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ARTICLE

Comparative Bioenergetics Modeling of Two Lake Trout Morphotypes

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Abstract

Efforts to restore Lake Trout *Salvelinus namaycush* in the Laurentian Great Lakes have been hampered for decades by several factors, including overfishing and invasive species (e.g., parasitism by Sea Lampreys *Petromyzon marinus* and reproductive deficiencies associated with consumption of Alewives *Alosa pseudoharengus*). Restoration efforts are complicated by the presence of multiple body forms (i.e., morphotypes) of Lake Trout that differ in habitat utilization, prey consumption, lipid storage, and spawning preferences. Bioenergetics models constitute one tool that is used to help inform management and restoration decisions; however, bioenergetic differences among morphotypes have not been evaluated. The goal of this research was to investigate bioenergetic differences between two actively stocked morphotypes: lean and humper Lake Trout. We measured consumption and respiration rates across a wide range of temperatures (4–22°C) and size-classes (5–100 g) to develop bioenergetics models for juvenile Lake Trout. Bayesian estimation was used so that uncertainty could be propagated through final growth predictions. Differences between morphotypes were minimal, but when present, the differences were temperature and weight dependent. Basal respiration did not differ between morphotypes at any temperature or size-class. When growth and consumption differed between morphotypes, the differences were not consistent across the size ranges tested. Management scenarios utilizing the temperatures presently found in the Great Lakes (e.g., predicted growth at an average temperature of 11.7°C and 14.4°C during a 30-d period) demonstrated no difference in growth between the two morphotypes. Due to a lack of consistent differences between lean and humper Lake Trout, we developed a model that combined data from both morphotypes. The combined model yielded results similar to those of the morphotype-specific models, suggesting that accounting for morphotype differences may not be necessary in bioenergetics modeling of lean and humper Lake Trout.

Lake Trout *Salvelinus namaycush* are coldwater, deep-dwelling apex predators that are native to North America, including the Laurentian Great Lakes region (McDermid et al. 2007). During the late 19th and early 20th centuries, Lake Trout populations throughout the Great Lakes declined or were extirpated due to a combination of factors, including overfishing, parasitism by Sea Lampreys *Petromyzon marinus*, and possibly degraded habitat (e.g., dioxin contamination; Coble et al. 1990; Bronte et al. 2003; Cook et. al 2003). Since the formation of the Great Lakes Fishery Commission in 1955, Lake

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Trout management has focused on restoring self-sustaining populations through Sea Lamprey control, harvest regulations, habitat restoration, and the stocking of various Lake Trout strains. However, with the exception of Lake Superior, the Great Lakes region still lacks self-sustaining Lake Trout populations (Paterson et al. 2009). Lake Trout populations are influenced by a wide variety of factors, including changes in trophic dynamics, introduced species, changes in habitat conditions, and poor recruitment, which are impeding restoration efforts (Coble et al. 1990; Burnham-Curtis et al. 1995; Bronte et al. 2003; Cook et al. 2003; Paterson et al. 2009; He et al. 2012).

Lake Trout management is further complicated by the presence of multiple body forms or morphotypes. Three main morphotypes are recognized—the lean, humper, and siscowet—although many other minor forms existed historically (Eshenroder et al. 1995). In general, the three main morphotypes are characterized by divergent life histories and differences in general attributes, such as percent lipid content, preferred depth and corresponding thermal preferences, growth rate, prey preference, body shape, and spawning preferences (e.g., timing and location; Moore and Bronte 2001; Page et al. 2004; Eshenroder 2008; Zimmerman and Krueger 2009). The lean and siscowet morphotypes have the largest degree of difference in the above characteristics, whereas the humper morphotype is generally intermediate. Lake Trout management plans have suggested the stocking of multiple Lake Trout morphotypes in order to explicitly consider genetic diversity and to allow for a broader use of available habitat (Page et al. 2004; Bronte et al. 2008; Markham et al. 2008). In response to this recommendation, the U.S. Fish and Wildlife Service (USFWS) developed and stocked a humper strain (Klondike-strain Lake Trout) for rehabilitation efforts in the Great Lakes (USFWS and GLFC 2013; www.glfc.org/fishstocking/).

Managers are reliant on tools that help guide management decisions, including information on the effectiveness of stocking a certain strain or morphotype given the biological and physiochemical properties of specific lakes. As a management tool, bioenergetics modeling uses the concepts of mass balance and energy transfer to relate fish physiology to corresponding habitat criteria (e.g., consumption, growth, or respiration at a given fish size and temperature). Because the primary use of bioenergetics models has been for management, consumption and growth parameters are of greatest interest to researchers that develop these models (Hansen et al. 1993). Although software has been developed for ease of use by managers (i.e., Fish Bioenergetics 3.0: Hanson et al. 1997), consumption and growth predictions with measures of uncertainty are not currently possible. The incorporation of uncertainty in bioenergetics estimation and inference would help managers to better compare alternative management scenarios, such as which morphotype may be most appropriate for stocking or reintroducing into a particular habitat.

Although useful, the current Lake Trout bioenergetics model developed by Stewart et al. (1983) offers an incomplete description of Lake Trout bioenergetics because (1) it is based solely on the lean morphotype and (2) the models developed for maximum consumption and respiration have limited temperature ranges (up to 10°C and 15°C, respectively). The consumption and respiration models were developed under the assumption that Lake Trout would seek out their preferred habitat. With global climate change models predicting increasing water temperatures, Lake Trout may not always be able to seek out their preferred temperature; thus warranting models that can be used to predict potential changes in growth, metabolism, and consumption in relation to increasing water temperatures (Lynch et al. 2010) that may be beyond Lake Trout's preferred range. Extrapolation of the Stewart et al. (1983) model to temperatures that were not included in the model is not appropriate. Because multiple Lake Trout morphotypes are actively stocked and because management plans have expressed interest in stocking all three main morphotypes in the Great Lakes, there is a need to investigate potential variation in bioenergetics among the commonly stocked morphotypes (Bronte et al. 2008; Markham et al. 2008).

Given the lack of information regarding potential physiological differences among Lake Trout morphotypes and the need to report bioenergetics predictions with measures of uncertainty, the objectives of this study were to (1) develop and validate Lake Trout bioenergetics models for consumption and respiration parameters of juvenile Lake Trout (up to 100 g) to account for morphotype variability, if present; (2) investigate alternate modeling frameworks (i.e., using Bayesian inference) to report bioenergetics estimates with measures of uncertainty; (3) examine potential global climate change implications by completing experiments at temperatures that exceed the Lake Trout's preferred range (i.e., >12°C); and (4) investigate management scenarios for Lake Trout morphotypes under varying environmental (water temperature) conditions. Because Lake Trout morphotypes differ in a wide range of characteristics, including lipid storage and ribosomal RNA sequences relating to metabolic processes, it was predicted that utilization of energy obtained from prey would differ between morphotypes, thus resulting in differences in consumption, respiration, and growth (Burnham-Curtis and Smith 1994; Goetz et al. 2010).

METHODS

Fish Acquisition

Representative strains of actively stocked Lake Trout morphotypes were acquired from disease-free federal (USFWS) fish hatcheries. Of the three main morphotypes, we were able to obtain fish representing the lean and humper morphotypes. The lean morphotype was represented by Lake Champlain-strain fish acquired from White River National Fish Hatchery (NFH) and Allegheny NFH; the humper morphotype was

represented by Klondike-strain fish obtained from Iron River NFH. It was not possible to obtain representative fish of the siscowet morphotype because it is not actively reared in state or federal hatchery systems and because the transfer of wild fish out of the Great Lakes basin is not permitted due to disease and fish health regulations. All experimental fish were housed at the USFWS Northeast Fishery Center in Lamar, Pennsylvania, and were reared in 1.8-m-wide × 0.9-m-deep circular tanks.

