

ENERGY ALLOCATION STRATEGY IN YOUNG FISH: ALLOMETRY AND SURVIVAL

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Abstract. We observed substantial variation in seasonal growth rates, autumn body size, and growing-season mortality among eight experimental cohorts of age-0 rainbow trout, *Oncorhynchus mykiss*. Wet mass, water, lipids (storage), and lipid-free dry mass (structure) had biphasic allometries with inflexions at ~10 cm in length. Dry:wet mass and storage:structure ratios were positively related to fish length, indicating that the relative quantities of these constituents change with body size. Lipid concentration varied according to a sigmoid relationship with wet mass which also had a growth-rate dependence. Independent assessments of the allometry of growing-season survival and winter metabolism facilitated assessment of the costs and benefits of two alternate energy allocation strategies of young fish. For cohorts with low growth rates and small autumn body size, a somatic growth rate maximization strategy is optimum, producing a 5% net survival advantage over an energy storage maximization strategy. For cohorts with intermediate growth rates and autumn mass, somatic growth and energy storage strategies lead to similar first-year survival. The fastest growing cohorts are estimated to have a net survival advantage of 7%, by adopting an energy storage maximization strategy over a growth rate maximization strategy.

Key words: allometry; energy allocation strategy; growth rate, fish; lipids; *Oncorhynchus mykiss*; rainbow trout; structure; trade-offs.

INTRODUCTION

Individuals and populations that live in seasonal environments must solve several problems to survive to reproduction. Some organisms (i.e., annual plants and many invertebrates), have life cycles timed to single annual cycles. Others live through multiple annual cycles. For this latter group, the primary determinant of success is survival to age-at-first-reproduction. In addition to seasonal variation in the environment itself, these organisms must cope with fluctuations in food supply and the often-substantial risk of predation associated with foraging, yet still accumulate sufficient energy stores for reproduction. These conflicting demands pose a constraint on an organism's ability to acquire, expend, and store energy, to survive to age-at-maturity, and to reproduce. The intensity of these conflicting demands, and apparent energy allocation strategies, have been explored for a number of taxa. By age-at-maturity, energy allocation to reproduction is a high priority for a wide variety of taxa, including planktonic rotifers, freshwater clams, reptiles, birds, and fish (Forsman and Lindell 1991, Rogers and Smith 1993, Jokela 1996, Jonsson and Jonsson 1997, Kirk 1997). For prereproductive organisms living in seasonal environments, there are tradeoffs between energy

allocation to growth, predation avoidance, and storage products for periods of resource scarcity. These have important fitness consequences, and are expected to have solutions that are unique locally, in response to the local intensity of selective environmental, resource, and predation pressures (Rogers and Smith 1993, Walters and Juanes 1993, Bull et al. 1996, Fullerton et al. 2000).

Temperate-zone fishes are ideal candidates for examining energy allocation strategies in the face of fitness-related selective pressures. Young fish are subjected to high rates of mortality that are related, in part, to risky behaviors involved in energy acquisition and to the allometry of energy metabolism during periods of resource scarcity. During the earliest larval life history stages, energy may limit morphological and physiological development because of the high energetic costs of mobility and somatic growth (Wieser 1991). During juvenile stages, energy acquisition limits somatic growth, and should therefore be inversely related to mortality if exposed to size-dependent and gape-limited piscivory (Tonn et al. 1992, Persson et al. 1996, Post et al. 1999). The first winter is usually a period of energy deficit for north-temperate fishes. Individuals or cohorts entering winter with enhanced energy stores are more likely to survive (Post and Evans 1989, Shuter and Post 1990, Johnson and Evans 1991, Schultz and Conover 1997). During the first growing season, juvenile north-temperate zone fishes face the competing

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TABLE 1. Morphometry of the experimental lakes in south-central British Columbia, Canada, the years that lipid data were collected, and initial densities of age-0 and older trout in the lakes.

Lake	Year	Physical characteristics			Initial density (trout/ha)	
		Surface area (ha)	Maximum depth (m)	Mean depth (m)	Age-0	Age-1
Crater Pothole 1	1991	4.2	20	10.0	9 940	86
Crater Pothole 2	1991	3.8	18	7.5	9 855	84
	1992				9 605	910
Crater Pothole 3	1992	3.3	18	9.3	10 758	296
Bluey Pothole 2	1992	1.4	6	2.8	1 016	802
Bluey Pothole 3	1992	1.4	6	NA	9 240	801
Cigar	1992	3.9	9	4.8	1 028	78
Smoke	1992	1.9	8	3.7	9 439	80

Note: There are data for Crater Pothole 2 Lake for both 1991 and 1992.

energy demands of maximizing somatic growth and energy storage. Under typical ecological and physiological conditions faced by north-temperate fishes, these energy allocation options have the potential to increase survival during the first year. Since energy availability is frequently limiting (i.e., it is common to see fish in the field growing at less than their physiological maximum rates given ambient temperatures), there is a conflict between these two allocation options. This conflict has important implications to first-year survival, and therefore, to overall fitness (Post et al. 1997, Walters and Juanes 1993, Conover and Schultz 1997). Similar conflicts in energy allocation have been observed for larger bodied, sexually mature fish, because energy is utilized for reproduction at the expense of somatic growth and energy storage (Booth and Keast 1986, Chelloppa et al. 1989, Meffe and Snelson 1993, Jonsson and Jonsson 1997).

These first-year selective pressures have strong allometries. A significant body of literature documents the common, but not exclusive, inverse relationship between body size or growth rate and survival in young fish (Tonn et al 1992, Persson et al. 1996, Post et al. 1999). This allometry implies that energy allocation to somatic growth during the growing season acts to increase growing-season survival. There is also substantial literature on the metabolic allometry and the body-size dependence of energy storage of juvenile north-temperate fishes (as reviewed in Shuter and Post 1990), implying that larger bodied individuals, and those with greater energy storage in a utilizable form (primarily lipids), have a greater likelihood of surviving periods of intense resource scarcity, such as northern temperate winters. This combination of selective pressures indicates that the conflict of demand over a limited energy supply, is strongest for the smallest fish in the youngest age classes.

