Development and Application of Juvenile Pallid Sturgeon Bioenergetics Model

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Executive Summary

We developed a bioenergetics model for juvenile pallid sturgeon -- a federally endangered species in the Missouri and lower Mississippi river basins. To evaluate the model, we compared bioenergetic estimates of food consumption to laboratory observations from feeding and growth trials. We then used field-derived information on growth, diets, and water temperatures from the Missouri River, SD to evaluate prey-specific consumption by two size classes of juvenile pallid sturgeon (200-400 mm FL and 500-700 mm FL). Water temperature had a significant influence on feeding and growth; feeding rates ranged from 0.007 to 0.12 g/g/d at temperatures from 13 to 28°C. Optimal temperatures for feeding and growth were 25-28°C, which rarely (or only briefly <2 wks) occur in the upper Missouri River basin during summer months. Bioenergetic estimates of food consumption agreed well with laboratory observations (+7%) across a broad range of water temperatures (13-28 °C). However, at low temperatures (<18°C), the model overestimated food consumption by 50 to 145%. Feeding rate also influence the reliability of model output. At low feeding rates ($\leq$2%/d), the model overestimated observed consumption by (78 to 143%). To account for model uncertainty, we developed a corrective equation that reduced mean error from 47 to -2%, thus improving the reliability of model output. Application of the model to field data showed that young pallid sturgeon (<300 mm FL) relied heavily on both invertebrates (Ephemeroptera, 44%) and fish (46%) prey, whereas the energetic contribution from fish prey (81%) was important to growth of larger juveniles (>400 mm FL). The model developed here provides a quantitative tool for

addressing growth dynamics and energy acquisition in juvenile pallid sturgeon and should prove useful to management and research questions focused on recovery efforts.

Introduction

The pallid sturgeon (*Scaphirhynchus albus*) is a long-lived species native to the Missouri and lower Mississippi River basins that has been listed as federally endangered since 1990 (Bergman et al. 2008). Over the last century, sturgeon habitat in the Missouri River has been greatly modified by human activities that include construction of large impoundments (Hesse and Mestl 1993; Galat et al. 1998). Outflows from Missouri River dams influence water velocities, turbidities, and water temperatures available to pallid sturgeon. Throughout much of the Missouri River system, the extant pallid sturgeon population is characterized by large, old fish (Bergman et al. 2008). Natural reproduction in pallid sturgeon is negligible in many reaches of the Missouri River and mechanisms for recruitment failure are not known. Due to the critical status of this species, short-term recovery efforts have focused on artificial propagation of juvenile fish and construction of shallow water habitat. Although much has been learned about propagation and rearing techniques, comparatively little is known about factors affecting growth of juvenile pallid sturgeon once they are stocked into the Missouri River.

Bioenergetics modeling provides a simple approach for quantifying feeding or growth rate of fishes and has been used to evaluate food web connections and habitat suitability for sturgeons (Bevelhimer 2002; Mayfield and Cech 2004;

Niklitschek and Secor 2005).   Prey availability and water temperature, in particular,

have important consequences for growth rate in fishes, but these factors have been

difficult to assess for pallid sturgeon in the Missouri River due to a general lack of

quantitative methods. Understanding the influence of diet composition and water

temperature on growth responses of juvenile pallid sturgeon would enhance

stocking and habitat enhancement efforts aimed at recovering the population.

In this study, we developed a juvenile pallid sturgeon bioenergetics model

and tested the model against independent observations across a broad range of

water temperatures and ration levels. Using information on diet composition and

growth, we model prey consumption by juvenile pallid sturgeon in the Missouri

River and estimate prey-specific energy contribution. We highlight implications for

model use and discuss potential limitations of the model for evaluating growth

dynamics of juvenile pallid sturgeon.