Overview of Experimentation

Consumption, growth, and respiration were measured on both morphotypes across a range of temperatures and fish sizes. Five test temperatures (4, 8, 12, 16, and 22°C) were selected to encompass a range that would include not only optimal temperatures (~12°C) but also representative suboptimal temperatures. Fish up to 100 g were used to evaluate potential variation in bioenergetics parameters due to the higher maximum growth rates observed in smaller fish (Stewart et al. 1983) and a greater ability to detect morphotype-specific differences at these small size ranges. The size ranges selected were also representative of juvenile Lake Trout (i.e., fingerlings) stocked in the Laurentian Great Lakes. Three size-classes (5–10, 25–40, and 75–100 g) were examined for each morphotype across the five temperatures. All consumption and respiration experiments were completed in a dark environment to mimic the low-light conditions that would be experienced by Lake Trout in the wild. A complete experimental trial, including both consumption and respiration experiments for a given temperature and fish size-class of interest (e.g., 5–15-g humper Lake Trout held at 4°C), occurred over a 21-d period.

Consumption Experiments

Consumption experiments consisted of an acclimation period and a feeding trial. The experiments were performed using seven 76-L tanks with eight fish in each tank for each morphotype × temperature × fish size combination. The number of experimental tanks was reduced to four for the 22°C trials due to high fish mortality. Prior to a feeding trial, a 2-week acclimation period occurred wherein the test temperature was achieved and fish were accustomed to the prey type that would be used during the feeding trial. Prey consisted of maggots (larvae of the blue bottle fly *Calliphora vomitoria*) for fish in the smaller size-classes (5–15 and 25–40 g) and mealworms (larvae of the darkling beetle *Tenebrio molitor*) for the largest size-class (75–100 g). Fish were fed in excess of satiation every other day to constitute a 50% feeding ration during the acclimation period, as recommended by Hartman and Hayward (2007). Uneaten food was collected approximately 24 h after the food was offered. Initial weights and lengths were measured 24 h prior to the start of the 5-d feeding trial, immediately after the food collection from the last acclimation feeding. Fish were anesthetized with tricaine methanesulfonate (MS-222) prior to measurements of weight (nearest 0.1 g) and length (nearest 1 mm). Fish were then fed daily in two feedings (morning and afternoon) in excess of satiation over a 5-d time period. Remaining uneaten food was collected approximately 24 h after the previous morning's feeding. A final weight measurement was taken 24 h after the last feeding day (day 5) to be consistent with weighing at the start of the trial.

Respiration Experiments

Respiration experiments consisted of an acclimation period and a temperature trial. Prior to the start of respiration experiments, fish were acclimated to the test temperature. Fish in the acclimation tanks were fasted for a period of time before completion of the respiration experiments to ensure that the measurements gathered were those of basal respiration, excluding costs associated with energy of assimilation. The duration of fasting was determined based on the temperature and gastric evacuation rates of other salmonids (e.g., Brook Trout *Salvelinus fontinalis*; Sweka et al. 2004). The 4°C trials required the longest period of withholding food (10 d), and the 22°C trials required the shortest period of withholding food (3 d). All respiration experiments were completed in respiration chambers using groups of five fish. Six respiration chambers were used for all temperature trials except the 22°C trial, in which the number of chambers was reduced to four due to mortality during the acclimation period. The size of the respiration chambers was 13 L for the smallest fish (5–10 g) and 37 L for the remaining size-groups (25–40 and 75–100 g). For all sizes, the ratio of water volume to fish volume exceeded the required minimum ratio of 30 (e.g., the lowest ratio was ~74 for the largest size-class).

Prior to the acclimation phase of the respiration experiments, five fish were randomly removed from the respiration holding tanks, anesthetized with MS-222, and weighed to the nearest 0.1 g before being placed into a chamber. Fish were acclimated to the test chamber for a period of 24 h prior to experimentation. Dissolved oxygen was measured at the start of the experiment by using a Hach HQ40d optical dissolved oxygen probe, and then the chamber was completely sealed using rubber gasket material and an air-tight lid. Fish were held in the chamber for a period of time that allowed them to respire at rest. The duration of the experiment varied (~1–4 h) depending on fish size and temperature. The goal was to achieve a minimum 1-mg/L decrease in dissolved oxygen during the experiment. The chamber was then unsealed, and an ending measurement of dissolved oxygen was taken. This process was repeated three times (i.e., three trials), resulting in multiple measurements for each chamber. For example, once the first trial ended, the chamber was flushed with new water and a new initial dissolved oxygen measurement was taken before the second trial began.

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Model Development

Bioenergetics modeling is based on concepts of mass balance or conservation of energy, where energy is transformed into different products (first law of thermodynamics). The overall bioenergetics equation is

$$C = (R + S) + (F + U) + G, \tag{1}$$

where C is consumption; R is metabolism in the form of respiration; S is the energy required to assimilate energy, also known as specific dynamic action; F is egestion; U is excretion; and G is growth. All physiological processes are expressed in terms of specific rates (e.g., g of oxygen consumed·g of fish^{-1}·d^{-1} or g of prey consumed·g of fish^{-1}·d^{-1}) and are converted into the proper units by using the oxycaloric coefficient (13.6 kJ/g O_2; Elliot and Davidson 1975) and the energy density of the experimental fish and prey such that final growth predictions are in relation to the experimental fish.

Within each physiological process are submodels that describe various relationships, including how processes vary with fish weight and temperature (see model descriptions below). We fitted statistical models to estimate consumption and respiration parameters by following the approach outlined by Hartman and Hayward (2007). Models and parameter estimates for egestion, excretion, and specific dynamic action were taken from Stewart et al. (1983), who modified values from Elliot (1976) and Beamish (1974). However, prior to model fitting, we plotted the raw consumption and respiration data to visualize temperature and weight dependence relationships and fitted ANCOVAs to test for temperature and weight interactions, as was recommended by Hartman and Hayward (2007). We evaluated differences between morphotypes by using posterior means and 80% and 95% credible intervals (CRIs) from the summarized posterior distribution for each physiological process of interest. Although the primary goal was to develop individual models for lean and humper Lake Trout, combined models of consumption and respiration parameters were also developed for comparative purposes (i.e., to evaluate whether a single model would exhibit performance similar to that of morphotype-specific models).

Consumption model.—The model developed to predict consumption was based on modeling the relationship between maximum consumption (C_{max}; g of prey consumed·g of fish^{-1}·d^{-1}) and fish weight and temperature (i.e., weight and temperature dependence functions). Hartman and Hayward (2007) recommended an initial model with $\log_{10}$ transformed consumption as the response variable and $\log_{10}$ transformed wet weight (ww) and linear and quadratic temperature effects as predictor variables. Traditionally, the relationship between C_{max} and fish weight has been described by a power function, and the relationship between C_{max} and temperature has been expressed as a polynomial relationship. However, in addition to linear and quadratic temperature predictors, we also investigated a cubic temperature term. Thus, the consumption model was a linear model with parameter estimates for each morphotype:

$$\log_{10}(C_{max})_{ij} = a_j + \left[b_j \log_{10}(\text{ww})_{i,j}\right] + (b_{2_j} T_{i,j}) + \left(b_{3_j} T_{i,j}^2\right) + \left(b_{4_j} T_{i,j}^3\right) + \varepsilon_{ij}, \tag{2}$$

where $\log_{10}(C_{max})_{i,j}$ is $\log_{10}$ transformed consumption measured at satiation (i.e., C_{max}) for observation i ($i = 1, \ldots, 169$) and morphotype j ($j = 1, 2$); a_j is the intercept for each morphotype; b_j describes the relationship between $\log_{10}$ transformed ww and C_{max} for each morphotype; $\log_{10}(\text{ww})_{i,j}$ is $\log_{10}$ transformed ww; $T_{i,j}$ is water temperature; b_{i_j} are slopes on the temperature terms; and ε_{ij} is the residual error, with $\varepsilon_{ij} \sim \text{N}(0, \sigma^2)$. All consumption estimates were back-transformed prior to use in the bioenergetics model. The consumption model in its final form incorporated C_{max} and the proportion of maximum consumption (p) to estimate consumption at a given feeding level ($C = p \cdot C_{max}$).

