwise influence survival in more productive lakes. Rainbow trout in a state of energy reserve depletion are more susceptible to predation and disease (Haddix and Budy 2005; Peters et al. 2007) which are additional factors that may have directly contributed to mortality and poor angling returns in First Bisby Lake.

Metrics of energy reserves and overall lipid content are generally more useful than morphological measurements for assessing overall fish condition (Hartman and Brandt 1995; Sutton et al. 2000; Ciancio et al. 2007). Our study confirms that Fulton's *K* and relative weight were not sufficient to detect the in-lake decline in energy reserves of rainbow trout that was evident when water content was measured (Copeland and Carline 2004; Trudel et al. 2005; Naesje et al. 2006). Fulton's *K* and relative weight were sufficient to detect differences between fed and food-deprived fish in the hatchery experiment where food deprivation was severe. However, in the field portion of this study, these measures were not sensitive to increasing water content corresponding to losses of lipid reserves. Our study shows that reliance on Fulton's *K* or relative weight measures in the field would have led to the conclusion that the condition of rainbow trout had not declined for rainbow trout stocked in First Bisby Lake in either spring or fall when, in fact, increasing water content signified a loss of lipids and a decline in energy reserves. The insensitivity of Fulton's *K* and relative weight to detect underlying changes in fish energy reserves in First Bisby Lake reaffirms the limitations associated with such measures.

Fishery managers interested in evaluating whether food limitation and energy reserve depletion are affecting survival and growth of stocked or wild fish populations should consider using fish tissue water content as an effective and easily obtained measure of energy reserves (e.g., lipid content). Water content measurements provide a cost-efficient proxy for managers to assess fish energy reserves. The major drawback of this technique is that fish must be sacrificed and processed in the laboratory to measure water content. New techniques like bioelectrical impedance analysis are becoming more widely used and offer the capability to reliably assess the energy reserves for larger numbers of fish in field settings without the need to sacrifice individuals (Pothoven et al. 2008).

Stocking rainbow trout in lakes and rivers with low productivity, coupled with the presence of competing fish species, is likely to result in poor survival and poor long-term return to anglers due to energy reserve depletion and ultimate mortality. Further, it is important to stock rainbow trout in good condition with low water content because fish with low energy reserves perform poorly after stocking (Babey and Berry 1989). Management practices such as stocking different sizes and strains of rainbow trout have a low probability of producing improved survival and return to anglers in food-limited systems. Given that stocked rainbow trout often exhibit poor survival, growth, and return to anglers in food-limited lake systems, the relative benefits of stocking these fish under such conditions are minimal.

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