Our goal was to experimentally analyze the resolution of energy allocation conflicts in cohorts of age-0 fish. We controlled for both genetic stock and potential environmental influences on energy allocation. At the same time, we ensured a substantial variation across

cohorts in available energy and growth rates, spanning the range typically observed in natural populations. To infer energy allocation strategy of age-0 fish *in situ*, we combined information on general metabolic allometry with empirical data on growth rates, mortality rates, and the allometry of body composition from experimental cohorts of age-0 rainbow trout.

MATERIALS AND METHODS

Field experiment

Our work is a component of a larger experimental assessment of the mechanisms involved in density-dependent growth, survival, and recruitment in size-structured and age-structured populations (see Post et al. 1998, 1999). The research involves assessments of exploitative and interference competition and predation in populations of rainbow trout that vary substantially in density and size structure. The assessments took place in 10 experimental lakes over a number of years. Multi-lake and multi-year population-level manipulations of density and size structure were involved. We have shown elsewhere (Post et al. 1999) that growth rates of trout in these experimental lakes are a function of several conditions, including density of their own age class, density of other age classes, and prey abundance. The strengths of these relationships suggest that there is little unexplained variance (<10%) remaining for lake and year effects (Post et al. 1999). This is not to say that there are no lake and year effects. Growth variation among lakes and years was dominated by ecological conditions that are included in the analysis. Our work involves a subset of eight lake-year combinations (Table 1), in which we also assessed the allometry of lipid and structural constituents in age-0 trout at the end of the growing season, prior to their first winter.

The experimental lakes are located in south-central British Columbia, Canada (49°50'–49°56' N, 120°33'–120°34' W). The lakes contained no fish prior to our experiments. They vary in size from 1.4 to 5.4 ha, with maximum and mean depths of 6 to 18 m, and 2.3 to

10 m, respectively. The lakes can generally be characterized as mesotrophic, with total phosphorus concentrations in the range of 15 to 30 $\mu\text{g/L}$ and total dissolved solids in the range of 300 to 500 mg/L .

Experimental populations were established through annual spring stocking of age-0 fish, and three non-overlapping size classes of age-1 fish raised from gametes collected annually from a wild population in Penask Lake, British Columbia, Canada. Although obviously of the same age, our three size classes of age-1 trout, raised in the hatchery, effectively represented the size structure of three age classes such as would be found in natural populations. Annual autumn gillnetting removed 40–70% of those fish that survived the growing season, resetting the conditions for the following year's treatment. Additional details of the methodology and mechanisms of density-dependent growth and mortality within these size-structured populations is reported in Post et al. (1998, 1999). The age-0 fish that are the subject of this study were stocked annually each spring, within seven days of yolk-sac absorption (ranging from 29 June to 11 July across years), at ~ 25 mm total length. As a function of the allocation of treatments in the larger scale experiment, age-0 fish in our experimental populations were subjected to densities of potential competitors and cannibals that varied among lakes and years (Table 1). The design involved two discrete levels of age-0 density that differed ~ 10 fold, and a graded range of older trout that was also ~ 10 fold. These treatments provide a wide range of growth conditions and predation risk, within which we examine energy allocation strategies of age-0 trout.

During the first two weeks of October, age-0 trout were captured from each lake for analysis, using fine-mesh gillnetting, over five successive days and nights. Floating and sinking nylon gillnets (stretched mesh sizes of 13, 16, 19, 25, 32, 38, 51, 64, 76 and 89 mm) were set in the littoral and pelagic zones at midday, and removed 18–24 h later. Captured fish were removed and nets reset. Captured fish were immediately put on ice, and were frozen within eight hours. Gillnet densities were standardized among lakes on an aerial basis, and ranged from 380–580 $\text{m}^2\cdot\text{ha}^{-1}\cdot\text{night}^{-1}$. We corrected for size-dependent vulnerability in all catch and size data from gillnets. Random subsamples of at least 500 age-0 rainbow trout per lake-year were measured for length (± 0.5 mm) and wet mass (± 0.05 g). Daily instantaneous growth rates were calculated from geometric mean mass at stocking, and from the size vulnerability adjusted geometric mean mass of trout caught in October. Daily instantaneous mortality rates were calculated from stocking density in the spring and autumn population estimates based on size-dependent vulnerability and total catches during the October gillnetting. Additional description of the lake environments, experimental design, field sampling, and growth

and mortality estimation are available in Post et al. (1999).

Lipid extraction

Random subsamples of 30 age-0 trout captured in each lake-year treatment were frozen for lipid analysis. In the laboratory, individual fish were thawed, measured, weighed, and dried at 50°C for 96 h. The dried carcass was then reweighed before being ground with a mortar and pestle. Lipids were extracted using the methanol and chloroform procedure detailed in Folch and Stanley (1957). This process involved measuring 0.5 ± 0.0001 g of powdered fish into a test tube, adding 16 mL of a 50:50 methanol-chloroform solution, and then heating the mixture in a water bath set at 61°C until it boiled. Upon removal from the water bath, the mixture was cooled to room temperature, then brought to 25 mL by adding chloroform. The solution was filtered through a No. 1 Whatman filter paper (Whatman Incorporated, Clifton, New Jersey) into a separatory funnel. After the addition of 10 mL of 9% saline solution, the mixture was shaken vigorously. The addition of the saline solution removed impurities from the mixture, leaving pure lipid in the methanol-chloroform layer to settle to the bottom of the funnel. The bottom layer was drained into a preweighed beaker, then evaporated to dryness on a hot plate at 70°C. The beaker was cooled to room temperature and weighted to the nearest 0.0001 g. The mass of lipid remaining in the beaker represented the mass of lipid per 0.5 g of dry fish tissue.

We ran a series of trials to determine the analytical error in the lipid determination technique. To do so, we selected three trout large enough to yield dry material for 9–10 independent analyses per fish. Extractions were run on these 30 subsamples. The coefficients of variation for the three fish ($n = 10, 9, 10$) were 6.09%, 5.95%, and 3.81% for a mean cv of 5.28%. This measurement error represents the combination of subsampling error associated with the random selection of 0.5 g dry material from the total dry material per fish, and the error associated with the extraction and weighing process itself.