Respiration model.—Similar to the consumption model, the respiration model was developed using methods outlined by Hartman and Hayward (2007) and included an exponential relationship between respiration and temperature and a power function between respiration and weight. The respiration model was a linear model with parameter estimates for each morphotype:

$$\log_e(R_r)_{i,j} = a_j + \left[b_j \log_{10}(\text{ww})_{i,j}\right] + (b_{2j} T_{i,j}) + \varepsilon_{ij}, \tag{3}$$

where $\log_e(R_r)_{i,j}$ is the natural log transformed specific respiration of undisturbed fish in a closed, dark chamber assumed at rest (R_r; measured in g of oxygen consumed·g of fish^{-1}·d^{-1}) for each observation i ($i = 1, \ldots, 155$) and morphotype j ($j = 1, 2$); a_j is the intercept for each morphotype j; b_j is the relationship between $\log_{10}$ transformed ww and R_r for each morphotype; b_{2_j} is the linear temperature effect for each morphotype; $T_{i,j}$ is water temperature; and ε_{ij} is the residual error, with $\varepsilon_{ij} \sim \text{N}(0, \sigma^2)$. All values were back-transformed prior to use in overall bioenergetics equations for respiration. Respiration was then transformed into the appropriate units using the oxycaloric coefficient (13.6 kJ/g O_2; Elliot and Davidson 1975) and energy content of the prey so that all bioenergetic physiological processes were in the units of grams of prey consumed·grams of fish^{-1}·d^{-1}. Because respiration was measured at rest, an activity multiplier (ACT) was applied to the respiration equation. We solved for an appropriate ACT using the growth data from the trials given all of the energetic costs associated with metabolism and waste and given the known consumption with a measure of uncertainty (i.e., mean and variance).

All models were fitted using Bayesian estimation and the program WinBUGS from R software (Lunn et al. 2000;

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R Development Core Team 2013). Diffuse priors were used for all parameters. Parameter values from the models developed by Stewart et al. (1983) were not used as priors because those authors used different models to describe some of the consumption and respiration relationships and because their parameters were estimated from data collected during experiments conducted on larger size-classes of fish than used here. After discarding 600 samples, three parallel chains were run with different initial values to generate 5,000 samples from the posterior distributions for each analysis. We retained every third sample for a total of 6,600 samples. For each parameter, we examined the scale reduction factor ($\hat{R}$; a convergence statistic), trace plots, and plots of posterior distribution to assess convergence. In addition to developing models for both of the Lake Trout morphotypes, we compared estimates of growth, consumption, and respiration from all trials by comparing posterior means based on overlapping 95% CRIs.

22°C Trials

We chose to evaluate growth and consumption at 22°C, a temperature near the upper threshold for Lake Trout survival (23.5°C; Gibson and Fry 1954). In doing so, we recognized the possibility of fish mortality occurring during these trials. Fish were not individually identifiable, so we were not able to track specific individuals that died during the trial; however, we wanted to incorporate the fact that if a fish died, it would no longer be consuming, which should be considered during calculations of C_{max}. We were concerned that if we removed the fish's weight from the trial, we could be biasing the results toward the survivors and yielding an overestimate of the true distribution of consumption at this high temperature. We were also concerned with using a dead fish's weight, because the fish often gained water weight after death, thus biasing the measurements of live weight. We decided to use the average fish weight from the trial to substitute for the weight of each fish that died in order to represent the fish throughout the trial. This mortality issue only existed with consumption trials because fish in respiration trials were weighed at the start of the first trial and were used throughout the trial (which only lasted a few hours).

Energy Density Analysis

Energy density (J/g ww) of Lake Trout was predicted by using dry weight and ww relationships, and the energy density of prey items was determined using oxygen bomb calorimetry. Different techniques were necessary because of logistical constraints, particularly related to our inability to dry all fish used in the experiments. In total, 165 fish (sampled across both morphotypes and all size categories; $n \geq 10$ per size category) were used for energy density estimation via a dry weight analysis. All fish used for the dry weight analysis were given a lethal dose of MS-222, ww was immediately measured, and fish were dried to a constant weight. The dry weight analysis consisted of using the percent dry weight and Hartman and Brandt's (1995) energy density equation to predict energy density for the 165 fish. We then used the relationship between predicted energy density (obtained in the dry weight analysis) and the ww of these same 165 fish (see Supplement in the online version of this article) to predict energy density (using a linear model) at the start of a day (where we only had ww information) for balancing the energy budget. Although there was uncertainty in the predicted energy density–ww relationship, the energy densities we predicted from this relationship were comparable to energy density values obtained by Stewart et al. (1983) using bomb calorimetry. Furthermore, we propagated this uncertainty through to final growth estimates. In addition to sampling fish for energy density estimation during the experiments, samples of fish were removed from a subset of consumption trials (4 trials) prior to the start of the trial and at the end of the trial. These fish were used to determine whether fish energy density changed during the course of a consumption trial; dry weight values were used with Hartman and Brandt's (1995) equation to predict energy density. We compared posterior means and 95% CRIs to evaluate whether the predicted energy density of the fish at the start and end of each trial changed over the duration of the consumption experiment.

Energy density of prey items was determined by performing oxygen bomb calorimetry on three separate shipments of each prey type (maggots and mealworms), with three 1-g dry weight samples taken from each individual shipment. Prior to calorimetry, prey samples were dried to a constant weight in a drying oven at 80°C (Cummins and Wuycheck 1971). Energy density was used to convert bioenergetics parameters into units that summarized growth estimates in relation to the Lake Trout. All energy density results are reported as mean ± SD.

Model Evaluation

Model evaluation was conducted using several approaches. First, we used raw data from the experimental trials to determine how well the consumption and respiration models were able to predict the data from which they were developed. We solved for the final ACT by using the observed growth data from the experimental trials with inclusion of variability (e.g., a variance of 0.1 was used as a starting point). Second, we performed validation trials on both of the Lake Trout morphotypes to assess how well the developed models predicted total consumption (g of prey consumed) and growth (g) in relation to temperature, fish size, and ration level. All validation experiments occurred over a 42-d time period and evaluated one size-class for each morphotype and ambient temperature condition. Ten circular tanks (five for each morphotype) measuring 0.91 m (3 ft) in diameter were used for validation trials. Validation trials were completed on groups of eight fish randomly assigned to the tanks; lean Lake Trout used during the experiments were in the 5–15-g size range, whereas humper

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Lake Trout were in the 75–100-g size range. These sizes were selected because they were the remaining fish available that were still within the limits of the developed model after having grown over the duration of the experiment.

Two different ration levels were used based on the proportion of feeding in relation to what was expected to satiate the fish, where satiation represents a value of 1.0 ($p = 1.0$). The two ration levels investigated were satiation (3 replicates) and 50% of satiation (2 replicates). Fish were offered the specified ration level each day during one feeding, and any waste or uneaten food was collected approximately 24 h after feeding. Fish growth was measured during the validation experiments by recording the weights and TLs of all fish on the day prior to the first feeding, followed by weekly measurements throughout the duration of the experiment and finally at the end of the trial, as recommended by Hartman and Hayward (2007). Validation trials occurred at ambient temperature, which fluctuated with seasonal changes throughout the trial period (15.8°C on day 1; 11.5°C on day 42).