Methods

Model Development

We developed a juvenile pallid sturgeon bioenergetics model using the mass-

balance equation,

$$C = (R + A + SDA) + (F + U) + (G),$$

where food consumption (C) is balanced by 1) respiratory demands (R, A, and SDA),

2) waste losses (F and U) and 3) growth processes (G). Here, R equals standard

metabolism, A is energy expenditure due to activity, SDA is specific dynamic action,

F and U are losses due to egestion and excretion, respectively, and G represents

somatic growth and gonad production (Winberg 1956; Hanson et al. 1997). Standard metabolism (R) is modeled as a function of body mass and water temperature. Other parameters are defined as either a constant proportion of consumed energy (i.e., SDA, F, and U) or as a fixed multiplier of standard metabolism (i.e., Ma; Winberg 1956). The model developed here is structured after the popular Wisconsin bioenergetics model where information on temperature and weight-dependent maximum food consumption (C_{max}) is used to adjust consumption to account for observed growth (i.e., P-value; Kitchell et al. 1977; Hanson et al. 1997).

Maximum Consumption

Juvenile pallid sturgeon (n=24, 21.5 to 58.7 g) were obtained from the USFWS Gavin's Point National Fish Hatchery in Yankton, South Dakota on 13 June 2005. Fish were transported to the laboratory, acclimated for 24 h in a holding tank (1.3 m^3) and then placed separately into 114 L aquaria (n=24) containing 17 °C water. The aquaria were connected to a recirculation system where water was pumped through a biofiltration tank and sand filter. Three 1500 w heaters and a 1 hp chiller unit were used to control water temperature in the system. Two temperature loggers (Optic StowAway, Onset Computer Corporation, Bourne, Massachusetts) recorded hourly water temperature and were placed in aquaria on each end of the recirculating system. Pallid sturgeon were acclimated to laboratory conditions for two weeks and fed an *ad-libitum* daily ration of live red wiggler worms (*Eisenia foetida*). In pilot feeding trials, we found that pallid sturgeon readily accepted chopped worms (~1 cm sections) over whole specimens.

We measured feeding and growth of juvenile pallid sturgeon over a three month period. To simulate seasonal changes in water temperature, we acclimated fish to 17, 21, 25, 28, or 13 °C; during this period, fish were maintained under natural photoperiods.   This design allowed us to collect information on temperature-dependent consumption as well as feeding and growth data (~3 mos) that could be used to evaluate the bioenergetics model (Figure 1; see Model Evaluation). Trials began on 27 June, 2005 at 17°C and fish were fed pre-weighed, *ad-libitum* rations of chopped, red wigglers twice a day for 5-d. Uneaten food was siphoned daily from each aquarium and weighed wet to the nearest 0.01 g. Water temperature in the recirculating system was then increased ~1°C/day and fish were fed *ad-libitum* daily rations until the next test temperature was achieved (e.g., 21 °C). Fish were acclimated and fed at this new temperature for 7-d before beginning the next 5-d feeding trial. After we completed feeding trials at 28°C, water temperature was decreased in the tanks ~1°C/d until we reached a test temperature of 13 °C. Fish were then acclimated/fed at 13°C for 7-d before beginning the 5-d feeding trial.   All fish were weighed to the nearest 0.001 g wet wt at 2 to 3 week intervals.

Daily food consumption (g/d) was calculated for each fish as the difference between the amount of food fed and that recovered from aquaria 24 h later. To account for measurement error due to leaching and residual metabolism of small, invertebrate prey (Wurstbaugh and Cech 1983), we measured prey recovery in tanks without fish. Five different amounts of chopped, red wigglers weighing 0.02, 0.25, 0.5, 1, or 2 g were introduced into fishless aquaria (three per treatment) at

22°C and recovered 24 h later. The ratio of recovered-to-initial prey mass was independent of the amount of prey introduced and averaged 0.82 (i.e., 18% loss). To estimate daily food consumption, the amount of prey recovered was divided by 0.82 and then subtracted from the amount of prey fed.