Allometric analysis

The allometry of wet mass and of its constituents (water, lipids, and lipid-free dry mass) was determined using a nonlinear fitting algorithm that (in addition to providing best fit slopes, intercepts, and associated confidence intervals), tests the hypothesis that the data is best represented by two rather than a single linear segment (Wilkinson 1990, Neter et al. 1996; and for an application, see Post and Lee 1996). This nonlinear piecewise regression was implemented in SYSTAT (Wilkinson 1990). If it is demonstrated that two linear segments fit the data significantly better than a single linear segment, then the analysis provides the best fit estimates of the slopes and intercept plus the value of

the independent variable that best defines the inflexion in the biphasic relationship (and associated confidence intervals). This method, therefore, provides an objective assessment of the adequacy of a single linear relationship not provided by a visual inspection of the data of the residual pattern. The nonlinear piecewise regression model fitted to the data was

$$Y = \begin{cases} b_0 + b_1X & \text{if } X \leq \text{BREAK} \\ b_0 + b_1X + b_2(X - \text{BREAK}) & \text{if } X > \text{BREAK} \end{cases}$$

where Y is log mass in g (of wet mass, or one of its constituents), X is log length of the fish (log cm), b_0 is the intercept of the first segment (log g), b_1 is the slope of the first segment, b_2 is the difference in slope between the first and second segments, and BREAK (log cm) is the inflection between the first and second segments. The slope of the second segment is calculated as $b_1 + b_2$. Confidence intervals (95%) are reported for each fitted parameter.

The following two allometric hypotheses were tested ($P < 0.05$) using this model

$$\text{Hypothesis 1} \quad H_0: b_1 = 3.0$$

$$\text{Hypothesis 2} \quad H_0: b_2 = 0.$$

Hypothesis 1 tests whether the mass allometry is isometric. Hypothesis 2 tests whether a single log-log linear relationship best represents the data. If Hypothesis 2 is rejected, then the parameter BREAK is interpreted as the log length at which there is a significant change in scaling from that of segment 1 for small fish to segment 2 for larger fish.

It has been argued that allometry should be examined using a Model II (also called geometric mean, functional, or reduced major axis) regression, rather than the Model I regression more typically used in biological data analysis (Ricker 1975, Giguere et al. 1988, Schultz and Conover 1997). The difference in slope estimates between Model I and II regressions is typically small in allometric relationships, because residual sums of squares are typically small (Jensen 1986). We report Model I regression coefficients here, because the nonlinear fitting algorithm that we used for the segmented regressions minimized sums of squares in the dependent variable, as in the Model I regressions procedure. This technique allows an objective assessment of Hypothesis 2, and if Hypothesis 2 is rejected, provides an estimate (with confidence interval) of the fish length at inflexion. Neither of these assessments are possible if we used a Model II algorithm.

The allometries of dry:wet mass and storage:structure ratio were also examined. It was assumed that total lipids extracted represent storage, and that lipid-free dry mass (primarily proteins and calcareous matter) represent structural components.

Assessment of the costs and benefits of alternate energy allocation strategies

The costs and benefits in terms of growth and survival were estimated from observed lipid density for

two extreme energy allocation strategies: (1) all energy in excess of a baseline lipid density is allocated to soma production (i.e., growth maximization), and (2) all energy available is allocated to lipid storage, up to an asymptotic lipid concentration. Baseline and asymptotic lipid concentration were estimated by fitting a sigmoid relationship to lipid concentration and wet mass for all individuals from all lake-year combinations. Potential growth rate and autumn mass, under each of these two extreme strategies, were estimated assuming that lipids are twofold the energy content of proteins (Brett and Groves 1979), and that somatic tissues are 75% water. These calculations were performed for the mean wet mass and mean lipid concentration observed for each of the eight experimental cohorts. Therefore, the resultant data set is comprised of: (1) the mean observed mass and seasonal growth rate for each cohort, (2) a predicted mean mass and growth rate, if the energy allocation strategy involved maximizing somatic growth, and (3) a predicted mean mass if the energy allocation strategy involved maximizing lipid concentration. The survival implications of the two alternate strategies, from stocking to autumn, were assessed using a regression relationship modified from that presented by Post et al. (1999). A function relating mortality to growth rate was developed using data for 15 cohorts of age-0 rainbow trout, from experiments conducted in 1991, 1992 and 1993, including those eight cohorts assessed for lipids in this study

$$\text{MORT} = 76.19 \times e^{-0.9888 \times \text{GROW}}$$

($n = 15$, $r^2 = 0.55$), where MORT and GROW are the mean mortality (percentage per day) and growth (percentage per day) for each cohort. Estimates of the change in survival, due to adoption of either extreme energy allocation strategy, is related to survival predicted for the observed seasonal growth rate.

Due to a reduction in growth rate, allocation of energy to lipid storage has a cost to growing-season survival, yet it confers longer term benefit because it increases the energy available during winter when trout experience an energy deficit. This energy deficit can be offset by mobilizing stored lipid energy. This mechanism has not been clearly established specifically for rainbow trout, but it is a common phenomena for many north-temperate fishes examined (Shuter and Post 1990). Salmonids such as sockeye salmon, *O. nerka*, lose mass over the winter (Eggers 1978). We assume that the rate of energy use over winter is proportional to $\text{MASS}^{2/3}$ (Shuter and Post 1990). The benefit of storing lipids is estimated as the quantity of lipids stored by autumn, divided by the rate at which lipids are mobilized over winter (which is size-dependent, as above). This estimate is proportional to time to starvation, or endurance time, and has been calculated for a variety of temperate freshwater vertebrate and invertebrate species (as reviewed in Shuter and Post 1990).

TABLE 2. Sample sizes, length (standard deviations and ranges), mass (standard deviations and ranges) at the end of the growing season, and seasonal growth rate estimates for eight cohorts of age-0 rainbow trout in the experimental lakes.