Models were evaluated by (1) predicting growth given observed consumption and (2) predicting consumption given observed growth. We used the posterior distributions from parameter estimates to propagate uncertainty through validation predictions. Observed growth data were summarized by using posterior means and 95% CRIs for each weighing period, and posterior means and 80% and 95% CRIs were calculated for model predictions. Total consumption data were represented as the mean in a given tank at the end of the experiment. Differences between predicted and observed growth and consumption values were compared by calculating the percent difference and are reported as mean ± SD. For both consumption and growth, linear regression was performed to compare predicted versus observed values. The coefficient of determination (R^2) and the slope of the fitted line (using 95% CRIs comparing the slope to 1.0) were used to assess how well the models predicted consumption and growth.

Model Simulations

Simulations were performed to provide stocking and management recommendations for Lake Trout stocked within the Great Lakes. We selected temperature from Lake Ontario for two different 1-month temperature scenarios: (1) temperatures near the Lake Trout's generally defined preferred range (average = 11.7°C; range = 10.3–13.7°C); and (2) temperatures that exceeded the Lake Trout's preferred range (average = 14.4°C; range = 10.5–17.5°C; Great Lakes Coastal Forecasting 2013; www.glerl.noaa.gov/res/glcfs/). Simulations were used to predict growth for the lean and humper morphotypes. We started simulations by assuming a 40-g fish, similar to the size of hatchery-stocked juvenile Lake Trout. We chose Alewives *Alosa pseudoharengus* as a representative prey type for juvenile Lake Trout in simulations (Elrod and O'Gorman 1991). Simulations for both morphotypes were performed using the same p-value ($p = 0.9$). The simulations were used to compare projected growth of the two morphotypes over the time duration to investigate whether there would be a preference for stocking the lean or humper morphotype given the temperature scenarios evaluated. Posterior means and 95% CRIs for predicted growth were calculated to compare between morphotypes.

RESULTS

Morphotype Comparisons

Consumption, respiration, and growth from all temperature trials and across the different size ranges varied little between the lean and humper Lake Trout morphotypes (based on overlapping CRIs). The differences that did exist varied across size ranges and temperatures. For example, 5–15-g humper Lake Trout consumed more, on average, than did 5–15-g lean Lake Trout (80% and 95% CRIs for consumption did not overlap), and humper Lake Trout had higher growth at 16°C (humper: growth = 0.031 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.028–0.035; lean: growth = 0.017 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.017–0.021). For the 25–40-g size-class, lean Lake Trout had higher consumption rates at 4°C and 8°C and higher growth at 4°C than did humper Lake Trout (humper: growth = 0.000 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = −0.003 to 0.003; lean: growth = 0.009 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.006–0.012), but humper Lake Trout had a higher growth rate at 16°C (humper: growth = 0.027 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.023–0.032; lean: growth = 0.015 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.013–0.018). We were unable to complete all bioenergetics experimental trials for the 75–100-g size-class of the lean morphotype (consumption at 16°C and 22°C and respiration at 22°C) due to disease-related mortalities. For the trials completed with 75–100-g fish, lean Lake Trout had higher consumption than humper Lake Trout at 4, 8, and 12°C and had higher growth at 8°C (humper: growth = 0.003 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.000–0.006; lean: growth = 0.012 $g{\cdot}g^{-1}{\cdot}d^{-1}$, 95% CRI = 0.009–0.015). Respiration rates did not differ between morphotypes for any temperature trial or size trial (all 95% CRIs overlapped).

Bioenergetics Models

Following the steps outlined by Hartman and Hayward (2007), we first created plots of temperature against consumption across the size-classes and temperatures tested (Figure 1). The patterns observed in the consumption and respiration data coincided with expected patterns described by Hartman and Hayward (2007), including (1) consumption data were polynomial in nature with respect to temperature, (2) respiration data increased across all temperatures (Figure 2), and (3) specific rates generally declined with fish size (except for lean Lake Trout consumption data, which displayed an inverse allometric relationship). There were no significant temperature × weight

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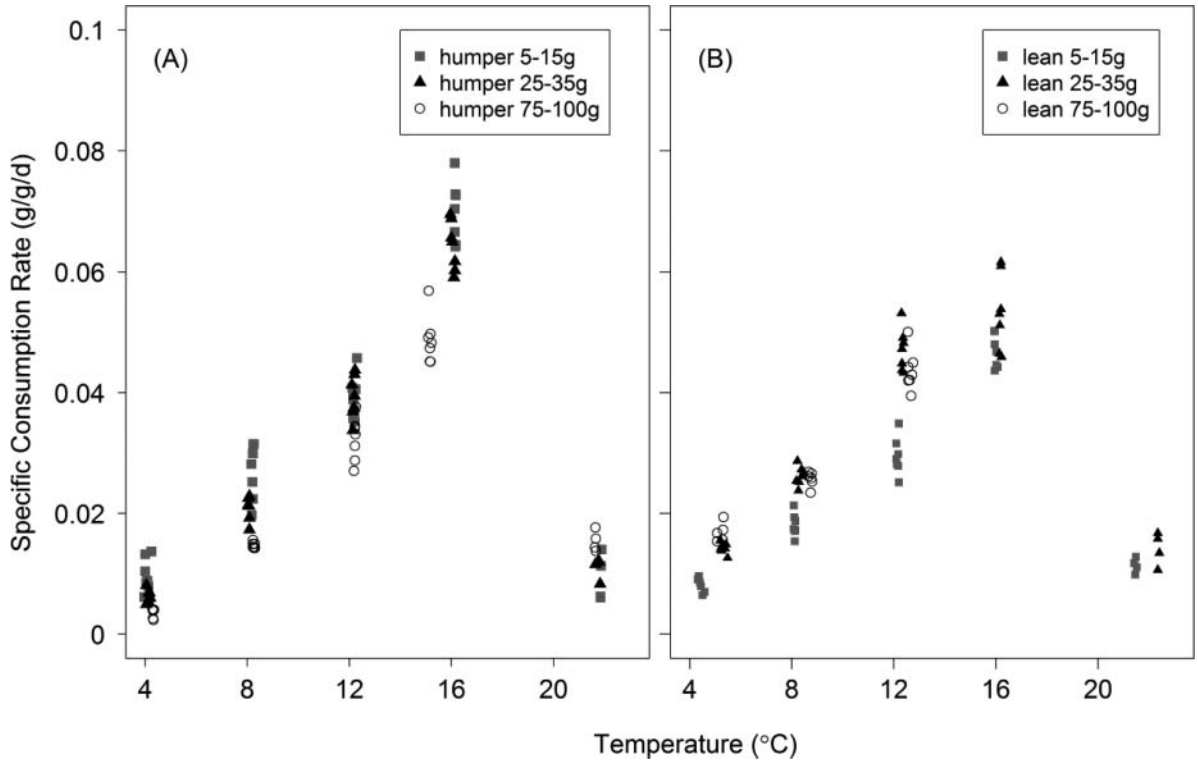

FIGURE 1. Temperature dependence relationships (i.e., specific consumption rate [g of prey consumed·g of fish^{-1}·d^{-1}] versus temperature [°C]) for three size-classes of Lake Trout belonging to the **(A)** humper morphotype or **(B)** lean morphotype. Seven experimental tanks were used for each temperature × size combination except the 22°C trials, during which four tanks were used. Each data point represents the mean specific consumption value for a tank of fish over the 5-d feeding trial.