We calculated mean daily food consumption (g/g/d) for each fish by averaging daily food consumed for each 5-d feeding trial at 17, 21, 25, 28, or 13 °C. Mean daily consumption was then plotted against water temperature to determine the optimal feeding temperature for juvenile pallid sturgeon. The relationship between body size and maximum food consumption was determined at optimal water temperature as,

$$C_{max} = aW^b \times f(T)$$

where C_{max} is maximum specific consumption rate (g/g/d), W is fish mass (g), a and b are regression coefficients, and $f(T)$ is a temperature rate multiplier, that at optimal feeding temperature(s) equals 1 (Hanson et al. 1997).

Respiration

We used static respirometry as outlined in Klumb et al. (2003) to quantify respiration rates of juvenile pallid sturgeon (n=215, 0.004 to 617 g) at temperatures ranging from 3 to 24°C. Experiments were conducted at the U.S. Fish and Wildlife Service, Bozeman Fish Technology Center in Bozeman, Montana, Garrison Dam National Fish Hatchery, Riverdale, North Dakota, and the Gavin's Point Dam National Fish Hatchery in Yankton, South Dakota. Fish were generally tested at ambient water temperatures in the hatcheries. Juveniles were acclimated for 15 – 24 h after

placement into static respirometers ranging from 1 to 20 L, depending on fish size, whereas, small larvae were not acclimated to the respirometer (Klumb et al. 2003). Larger juvenile fish (161-617 g), located at the Bozeman Fish Technology Center, were acclimated to one of six water temperatures (13, 16, 18, 20, 22, and 24 C) for 1 – 2 weeks and oxygen consumption was measured in a 200 L respirometer. Each experimental chamber contained one fish with 1-4 fishless chambers used as controls to account for microbial respiration. Water temperature was measured every 15 minutes using submersible temperature loggers. To minimize the influence of specific dynamic action (SDA) on metabolism measurements, fish were starved for at least 24 h prior to measuring oxygen consumption. Small larvae that continuously feed at the hatcheries were not starved prior to experimentation (Klumb et al. 2003).

To ensure adequate oxygen draw and avoid hypoxic conditions in the chambers, trial duration varied depending on temperature and/or fish size. Initial and final dissolved oxygen concentration was determined using the azide-modification of the Winkler method (American Public Health Association (APHA) 1998) and expressed to the nearest 0.01 mg/L. Replicates where final oxygen concentrations fell below 5 mg/L were not used. Oxygen depletion was calculated as the difference between initial and final g of O_2 in the respirometer, corrected for the volume of pallid sturgeon (assuming a displacement of 1 ml water per g of fish); this value was then divided by time (h) and expressed as oxygen consumption rate (g O_2/d) for each fish.

We used multiple regression to quantify the influence of body mass (B) and water temperature (T) on daily oxygen consumption (M) as,

$$M \ (g \ O_2/d) = x + bB + cT$$

where x, b and c are regression coefficients. We then estimated oxygen consumption for a 1-g fish at temperatures ranging from 4 to 30 °C. Although this procedure extrapolated beyond the highest temperature tested (i.e., 24°C), we included temperatures up to 30°C because 1) feeding experiments indicated that optimal feeding temperatures were 28 °C and 2) lethal temperature for juvenile pallid sturgeon exceeded 33 °C (see below). Metabolism was then expressed as

$$R = aW^b \ x \ ACT \ x \ f(T),$$

where R is resting metabolism (g O_2/g/d) at optimal water temperature, W is fish mass in g of wet weight, a is the intercept value for a 1-g fish, b is the weight-dependent slope component, ACT is activity, and $f(T)$ is a temperature rate multiplier (Hanson et al. 1997). We used information developed for Atlantic sturgeon to model activity cost (Niklitschek and Secor 2005). Because activity in sturgeons increases with water temperature (Mayfield and Cech 2004), we set A equal to 1 for simulations with temperatures ≤20°C and 1.5 for water temperatures >20°C (Niklitschek 2001).