Lake	Year	n	Fork length (mm)		Mass (g)		Mass growth rate (%/d)
			Mean (1 SD)	Range	Mean (1 SD)	Range	
Crater Pothole 1	1991	474	117 (12)	79–156	18.5 (5.9)	4.5–43.6	4.32
Crater Pothole 2	1991	967	120 (14)	79–164	20.5 (8.0)	5.9–50.9	4.26
	1992	291	83 (10)	52–110	6.7 (2.2)	1.8–14.9	3.21
Crater Pothole 3	1992	287	89 (11)	54–120	8.2 (2.8)	2.0–18.1	3.22
Bluey Pothole 2	1992	68	112 (11)	87–137	15.8 (4.6)	7.3–30.3	3.87
Bluey Pothole 3	1992	88	106 (11)	87–131	13.4 (4.2)	7.3–24.3	3.73
Cigar	1992	157	132 (15)	101–167	28.7 (10.2)	11.9–56.2	4.40
Smoke	1992	89	114 (16)	88–147	17.7 (7.9)	8.0–38.1	3.94

Note: There are data for Crater Pothole 2 Lake for both 1991 and 1992.

RESULTS

Allometry of storage and structure

Substantial variation in autumn size and seasonal growth rates of age-0 rainbow trout was observed within and among the experimental populations (Table 2). Variation in autumn fork length, and mass among individuals within lakes, ranged from 1.5–2 fold and from 3–10 fold respectively. Variation in autumn fork length, mass, and growth rate among lakes was 1.6, 4, and 1.4 fold, respectively. This magnitude of variation in size

and growth rate of age-0 trout observed in our eight experimental populations, covers the range we observed within a larger data set of 26 yr classes (Post et al. 1999), and was also observed in natural rainbow trout populations in southern British Columbia (J. R. Post, unpublished data).

Examination of the allometry of total wet mass and of its constituents—water, lipid-free dry mass (structure), and lipids (storage)—show biphasic patterns (Table 3, Fig. 1). Total wet mass was isometric for lengths less than ~10 cm. At this size, the slope increased

TABLE 3. Results from the piecewise regression of the allometry of: (A) body constituents and (B) ratios of dry:wet mass and storage:structure on length of age-0 rainbow trout from eight cohorts at the end of the growing season.

Dependent variable (log units)	Intercept (log g) (b_0)	Segment 1 slope (b_1)	Change in slope (b_2)	Segment 2 slope (calculated; percentage change in parentheses)	Inflection (log length) (BREAK)	R^2
A) Body constituents						
Wet mass	-1.823 (-2.097, -1.549)	2.903 (2.606, 3.199)	0.375‡ (0.034, 0.717)	3.278 (+12.9%)	0.944 ^a (0.923, 0.966)	0.97
Water	-1.780 (-2.019, -1.542)	2.742‡ (2.486, 2.998)	0.411‡ (0.100, 0.721)	3.153 (+15.0%)	0.954 ^a (0.942, 0.966)	0.97
Lipid-free dry mass	-3.464 (-3.621, 3.306)	3.933‡ (3.771, 4.094)	-0.352§ (-0.680, -0.023)	3.581 (-8.9%)	1.029 ^b (1.010, 1.049)	0.97
Lipid	-5.292 (-5.642, -4.943)	5.095‡ (4.735, 5.455)	-1.006§ (-1.746, -0.265)	4.089 (-19.7%)	1.031 ^b (0.982, 1.080)	0.91
B) Ratios						
Dry:wet mass	0.068 (0.036, 0.101)	0.018 (0.014, 0.021)	-0.011§ (-0.015, 0.007)	0.009 (-61%)	10.027 (9.391, 10.664)	0.64
Storage:structure	-0.038 (-0.085, 0.009)	0.026 (0.021, 0.031)	-0.016§ (-0.025, -0.008)	0.010 (-62%)	10.700 (10.364, 11.036)	0.48

Notes: The estimates of the intercept and slope of the first segment of the regression, the change in slope from the first to second segment, the slope of the second segment (calculated by addition of the slope of the first segment and the change in slope from the first to second segment with percentage change in parentheses), the length at inflection, and the explained variation in the dependent variable are indicated. Confidence intervals are given in parentheses below the estimates. The slopes of segment 1 were assessed for significant deviation from isometry for each body constituent. A change in slope from segment 1 to segment 2 was assessed for significant deviation from zero for each body constituent and ratio. The results of an a posteriori contrast of the inflection points for body constituents is reported. BREAK is the parameter in the model that is fitted to determine the inflection point. Values of BREAK followed by different superscript letters are significantly different from one another.

‡ The exponent is significantly different than isometry ($P < 0.05$).

‡ Significant ($P < 0.05$) increase in slope from phase 1 to phase 2.

§ Significant ($P < 0.05$) decrease in slope from phase 1 to phase 2.