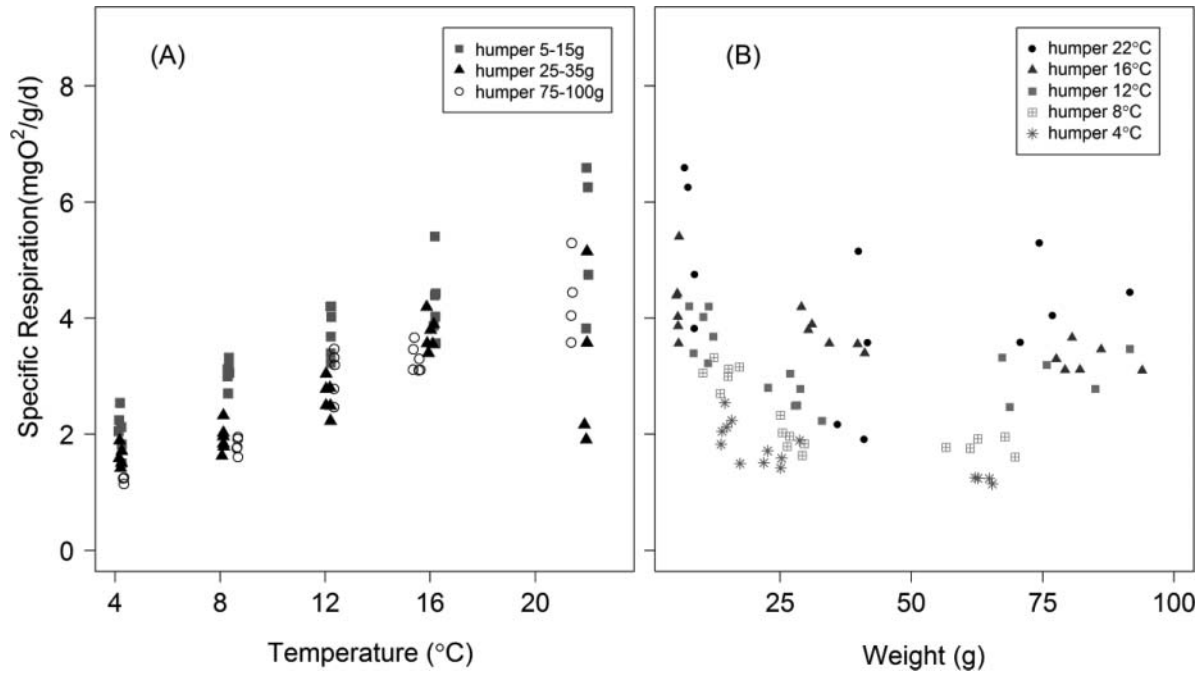

FIGURE 2. Specific respiration (mg O_2·g fish^{-1}·d^{-1}) for humper Lake Trout **(A)** across all temperatures tested for the three size-classes (i.e., temperature dependence) and **(B)** across all size-classes tested for each temperature (i.e., weight dependence). The lean Lake Trout morphotype exhibited the same patterns for both relationships. Six respiration tanks were used for each temperature × size combination except the 22°C trials, during which four tanks were used. Each data point represents the mean specific respiration value for a tank of fish over three respiration trials.

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interactions for either respiration or consumption, with the exception of humper Lake Trout respiration data. The respiration data for humper Lake Trout at 4°C was based on a smaller range of fish sizes tested (fish weight range = 15–65 g) relative to the other temperature trials; thus, we investigated whether this trial was driving the significant interaction. After removing the 4°C trial, the temperature × weight interaction term was no longer significant. Because the interaction was driven by a single trial with a limited size range, we chose not to incorporate an interaction term in the model.

Morphotype-specific parameter estimates for consumption and respiration (equations 2 and 3) were very similar to one another (Table 1), and parameter estimates borrowed from Stewart et al. (1983) were used for the remaining physiological processes (Table 2). However, there were missing data for model development for the 75–100-g lean morphotype trials. Because we were unable to complete the 16°C and 22°C trials for consumption and 22°C trials for respiration, we allowed missing data to be estimated given the relationships displayed at the other size ranges and temperatures. In the combined model, data collected for both morphotypes were combined and data from 5–15-g lean Lake Trout were omitted due to the inverse allometric relationship exhibited (Table S.2). The combined model was still limited in scope to 100-g fish but used data from both morphotypes to obtain parameter estimates.

Energy Density

Prey types used for experimentation consisted of maggots for the smallest two size-classes (5–15 and 25–40 g) and mealworms for the largest size-class (75–100 g). Predicted fish energy density from the dry weight analysis using Hartman and Brandt's (1995) equation ranged from 4,466 to 8,181 J/g ww for lean Lake Trout and from 3,861 to 8,540 J/g ww for humper Lake Trout. Predicted energy density of Lake Trout did not change over the duration of the consumption experiments, as there was no difference between samples taken at the beginning and end of the experiments (all 95% CRIs overlapped). Prey energy density was greater than fish energy density. Maggot energy density was 8,624 ± 262.1 J/g ww (mean ± SD), and mealworm energy density was 9,080.8 ± 336.9 J/g ww.

Model Evaluation

In general, both models predicted consumption and respiration within the 95% CRIs of observed consumption and growth for all sizes and temperatures tested (predictions fell outside of the observed data in only 3 of 28 trials). After an iterative process of comparing ACT values, the final ACT was assumed to be normally distributed with a mean of 2.6 and a variance of 0.1 (i.e., ACT $\sim$ N[2.6, 0.1]). Using this ACT value, 21 of 28 growth predictions from the trials (75% of trials) had 95% CRIs that overlapped observed growth.

Model Validation

During the 42-d period used in validation experiments, temperature ranged from 11.4°C to 15.9°C. For both morphotypes, models predicted growth at the higher ration level within 19% of observed values (humper: −8.1 ± 3.3%; lean: −13.5 ±

TABLE 1. Posterior means (95% credible intervals in parentheses) of parameter estimates for physiological processes in Lake Trout bioenergetics modeling (C = consumption; C_{max} = maximum consumption; p = proportion of maximum consumption; R = respiration with inclusion of activity; R_r = respiration at rest; ACT = activity multiplier). The parameters for C_{max} (equation 2) and R_r (equation 3) were estimated using respiration and consumption data from the experimental trials. Estimates are from separate models for lean and humper morphotypes of Lake Trout. Model residual variance is reported as σ^2 (lean and humper models were completed assuming equal variability and have a single σ^2 parameter). The same ACT was used for both morphotypes.

Parameter	Lean morphotype	Humper morphotype
	Consumption ($C = p \cdot C_{max}$)	
a	−2.350 (−2.644 to −2.053)	−2.321 (−2.547 to −2.099)
b	0.160 (0.094–0.224)	−0.159 (−0.210 to −0.108)
b_2	−0.001 (−0.90 to 0.087)	0.053 (−0.014 to 0.121)
b_3	0.011 (0.003–0.018)	0.010 (0.004–0.016)
b_4	−0.0005 (−0.001 to 0.000)	−0.0005 (−0.001 to 0.000)
σ^2	0.105 (0.094–0.116)	
	Respiration ($R = R_r \cdot$ACT)	
a	0.870 (0.677–1.071)	0.859 (0.658–1.055)
b	−0.346 (−0.463 to −0.227)	−0.357 (−0.478 to −0.237)
b_2	0.058 (0.049–0.066)	0.055 (0.048–0.063)
σ^2	0.201 (0.179–0.225)	
	Activity multiplier	
ACT	2.595 (1.969–3.202)	

TABLE 2. Borrowed parameter estimates from the Stewart et al. (1983) models for Lake Trout egestion (F) and excretion (U). The specific dynamic action (SDA) estimate was borrowed from Beamish (1974; T = temperature; p = proportion of maximum consumption; C = consumption; all other parameters are defined in the table). Units for F, U, and energy of assimilation (S) are grams of prey·gram of fish^{-1}·d^{-1}.