Egestion, Excretion, SDA

Energy losses due to egestion and excretion are generally modeled as constant proportions of consumed energy (cit). In a detailed study of Atlantic sturgeon *Acipenser oxyrinchus*, Niklitschek (2001) reported values of 0.10 and 0.04

for egestion and excretion, respectively. Similar values were used to model egestion (0.15) and excretion (0.05) in a white sturgeon *A. transmontanus* bioenergetics model (Bevelhimer 2002).   Here, we used values of 0.1 and 0.04 to represent waste losses in the pallid sturgeon bioenergetics model.   Specific dynamic action (SDA) was assumed to represent a constant proportion of consumed energy (0.13) based on work with Atlantic sturgeon (Niklitschek 2001).

Thermal tolerance

To quantify temperature tolerance, we used an adaptation of the acclimated chronic exposure (ACE) method (Zale 1984; Selong et al. 2001) to measure pallid sturgeon survival at water temperatures of 29, 33, and 35°C. Eighteen juvenile pallid sturgeon (18 to 38 g) were available for use, limiting our ability to evaluate multiple acclimation temperatures or calculate LD50s. In an effort to determine both a critical thermal maximum (CTM; Fry 1947; Brett 1956) and gain information on exposure time (i.e., upper incipient lethal temperature; Kilgour and McCauley 1986), we acclimated fish to a water temperature of 26°C for 18-22 d. This temperature falls within the range of summer maxima (23-28 °C) observed in the Missouri River, South Dakota (Elliot et al. 2004).

To begin trials, six fish were transferred from 114 L acclimation tanks and individually placed into six, 38 L test chambers that were set up in a water bath system heated by two 1500 w heaters. Fish were starved for 48 h before transferring them to the test chambers and each chamber was insulated to help regulate water temperature which varied < 0.3 °C for any given temperature. Initial

water temperature in the chambers was 26°C and this was heated at a rate of 1°C/h and maintained at the desired test temperature (29, 33 or 35 °C) for 4-d. At the start of each temperature trial, we observed fish for 30 min and recorded any loss of equilibrium (e.g., CTM value; Kilgour and McCauley 1986; Selong et al. 2001). Survival was monitored at 0.5 h intervals for the first 8 h, and 1 h intervals thereafter. Because water temperature was increased faster (1°C/h) than that typically used in the ACE approach (i.e., 1°C/d; Selong et al. 2001), our findings were more representative of acute temperature tolerance used to measure critical thermal maxima (CTM). This approach allowed us to reliably estimate a CTM value (for modeling purposes), while providing additional information related to lethal exposure time for fish acclimated to a realistic upper temperature.

Other Input Parameters

Other input variables required to model feeding and growth of pallid sturgeon included water temperature, diet composition, and energy density of predator and prey. Water temperatures were recorded hourly in aquaria using submersible temperature loggers. Hourly water temperatures were averaged over each 24 h period to calculate mean daily water temperature experienced by fish. Diet composition was held constant at 100% (red wigglers).

We used bomb calorimetry to determine energy density of juvenile pallid sturgeon and red wiggler worms. Energy density of juvenile pallid sturgeon averaged 2,698 J/g wet wt (n=10, SE=292) whereas energy density of prey averaged

4,188 J/g wet wt (n=42, SE=100); these values were used as input in the
bioenergetics model to estimate food consumption.

Model Evaluation

Effects of Variable Water Temperature

We examined the influence of water temperature on feeding and growth of
juvenile pallid sturgeon reared at temperatures ranging from 13 to 28°C. We
modeled five simulation periods where information on growth, water temperature,
and predator/prey energy density were used as inputs in the model to predict food
consumption for each fish (Figure 1). Mean total food consumption predicted by the
model was compared to mean observed consumption using a paired t-test (SAS
2003). Sources of error in model predictions were evaluated by decomposition of
mean square error (MSE), obtained from least-squares regression of total observed
consumption against total consumption predicted by the model. The MSE
represents the variance around the 1:1 line, where sources of error from the mean
component (*Z*) are due to differences in predicted and observed values, the slope
component (*S*) represents error due to deviation of the slope from unity, and the
residual component (*R*) represents random error (Rice and Cochrane 1984; Wahl
and Stein 1991; Chipps and Wahl 2004). To evaluate systematic errors (*Z* and *S*), we
regressed total observed consumption against predicted values and used Bonferroni
joint confidence intervals to test the joint hypothesis that regression parameters
had an intercept of 0 and a slope of 1 ($P<0.05$; Neter et al. 1985). If the joint
hypothesis was rejected, we tested for differences between means and slope

separately (Rice and Cochrane 1984; Wahl and Stein 1991). Statistical analyses were performed using SAS 9.1 (SAS 2003, Cary, NC).