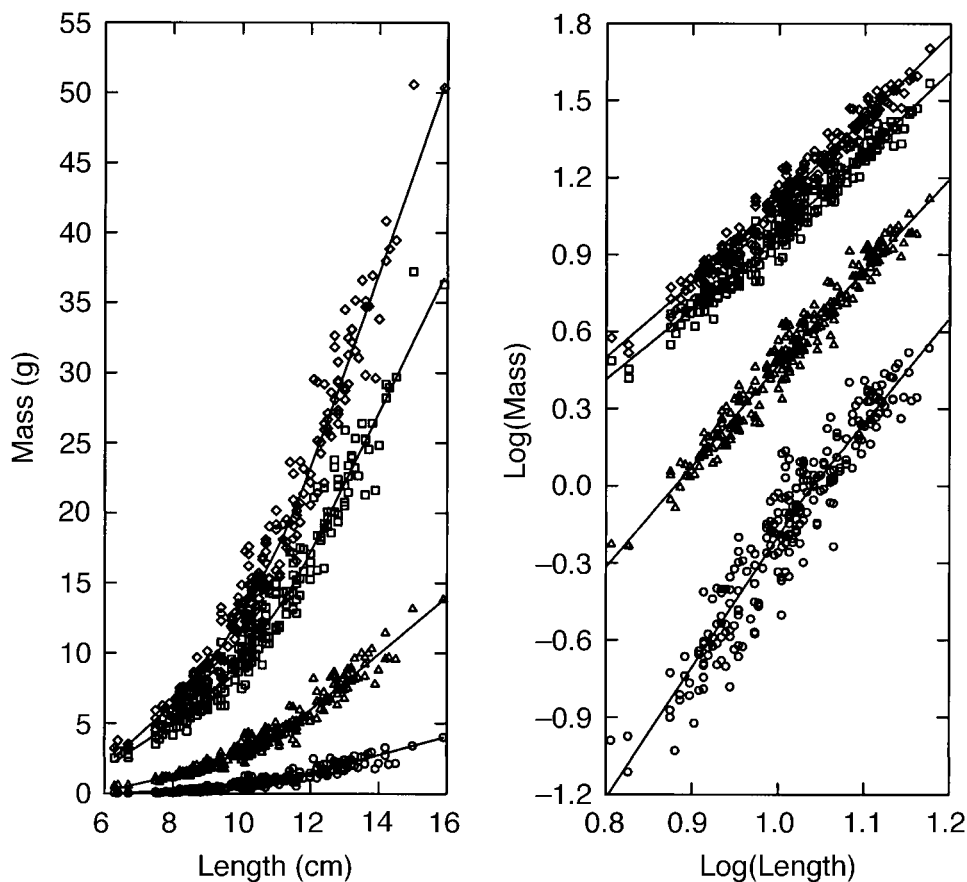


FIG. 1. The allometric relationships between fork length and total wet mass (diamonds), water mass (squares), lipid-free dry mass (triangles), and lipid mass (circles) are shown on arithmetic and log-log axes. The fitted piecewise regression curves are indicated, and coefficients are reported in Table 3.

significantly to hyperallometry. This same allometry is reflected in water content. In contrast, lipid-free dry matter and lipids were hyperallometric at lengths less than ~10 cm, and became significantly less hyperallometric at greater lengths. For fish <10 cm, the rate at which constituents are acquired as a function of increases in length was highest for lipids, intermediate for soma, and lowest for water. At larger body sizes, the rate of increase of lipids and soma as a function of increasing length decreased from the rate observed for smaller fish. The rate of water accumulation increased.

Dry:wet mass and storage:structure ratios are both positively related to fish length, and both show significant biphasic patterns (Table 3, Fig. 2). Small age-0 trout increase in dry:wet mass and storage:structure ratios with length at a higher rate than do larger individuals. There are significant changes in the relationships at the inflexion of 10–11 cm. The dry:wet mass and storage:structure ratios increase from means of ~0.20 to 0.30 and ~0.15 to 0.30, respectively, over the range in fish sizes we observed in the experimental lakes in autumn.

In the autumn, lipid concentration of age-0 rainbow

trout varied nonlinearly with the mass of individual fish (Fig. 3). We fitted a sigmoid curve to these data

$$\text{LIPID} = \min + (\max - \min) \times [W^b / (k^b + W^b)]$$

($n = 240$, $R_2 = 0.64$), where LIPID is the percentage of lipids in an individual fish of wet mass W in grams, min is the minimum percentage of lipids, max is the asymptotic lipid content of large fish, k is the mass at which LIPID is halfway between min and max, and b is a parameter that determines the steepness of the curve near k . The least squares estimates (and asymptotic standard errors) are: min is 2.27% lipid (0.59), max is 7.4% lipid (0.863), k is 11.49 g (1.15), and b is 2.32 (0.57). When residuals from this curve are plotted for individual lakes, the slope estimates are consistently negative (Fig. 4), but only five of eight lakes have slopes that are significantly less than zero ($P < 0.05$). The relationship between mean mass of fish in each of the eight cohorts and the slope of the residuals for each cohort, has a slope that is negative ($P < 0.01$). There is no obvious pattern when the residuals from all lakes are grouped in a single analysis. Lakes with the slowest growth rates have the largest negative

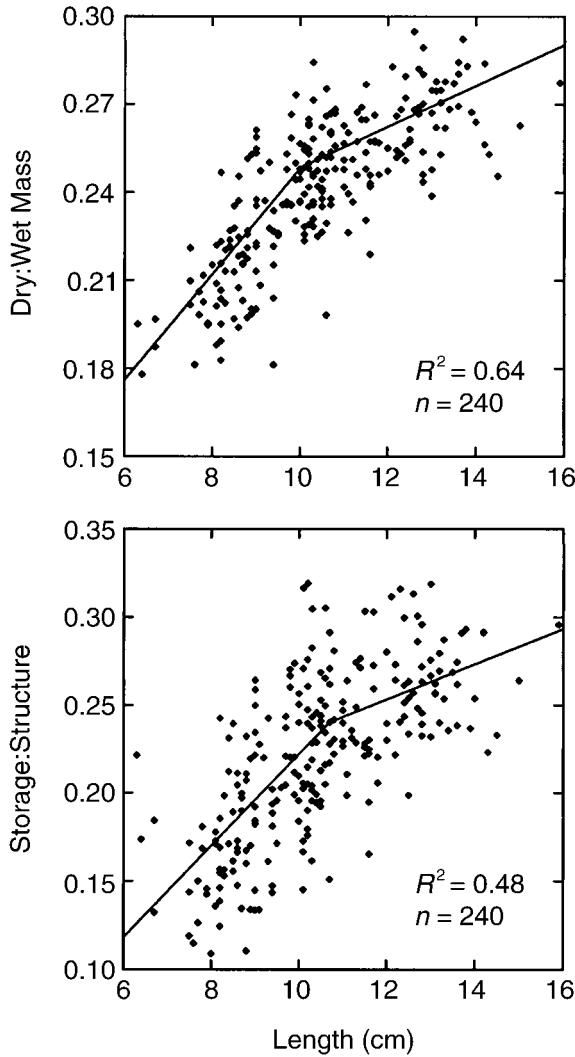


FIG. 2. The relationships between the percentage dry:wet mass and storage:structure ratios (mass of lipid per mass of lipid-free dry mass) and fork length of age-0 rainbow trout. The fitted piecewise regression curves are indicated, and coefficients are reported in Table 3.

slopes ($P < 0.01$). This pattern of residuals suggests that the sigmoid curve is actually a family of curves, rather than a single curve. The differences among lakes are due to the fact that fish from a slower growth lake tend to have a lower lipid content than fish of the same size from a faster growth lake.