Equation and parameter	Estimate
Egestion: $F = \mathrm{FA}\cdot T^{\mathrm{FB}}\cdot e^{(\mathrm{FG}\cdot p)}\cdot C$	
FA = intercept[a]	0.212
FB = temperature dependence relationship[a]	−0.222
FG = consumption coefficient[a]	0.631
Excretion: $U = \mathrm{UA}\cdot T^{\mathrm{UB}}\cdot e^{(\mathrm{UG}\cdot p)}\cdot (C - F)$	
UA = intercept[a]	0.0314
UB = temperature dependence relationship[a]	0.580
UG = consumption coefficient[a]	−0.299
Energy of assimilation: $S = \mathrm{SDA}\cdot(C - F)$	
SDA = proportion of assimilated energy	0.172

[a]Stewart et al. (1983), modified from Elliot (1976).

5.2%; combined morphotypes: −10.8 ± 4.9%) and predicted consumption within 27% of observed values (humper: 11.8 ± 4.9%; lean: 21.1 ± 9.6%; combined morphotypes: 16.5 ± 8.5%; Table 3). At the reduced ration level, growth was underestimated by up to 36% (combined models: −28.8 ± 8.2%) and consumption was overestimated by up to 92% (combined models: 67.0 ± 25.4%) compared with observed values (Table 3). We plotted predicted consumption and growth trajectories with posterior means and 95% CRIs for each day of the experiment (see Figure 3 for an example from one of the validation tanks). In general, consumption predictions fell outside of the CRIs more than did growth, which overlapped for all tanks investigated, even at the lower ration level. An additional evaluation of predicted growth and consumption was completed by plotting observed consumption and total growth against predictions. We combined the data for both morphotypes and ration levels for an overall evaluation of both models and different ration levels. Even with the lower ration level included, the correlation between predicted and observed values for both growth ($R^2 = 0.78$) and consumption ($R^2 = 0.97$) was high, and neither slope differed from 1.0 (95% CRIs of both slopes overlapped with 1.0; consumption: 95% CRI = 0.92–1.28; growth: 95% CRI = 0.38–1.08). The combined model produced similar predictions of consumption and growth for each morphotype (Table S.3).

Management Simulations

In the simulation that was representative of the Lake Trout's preferred conditions (temperature range = 8–12°C; McCauley and Tait 1970; Stewart et al. 1983), temperatures ranged from 10.3°C to 13.9°C. In the elevated temperature simulation, temperatures ranged from 10.5°C to 17.5°C, and the Lake Trout's preferred temperature range was exceeded on 19 d. For the two temperature scenarios, predicted growth for a 40-g fish did not differ between the two morphotypes. The 95% CRIs for weight gain overlapped for both temperature scenarios (preferred temperature, humper: weight gain = 4.3 g, 95% CRI = −1.0 to 9.8; preferred temperature, lean: weight gain = 5.3 g, 95% CRI = −0.5 to 11.5; elevated temperature, humper: weight gain = 6.2 g, 95% CRI = −0.4 to 13.4; elevated temperature, lean: weight gain = 6.2 g, 95% CRI = −1.1 to 14.2).

TABLE 3. Percent error for observed and predicted consumption and growth of Lake Trout in all tanks in the validation experiment (humper morphotype in tanks 1–5 [H1–H5] and lean morphotype in tanks 6–10 [L6–L10]). Two ration levels were tested: satiation (SR) and 50% reduced ration (RR). Weight$_i$ and Weight$_f$ represent average initial and final observed weights; predicted weight is the final weight predicted by the morphotype-specific model. For consumption, both observed and predicted total average rates are given.

		Growth					Consumption			
Tank	Ration	Weight$_i$ (g)	Weight$_f$ (g)	Predicted weight (g)	% Error	Absolute difference (g)	Observed consumption (g)	Predicted consumption (g)	% Error	Absolute difference (g)
H1	SR	96.2	143.7	126.7	−11.8	−17.0	127	149	17.3	22
H2	SR	86.7	127.7	120.3	−5.8	−7.4	121	131	8.3	10
H3	SR	90.5	131.7	122.9	−6.7	−8.8	123	135	9.8	12
H4	RR	69.4	96.8	70.6	−27.1	−26.2	69	103	49.3	34
H5	RR	84.5	116.1	95.4	−17.8	−20.7	80	113	41.3	33
L6	RR	10.9	16.8	15.4	−8.3	−1.4	20	22	10.0	2
L7	RR	14.0	22.2	19.2	−13.5	−3.0	23	29	26.1	6
L8	RR	13.6	21.9	17.8	−18.7	−4.1	22	28	27.3	6
L9	RR	13.6	18.6	11.9	−36.0	−6.7	12	23	91.7	11
L10	RR	15.3	21.1	13.9	−34.1	−7.2	14	26	85.7	12

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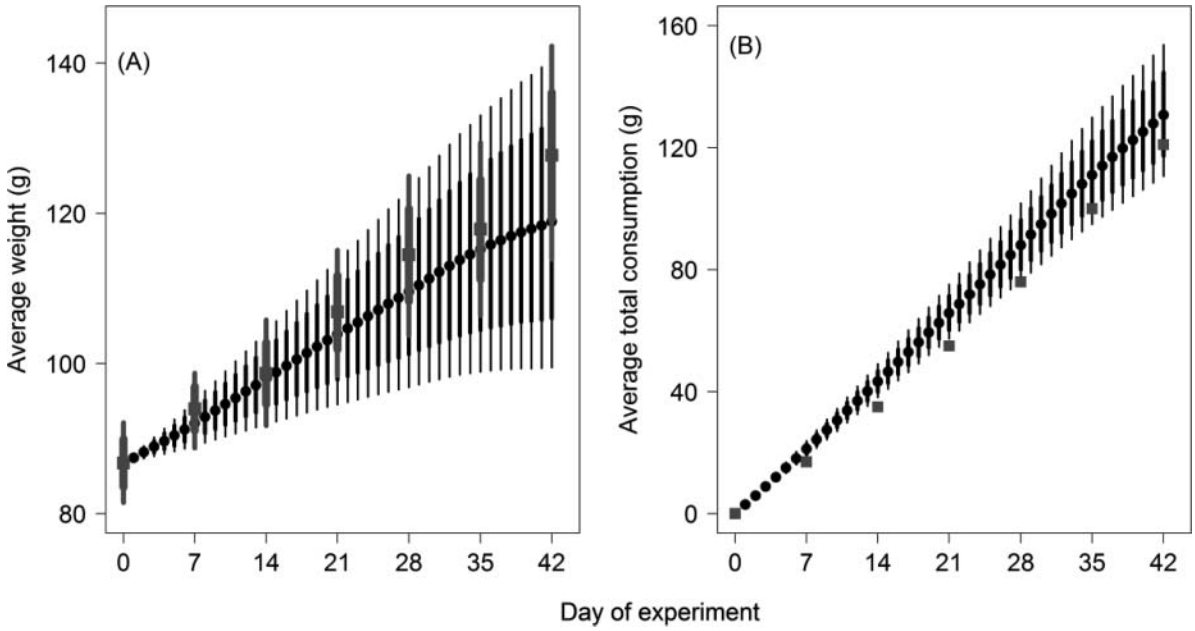

FIGURE 3. Plots of **(A)** average weight gain (g) and **(B)** average total consumption (g) by Lake Trout over time for one of the tanks used in the 42-d validation experiment. In both plots, black circles and lines represent predicted values. In panel A, gray squares and lines represent observed values; both predicted and observed weights are represented by posterior means with 80% (thick vertical bars) and 95% (thin vertical bars) credible intervals. In panel B, gray squares represent average observed consumption values.

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DISCUSSION

Evaluation of the Bioenergetics Models

Our bioenergetics models for lean and humper Lake Trout weighing less than 100 g produced reasonable estimates of consumption and growth under high (ad libitum) ration levels. These models should only be applied to juvenile Lake Trout up to 100 g in size. As defined by Chipps and Wahl (2008), "reasonable" estimates of consumption and growth are those less than 15% different from observed values. This reasonable difference was generally attained by all models at satiation, although for lean Lake Trout the average percent difference for consumption fell slightly outside of this range. At the lower ration level, however, both consumption and growth estimates fell outside of the reasonable range. The inability to reasonably predict consumption and growth at lower ration levels is a limitation of our model. There are several possible reasons to explain the poor estimation, including (1) use of a constant ACT across ration levels and (2) error caused by estimating Lake Trout energy density without the use of bomb calorimetry. We were unable to complete calorimetry on Lake Trout samples for energy density analysis; instead, we used the model developed by Hartman and Brandt (1995) to estimate energy density and then predict energy density from ww. Fish energy density is critical in the conversion process, and recent studies (i.e., Madenjian et al. 2012, 2013) have demonstrated that the accuracy of energy density affects model predictions. The equation used to estimate energy density in our model was developed based on a large sample size of Lake Trout >100 fish) and had a high R^2 value (0.97; Hartman and Brandt 1995). However, we recognize that estimating the energy density rather than performing direct measurements could have contributed to inaccurate predictions in our validation experiments.

Another concern is how the energy budget of the fish is balanced (i.e., by using fish energy density either at the start or end of the day) when developing the model. Madenjian et al. (2012) evaluated this issue with previous Lake Trout validation experiments and found that predictions for consumption were improved by using the energy density of fish at the end of the day. Our estimates of energy density did not exhibit large changes throughout the experimental trials or the validation experiments (e.g., energy density for a ~100-g fish ranged from 7,024 to 7,104 J/g ww over the validation experiments), thus leading us to use a simplified algorithm that may have produced inaccuracies in the overall balancing of the energy budget. However, the energy density estimates may not have characterized the actual range of energy densities in our experiments. Even if energy density had been directly measured from the experimental fish, the beginning energy density of experimental fish would have to be assumed based on lethal measurements from a separate sample of (nonexperimental) fish. Future experiments need to consider which energy density conversion is most appropriate and should directly determine energy density.

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Another potential limitation was the use of a constant ACT value across the different ration levels tested in the validation trial. An ACT that varies across ration levels may be more appropriate; this further demonstrates the need to test models under a wide range of variables prior to application. Bajer et al. (2004) also cautioned that many bioenergetics models are not tested over the temperature ranges and fish size ranges that are observed under wild conditions. The laboratory validation portion of this project allowed temperatures to fluctuate according to ambient levels that covered the Lake Trout's optimal range, but we did not test the wide range of potential environmental conditions. Recent development of a model for Bull Trout *Salvelinus confluentus* similarly used an ad libitum ration for development and a reduced ration for validation (Mesa et al. 2013). Although the validation performed by Mesa et al. (2013) yielded reasonable estimations for the reduced ration level (i.e., mean differences were $<15\%$ for predicted and observed consumption and growth), this again displays a limited evaluation of a newly developed model. Mesa et al. (2013) acknowledged limitations similar to those of our Lake Trout model, indicating the complexity involved in developing and validating models to accommodate the wide range of fish sizes, temperatures, activity levels, ration levels, and other characteristics experienced by fish under natural conditions. In this study, ACTs were solved from laboratory trials and may not have been representative of field conditions. Our bioenergetics models were used to examine the differences between the two Lake Trout morphotypes when held at similar conditions, but we did not investigate the activity levels of active fish in their natural environment. Given this limitation, we recognize that future field and laboratory validation trials are warranted before these models can be applied to a wider range of temperatures, ration levels, and activity levels.

The models developed here provide a useful comparison of energetics between juvenile humper and lean Lake Trout when held under similar conditions. However, these models must be validated across a range of field and laboratory conditions before their application to natural environments (Chipps and Wahl 2008). Limitations in ACT estimation and fish size range are potential sources of concern for field estimation. During model development, the ACT was estimated from fish at rest, which may not be comparable to field measurements (Christiansen and Jobling 1990). Additionally, Lake Trout used in this experiment were limited to 100 g in size. The model is therefore limited in scope to 100-g Lake Trout and should not be extrapolated beyond this weight.

We also observed an inverse allometric relationship for consumption by lean Lake Trout. We acknowledge that a relatively small size range (5–100 g) was evaluated, but we also believe that the allometric relationship should have been apparent over this range. A typical allometric relationship was evident for the humper morphotype. However, consumption of prey by 5–15-g lean Lake Trout in the laboratory was unexpectedly low. Experiments with both morphotypes were completed under the same conditions, but the 5–15-g lean Lake Trout appeared to have specific consumption rates that were much lower than expected. To investigate the influence of the inverse allometric relationship on model predictions, we developed the combined model using data from both morphotypes but with data from 5–15-g lean fish omitted. When we validated the model, reasonable estimations were given for the lean Lake Trout used for the validation experiments, suggesting that the estimates were not sensitive to this relationship. The temperature dependence relationships exhibited with the respiration and consumption data were also consistent across all fish size ranges tested. To further refine the model, we suggest running experiments across a wider range of fish sizes, which would allow for further investigation of the allometric relationship.

By using Bayesian inference, we were able to propagate parameter uncertainty through to growth predictions, thus providing estimates of uncertainty that managers can incorporate into decision-making processes. Ours is not the first bioenergetics model to incorporate uncertainty in parameter estimates and model predictions; Adameck et al. (2012) used a similar approach for brown shrimp *Farfantepenaeus aztecus*. In addition to providing uncertainty estimates that can help to inform decision-making, the incorporation and propagation of uncertainty throughout the modeling process also provide an alternative method for evaluating model fit (e.g., by examining the degree of CRI overlap) compared to the traditional approach of examining percent differences in observed versus predicted values. Additionally, efforts to update bioenergetics models can incorporate information from previously performed experiments in the prior distribution for bioenergetics model parameters.

Summary of Management Simulations

We investigated two water temperature scenarios representing current and potential future environmental conditions in Lake Ontario, and we found no indication that one morphotype would be more suitable for stocking than another under an elevated temperature regime (average temperature $= 14.4^{\circ}$C) or a preferred temperature regime (average temperature $= 11.7^{\circ}$C). The two Lake Trout morphotypes had similar estimates for final growth over the 30-d period, and all CRIs overlapped for both morphotypes. These results provide some evidence that differences in growth between the lean and humper morphotypes are unlikely to occur under the temperature scenarios evaluated. This is important because Lake Trout stocking recommendations now include the use of multiple morphotypes, and an understanding of potential differences between morphotypes is needed to best utilize available resources, including variability in occupied habitats and prey composition in those habitats (Page et al. 2004). Managers who are looking to utilize bioenergetics models may opt to use

the combined model given the subtle difference between the two morphotypes at the size ranges tested in this study.

Although we found only slight differences in consumption, growth, and metabolism between the lean and humper morphotypes, this does not imply that future research should not continue to evaluate differences between the morphotypes. First, a wider range of fish sizes (>100 g) for these morphotypes should be investigated. Second, the siscowet Lake Trout morphotype should also be evaluated in comparison with the lean and humper morphotypes. Metabolic differences between the lean and siscowet morphotypes have been identified (Goetz et al. 2010), and among the three main morphotypes, the lean and siscowet would be expected to be most dissimilar energetically. In contrast, the humper morphotype is considered more of an intermediate form between the lean and siscowet morphotypes (Burnham-Curtis and Smith 1994), which may explain the lack of bioenergetic differences observed between humper and lean Lake Trout in this study.