This family of curves cannot be generated by fitting different curves to the empirical data from individual lakes, because the size range within most lakes is not wide enough to generate good estimates of all four parameters for the sigmoid model. Instead, we assumed that all lakes had the same values for min, max, and b , and that the differences among lakes were due to differences in the half value, k , which is a function of lake-specific mean growth rates (G_m). If the relationship between k and G_m is log-linear, and min and max

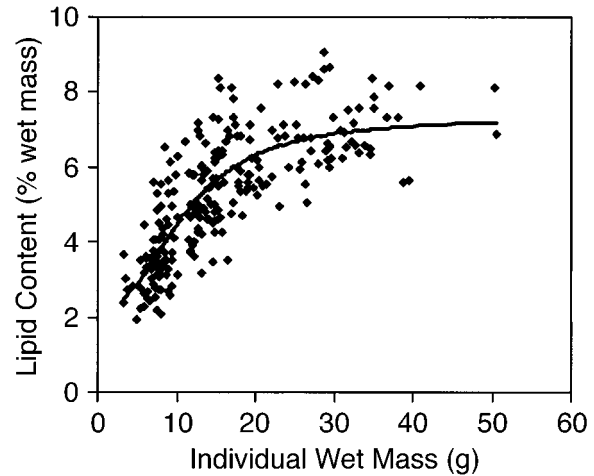


FIG. 3. The relationship between lipid concentration as a percentage of wet mass and individual wet mass for age-0 rainbow trout. A sigmoid curve is fitted to the data using least squares.

have been established in the common curve, the simple sigmoid curve can be reparameterized to incorporate the growth-rate dependence of lipid concentration by

$$\text{LIPID} = 2.13 + 5.06 \times (W^b / \{[a \times \ln(G_m) + c]^b + W^b\})$$

$$n = 240, \quad R^2 = 0.71$$

where a and c are additional constants, describing the growth-rate dependence. This curve can be fitted to the empirical data using a minimum least squares. The resulting estimates for b , a and c (with asymptotic standard errors) are 1.629 (0.154), -31.975 (5.416), and 54.122 (7.359). These parameter values produce a family of curves where lipid content of individual fish is a function of the individual fish mass and the average

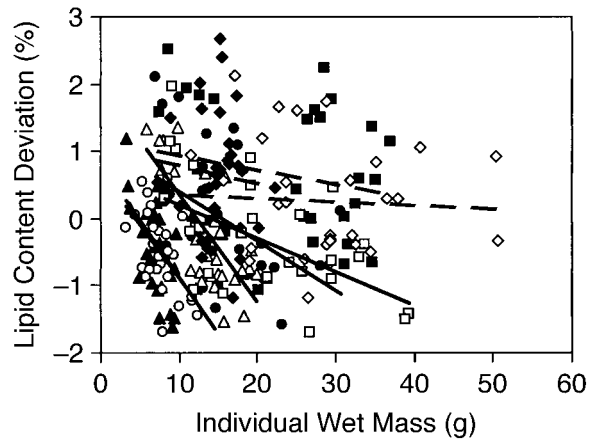


FIG. 4. Residual lipid concentrations from the sigmoid curve plotted in Fig. 3. Data from each cohort are plotted with different symbols, and linear regressions are fitted to the data for each cohort (solid lines represent significant negative slopes; dashed lines represent nonsignificant negative slopes).

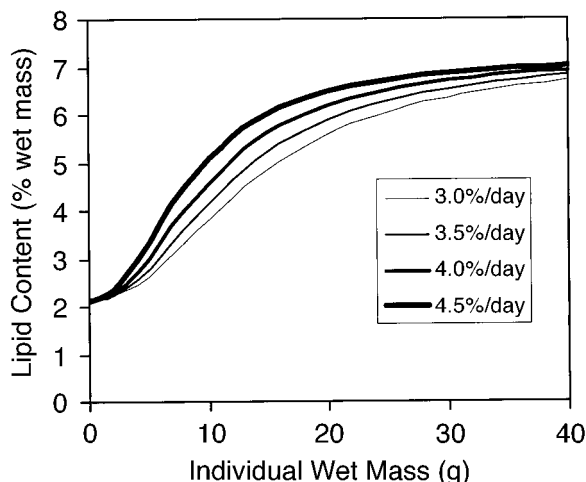


FIG. 5. The predicted relationship between lipid concentration as a percentage of wet mass and individual wet mass for age-0 rainbow trout, using the sigmoid model with growth-rate dependence. Growth rates that encompass the range that we observed among the eight experimental cohorts of age-0 trout are shown.

growth rate in the lake. Although the explained variance for the new model increased only modestly, the significance of the residual patterns in Fig. 3 suggests that effect of growth rate is important. This small improvement is likely due to the fact that the new curves are the same as the common curve, except for a relatively small region around k . This relationship indicates that k is large (~ 13 g) in lakes with the slowest average growth (i.e., even the largest fish have low lipid content) and decreases to a minimum of ~ 7 g in lakes with the highest observed growth rates (Fig. 5).

Survival gains and losses under alternative energy allocation strategies

Mortality of trout during their first summer is related to growth rate (Post et al. 1999). We used a subset of their data, collected in the same years as our lipid data, and assumed that mortality was proportional to the logarithm of growth rate. Our conclusions are insensitive to the exact form of this relationship; any curve that approaches zero mortality at high growth rates will produce similar results. Figs. 3 and 4 suggest that individuals switch between two alternative strategies, with small, slow-growing fish maximizing somatic growth, and large, fast-growing fish maximizing lipid storage. Therefore, we can estimate the gains and losses in survival that would occur if all fish in each lake followed one or the other strategy throughout their first growing season.

Under the somatic growth maximization scenario, estimated gains in growing-season survival were largest in the lakes with highest growth (Fig. 6), but the differences among lakes were relatively minor. The benefit for the group with the highest growth rate was

a 1.30-fold increase in survival. This is only slightly greater than the 1.26-fold increase in survival estimated for the group with the lowest growth rate. Fish in low-growth lakes had little excess lipid that could be reallocated to somatic growth. This resulted in modest increases in size, and therefore, in survival, under a growth-maximization strategy. Fish in lakes with high growth rates had large amount of lipids that, when reallocated to somatic growth, resulted in large estimated increases in size. This large increase in size, however, failed to produce substantial estimated gains in survival, since survival of these fish was already high.

Under a lipid maximization scenario, estimated losses in growing-season survival were largest in lakes with slow growth (Fig. 6), and the differences were relatively large. Fish in lakes with fast growth rates were already close to maximum lipid storage, and were only slightly smaller when all fish in these groups were assumed to maximize lipid content. In contrast, many fish in slow-growth lakes had low lipid content. As a result, their estimated somatic growth under the lipid-maximization strategy was much slower. Because of the negative logarithmic relationship between growth and survival, this slower growth led to relatively large projected losses in terms of growing-season survival.