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REFERENCES

Adameck, A. J., C. A. Stow, D. A. Mason, L. P. Rozas, and T. J Minello. 2012. Predicting the effects of freshwater diversions on juvenile brown shrimp growth and production: a Bayesian-based approach. Marine Ecology Progressive Series 44:155–173.

Bajer, P. G., G. W. Whiteledge, and R. S. Hayward. 2004. Widespread consumption-dependent systematic error in fish bioenergetics models and its implications. Canadian Journal of Fisheries and Aquatic Sciences 61:2158–2167.

Beamish, F. W. H. 1974. Apparent specific dynamic action of Largemouth Bass, *Micropterus salmoides*. Journal of the Fisheries Research Board of Canada 31:1763–1769.

Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community change in Lake Superior, 1970–20001. Canadian Journal of Fisheries and Aquatic Sciences 60:1552–1574.

Bronte, C. R., C. C. Krueger, M. E. Holey, M. L. Toneys, R. L. Eshenroder, and J. L. Jonas. 2008. A guide for the rehabilitation of Lake Trout in Lake Michigan. Great Lakes Fishery Commission, Miscellaneous Publication 2008-01, Ann Arbor, Michigan. Available: http://www.glfc.org/pubs/pub.htm#misc. (January 2013).

Burnham-Curtis, M. K., C. C. Krueger, D. R. Schreiner, J. E. Johnson, T. J. Stewart, R. M. Horrall, W. R. MacCallum, R. Kenyon, and R. E. Lange. 1995. Genetic strategies for Lake Trout rehabilitation: a synthesis. Journal of Great Lakes Research 21:477–486.

Burnham-Curtis, M. K., and G. R. Smith. 1994. Osteological evidence of genetic divergence of Lake Trout (*Salvelinus namaycush*) in Lake Superior. Copeia 1994:843–850.

Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Transactions of the American Fisheries Society 137:298–313.

Christiansen, J. S., and M. Jobling. 1990. The behavior and the relationship between food intake and growth of juvenile Arctic Charr, *Salvelinus alpinus* L., subjected to sustained exercise. Canadian Journal of Zoology 68:2185–2191.

Coble, D. W., R. E. Brusewitz, T. W. Fratt, and J. W. Scheirer. 1990. Lake Trout, Sea Lampreys, and overfishing in the upper Great Lakes: a review and reanalysis. Transactions of the American Fisheries Society 119:985–995.

Cook, P. M., J. A. Robbins, D. D. Endicott, K. B. Lodge, P. D. Guiney, M. K. Walker, E. W. Zabel, and R. E. Peterson. 2003. Effects of aryl hydrocarbon receptor-mediated early life stage toxicity on Lake Trout populations in Lake Ontario during the 20th century. Environmental Science and Technology 34:3864–3877.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. International Association of Theoretical and Applied Limnology, Communication 18, Hickey Corners, Michigan.

Elliot, J. M. 1976. The energetics of feeding, metabolism and growth of Brown Trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 1976:923–948.

Elliot, J. M., and W. Davidson. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19:195–201.

Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile Lake Trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. Transactions of the American Fisheries Society 120: 290–302.

Eshenroder, R. L. 2008. Differentiation of deep-water Lake Charr *Salvelinus namaycush* in North American lakes. Environmental Biology of Fishes 83:77–90.

Eshenroder, R. L., N. R. Payne, J. E. Johnson, C. Bowen II, and M. P. Ebener. 1995. Lake Trout rehabilitation in Lake Huron. Journal of Great Lakes Research 21:108–127.

Gibson, E. S., and F. E. J. Fry. 1954. The performance of the Lake Trout, *Salvelinus namaycush*, at various levels of temperature and oxygen pressure. Canadian Journal of Zoology 32:252–260.

Goetz, F., D. Rosauer, S. Sitar, G. Goetz, C. Simchick, S. Roberts, R. Johnson, C. Murphy, C. R. Bronte, and S. Mackenzie. 2010. A genetic basis for the phenotypic differentiation between siscowet and lean Lake Trout (*Salvelinus namaycush*). Molecular Ecology 19:276–196.

Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122:1019–1030.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Technical Report WIS-CU-T-97-001, Madison.

Hartman, K. J., and S. B. Brandt. 1995. Estimating energy density of fish. Transactions of the American Fisheries Society 124:347–355.

Hartman, K. J., and R. S. Hayward. 2007. Bioenergetics. Pages 515–560 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

He, J. X., M. P. Ebener, S. C. Riley, A. Cottrill, A. Kowalski, S. Koproski, L. Mohr, and J. E. Johnson. 2012. Lake Trout status in the main basin of Lake Huron, 1973–2010. North American Journal of Fisheries Management 32:402–412.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Lynch, A. J., W. W. Taylor, and K. D. Smith. 2010. The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries. Journal of Fish Biology 77:1964–1982.

Madenjian, C. P., S. R. David, and S. A. Pothoven. 2012. Effects of activity and energy budget balancing algorithm on laboratory performance of a fish bioenergetics model. Transactions of the American Fisheries Society 141:1328–1337.

Madenjian, C. P., S. A. Pothoven, and Y. Kao. 2013. Reevaluation of Lake Trout and Lake Whitefish bioenergetics models. Journal of Great Lakes Research 34:358–364.

Markham, J. L., A. Cook, T. MacDougall, L. Witzel, K. Kayle, M. Murray, M. Fodale, E. Trometer, F. Neave, J. Fitzsimons, J. Francis, and M. Stapanian. 2008. A strategic plan for the rehabilitation of Lake Trout in Lake Erie, 2008–2020. Great Lakes Fishery Commission, Miscellaneous Publication 2008-02, Ann Arbor, Michigan. Available: http://www.glfc.org/pubs./ (March 2013).

McCauley, R. W., and J. S. Tait. 1970. Preferred temperature of yearling Lake Trout, *Salvelinus namaycush*. Journal of the Fisheries Research Board of Canada 27:1729–1733.

McDermid, J. L., P. E. Ihssen, W. N. Sloan, and B. J. Shuter. 2007. Genetic and environmental influences on life history traits in Lake Trout. Transactions of the American Fisheries Society 136:1018–1029.

Mesa, M. G., L. K. Weiland, H. E. Christiansen, S. T. Sauter, and D. A. Beauchamp. 2013. Development and evaluation of a bioenergetics model for Bull Trout. Transactions of the American Fisheries Society 142:41–49.

Moore, S. A., and C. R. Bronte. 2001. Delineation of sympatric morphotypes of Lake Trout in Lake Superior. Transactions of the American Fisheries Society 130:1233–1240.

Page, K. S., K. T. Scribner, and M. Burnham-Curtis. 2004. Genetic diversity of wild and hatchery Lake Trout populations: relevance for management and restoration in the Great Lakes. Transactions of the American Fisheries Society 133:674–691.

Paterson, G. D., M. Whittle, K. G. Drouillard, and G. D. Haffner. 2009. Declining Lake Trout (*Salvelinus namaycush*) energy density: are there too many salmonid predators in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 66:919–932.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org. (January 2013).

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetic model for Lake Trout, *Salvelinus namaycush*: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681–698.

Sweka, J. A., M. K. Cox, and K. J. Hartman. 2004. Gastric evacuation rates of Brook Trout. Transactions of the American Fisheries Society 133:204–210.

USFWS (U.S. Fish and Wildlife Service) and GLFC (Great Lakes Fishery Commission). 2013. Great Lakes fish stocking database. USFWS, Region 3 Fisheries Program and GLFC, Ann Arbor, Michigan. Available: http://www.glfc.org/fishstocking/. (May 2013).

Zimmerman, M. S., and C. C. Krueger. 2009. An ecosystem perspective on reestablishing native deepwater fishes in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:1352–137.

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