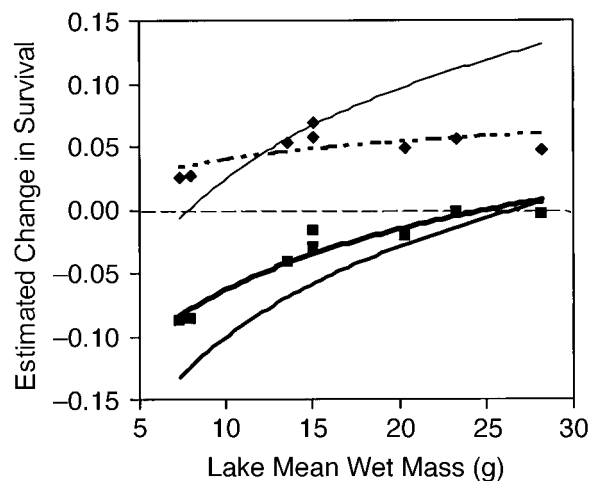


FIG. 6. Estimated changes in survival of age-0 rainbow trout under alternate energy allocation strategies. Survival change during the growing season under a somatic growth rate maximization scenario is represented for each experimental cohort at observed mean wet mass in the autumn (diamonds for each cohort and dashed line). Survival change during the growing season under an energy storage maximization scenario is represented for each experimental cohort at observed mean wet mass in the autumn (squares for each cohort and heavy solid line). Survival change during the growing season and winter under an energy storage maximization scenario is discounted for metabolic allometry, assuming no future benefit of energy storage (medium solid line). Survival change during the first year of life under an energy storage maximization scenario assumes that there is a benefit of energy storage for winter survival and that there is a switch in allocation strategy at wet mass k (fine solid line).

This difference is accentuated by the allometry of metabolism. Metabolic rates are higher in small fish. A higher proportion of lipid is necessary to achieve the same benefit in smaller fish, in terms of resistance to starvation during times of food shortage. By assuming that all fish need to store the same energy supply, in terms of days to starvation death the effect of the allometry of metabolism can be included as an additional cost in the lipid-maximization scenario (Fig. 6).

Lipid storage may result in losses in somatic growth, and therefore, in survival during the growth period, but stored energy can be beneficial during winter. If these fish follow an optimal energy allocation strategy, this benefit can be estimated by determining the point at which individuals switch from a somatic growth maximization strategy to a lipid maximization strategy. For the common curve, k is the point halfway between maximum and minimum lipid content. If this is the point where a lipid-maximization strategy becomes more beneficial than a growth-maximization strategy, then the two curves in Fig. 6 should cross at this point. The future benefit of lipid storage can be estimated from the additional survival benefit that is necessary to force the lipid-maximization curve through the somatic growth-maximization curve at this point. This analysis of survival advantages of adopting one extreme strategy or the other suggests that the benefits are strongly size dependent, whether for the first growing season or for the winter. For trout from the lake where we observed the lowest growth rate, a somatic growth maximization strategy would produce a survival benefit of ~5% over a lipid storage maximization strategy. For individuals in lakes where growth was intermediate, with a mean autumn mass of ~10 g wet mass, both energy allocation strategies would result in approximately equal survival. For fish in lakes where seasonal growth was the highest observed, over the combination of the growing season and winter, the lipid-maximization strategy had an estimated survival advantage of ~7%.

DISCUSSION

Small-bodied animals are faced with strong competing demands for surplus energy. Ecological and metabolic allometry demonstrate that small organisms have the highest rates of food consumption, growth, respiration, and starvation. In addition, small fish are the prey base on which piscivorous food webs depend. Therefore, individuals or cohorts that grow fast minimize the time that they are susceptible to gape-limited and size-dependent predators. Individuals or cohorts that maximize energy storage in the form of utilizable lipids reduce their susceptibility to starvation, which can be acute in north-temperate fishes during winter. Therefore, there are competing demands for consumed energy to grow rapidly and to accumulate energy stores in an effort to maximize fitness. The resolution of this conflict can be observed in the allometry of proximate

composition. Below a size of ~10 cm, age-0 trout grow isometrically and have a high water content, but are differentially accumulating lipid energy and structure faster than water. At ~10 cm, a distinct shift takes place. Growth is now allometric, with wet mass accumulating faster than length. Lipid energy is still being accumulated more quickly than other constituents, but a greater proportion goes into structural components as indicated by a reduced rate of increase in storage:structure ratios as a function of length.

The importance of competing demands for energy storage and somatic growth to age-0 trout can be inferred from our data. Fish with the highest growth rates had lipid contents of up to 9% by mass. This represents ~40% of the total energy content of these fish. This indicates that lipid storage is a major component of the energy budget and is likely of importance to age-0 rainbow trout. In contrast, lipid content in trout with the slowest growth rates was as low as 2%. This is close to the minimum lipid content of fish undergoing starvation (Newsome and Leduc 1975, Oliver et al. 1979, Gardiner and Geddes 1980, Toney and Coble 1980, Henderson et al. 1988). However, even the slowest growing fish in our experiments were growing at rates >3% per day. Clearly these fish have energy-acquisition rates that are well above maintenance metabolic requirements, but have channeled that energy preferentially into somatic growth rather than into storage.

We can draw inferences about energy allocation strategies in age-0 trout using our quantitative descriptions of storage and structure allometry, coupled with independent estimates of the growth-rate dependence of growing-season mortality and the metabolic allometry of winter energy utilization. For cohorts with low growth rates and small autumn body size, a somatic growth rate maximization strategy is optimal, producing an ~5% net survival advantage over an energy storage maximization strategy. This outcome is logical, since somatic growth should be a high priority for small, slow-growing fish, since their mortality rates are high and relatively small increments in growth rate result in substantial survival benefits over the course of a growing season. For cohorts with intermediate growth rates and an autumn mass of ~10 g wet, somatic growth and energy storage strategies lead to approximately the same first-year survival. The fastest growing cohorts that we observed are estimated to have a net survival advantage of ~7% by adopting an energy storage maximization strategy over a growth rate maximization strategy. As demonstrated by the allometry of body constituents, mortality, and metabolism, these relationships are strongly nonlinear. Across ranges of body sizes for small and particularly for large fish, energy storage concentration is relatively invariant. Conversely, trout of intermediate body sizes show a rapid increase in storage energy concentration over relatively narrow ranges of body size, with a distinct

switch point as identified in the log–log piecewise and nonlinear sigmoid regression models.

Our analysis involving the coupling of the allometry of storage and structure with the allometry of growing-season mortality and winter energy utilization, is unique. However, our inferences of energy allocation strategies are likely general for other species of north-temperate fishes. For example, age-0 Atlantic silversides (*Menidia menidia*) had size-dependent lipid concentrations similar to what we saw in age-0 trout (Schultz and Conover 1997). In addition, observations of increasing lipid concentrations from summer to autumn is common among temperate fishes (Booth and Keast 1986, Griffiths and Kirkwood 1995, Schultz and Conover 1997). This is likely an adaptive response to a strong selective pressure to acquire sufficient energy stores to enable the fish to survive winter energy deficits. Body-size dependent and growth-rate dependent growing-season mortality is also a common observation in cohorts of young fish (Tonn et al. 1994, Post et al. 1997, 1999), and somatic growth rate maximization should increase survival during the growing season (Ebenman and Persson 1988, Miller et al. 1988, Walters and Juanes 1993). Body-size dependent overwinter starvation mortality also appears to be a common phenomena in age-0 cohorts of north-temperate fishes (Shuter et al. 1980, Post and Evans 1989, Schultz and Conover 1997). The ability to survive a period of resource scarcity, such as the winter, is based on accumulated energy stores and the rate at which they are utilized metabolically (Shuter and Post 1990). Therefore, the strong selective pressure to grow fast and survive the growing season in the face of substantial piscivory, competes with the selective pressure to accumulate energy reserves to survive periods of winter food scarcity. These competing pressures are probably important for young fish across taxa. Given these observations, the phenotypic variation in energy allocation strategy that we observed as a function of autumn body size and growth rate for age-0 rainbow trout are likely to be general across species of north-temperate fishes.

If the allometry of lipid and somatic tissues we observed in a single genetic stock of rainbow trout is adaptive, we would expect that other genetic stocks may have different solutions to the competing forces of energy allocation to soma and storage (Schultz and Conover 1997, Fullerton et al. 2000). A body-size dependent and growth-rate dependent switch in strategies may be absent when one or the other of these competing forces dominates mortality during the first year of life. In many other situations, however, both forces are likely important contributors to first-year mortality, and a switch from a somatic growth to a lipid maximization would be predicted. We would predict that populations exposed to more extreme winter conditions would have relatively greater selective pressure for lipid accumulation, and that lipid allometry would be more hyper-

allometric, with a lower inflection point, compared to populations that have adapted to less severe winter conditions. This is the general allometric pattern observed over a latitudinal gradient for Atlantic silversides (Schultz and Conover 1997), although they did not examine for evidence of within population biphasic lipid storage allometry. It is unclear if differential levels of size-dependent, gape-limited piscivory would lead to the evolution of energy allocation strategies across populations. What is clear, is that lipid concentration in young fish during the growing season, when piscivory is likely most intense, tends to be low, increasing as winter approaches. This is consistent with the inference that seasonal energy allocation is sensitive to seasonal patterns in size and growth-rate dependent intensity of piscivory. The observations and experiments to critically assess these hypotheses have not yet been conducted.

Analysis of the allometry of energy allocation and growth-rate dependent mortality is incomplete unless all body constituents are considered. Our understanding of the prey-size dependence of piscivory is based on length and wet mass of the prey and predators. Our analysis demonstrated that a significant positive relationship exists between size of age-0 trout and the proportion of wet mass made up of dry material (storage plus structural components). The smallest trout that we observed in the autumn had dry:wet mass ratios of ~60% of those of the largest bodied trout of the same age. This inverse relationship between lipid and water content is commonly seen in fish, and leads to an interesting speculation that this may be adaptive in small fish because increased water content increases overall body size. This may, therefore, decrease susceptibility to size-dependent and gape-limited predators at no energetic cost.

The growth-rate dependence of the switch point from somatic to storage maximization strategies, as indicated by the residuals of the general sigmoid model, is interesting and somewhat perplexing. Despite originating from the same genotype, individuals in a lake that on average provided higher growth rate conditions, appeared to switch from somatic to lipid maximization at smaller sizes. This appears counterintuitive. If high growth-rate conditions are predictable, an optimal solution should be to maximize somatic growth and reduce mortality losses to predation, and therefore, switch later to energy storage. One potential explanation of this inconsistency involves the derivation of the empirical relationship that we used as a description of the growth-rate dependence of growing-season mortality (Post et al. 1999). The regression model was developed for cohorts of age-0 trout exposed to a range of food and predation conditions. Walters and Juanes (1993) argue that there should be strong selection for genotypes that, through behavior, vary exposure to risk of predation with prey availability, such that growth rate and energy stores are sufficient for surviving the

winter to subsequent reproduction. In this context, the average relationship that we used to characterize growth-rate dependent mortality during growth season, is likely a family of curves involving higher risk-taking (and hence, higher mortality) when growth conditions are poor, and lower risk-taking (and lower mortality) when growth conditions are favorable. Therefore, when growth conditions are good, it may be reasonable to suggest an earlier switch to an energy storage maximization strategy, if the growth-rate dependent selective pressure is less intense than we assume, since risk-taking to consume food and grow quickly is unnecessary to ensure a high likelihood of survival. We plan to explore this hypothesis further empirically and theoretically.

The energy allocation patterns and processes that we observed in juvenile trout may also be general for other organisms that are exposed to size-dependent and gape-limited predation in a seasonally harsh, energy-limited environment. The selective processes imposed by predation and the allometry of metabolism during periods of resource scarcity, create tradeoffs associated with alternate energy allocation strategies that would be expected to vary phenotypically and/or genotypically in north-temperate organisms. It is, therefore, necessary to understand the form and intensity of these selective pressures, in order to understand empirical patterns in the allocation of energy to storage and structural components as a function of body size and ontogeny.

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