Effects of Variable Ration Level

Accuracy of bioenergetics models can be influenced by feeding rates in fishes (Chipps et al 2000a; Bajer et al. 2004; Chipps and Wahl 2008).   To explore the influence of feeding rate on bioenergetics output, we evaluated feeding and growth of juvenile pallid sturgeon at four ration levels. Juvenile pallid sturgeon (n=24, mean mass = 15.4 g, range 3.9 to 32.0 g) were obtained from the USFWS Gavin's Point National Fish Hatchery on October 8, 2005. Individual fish were placed into 114 L rearing aquaria, held at 20 °C, and fed chopped, red wigglers for two weeks prior to experiments. After the two week acclimation period, six fish were randomly assigned to one of four ration levels of 1, 2, 3, or 5% body weight/d. All fish were fed twice daily for 29 d and weighed on four occasions (days 1, 9, 22, and 29) to determine growth. After each weighing, rations (% body wt/d) were recalculated based on new fish weights.

Information on growth (initial and final mass), water temperature (20 °C), and predator (2,698 J/g) and prey (4,188 J/g) energy density was used as input in the model to estimate total food consumption. For each fish, daily food consumption (g/d) was calculated as the difference between the amount of prey fed and the wet weight of prey remaining in the aquaria 24-h later, corrected for recovery error. Mean total food consumption predicted by the model was then compared to mean observed consumption for each ration level and analyzed using a paired t-test.

Sources of error in model predictions were evaluated for each ration level using decomposition of MSE and systematic error was assessed by regressing total predicted consumption against total observed consumption (SAS 2003, Cary, NC).

Model Application

We used information on growth and diet composition for juvenile pallid in the Fort Randall reach of the Missouri River to estimate prey-specific consumption using the bioenergetics model (Wanner et al. 2007; Berg 2008). Because consumption of fish prey increases with body size of juvenile pallid sturgeon, we used size-dependent diet data reported by Berg (2008) to model food consumption for two size classes of juvenile pallid sturgeon (200-400 mm FL and 500-700 mm FL). Diet information collected from June through October, 2006 were used as input in the model to estimate food consumption. Stocking and recapture data from tagged fish (2003-2007) were used to estimate mean growth of juvenile pallid sturgeon (Berg 2008). Based on recaptures, daily growth rate for juvenile pallid sturgeon averaged 0.44 g/d (n=6, SE=0.12) for 200-400 mm fish and 0.19 g/d (n=31, SE=0.03) for 500-700 mm pallids. For modeling purposes, we set model day 1= June 1; initial (June) and final (October, day 120) mass was 105 and 158 g for the smaller fish (200-400 mm) and 598 and 620 g for the larger juvenile pallids. Information on seasonal water temperatures (June-October) were measured in 2006 using temperature loggers at locations described by Klumb (2007). Mean daily water temperatures in the Missouri River increased from 18°C in June (day 1) to 24°C in August (day 60), then declined to 17°C by October (day 120). Other input

variables required to model food consumption, included energy density pallid sturgeon and their prey. Energy density of juvenile pallid sturgeon was set to 2,698 J/g; prey energy densities were obtained from the literature and used as input in the model to estimate prey-specific consumption. Prey consumption (g wet wt) was then converted to energy equivalents (Joules) and expressed as a percentage of total consumption (in J) for each prey taxon.

Results

Model Development

Maximum Consumption

Mean daily food consumption increased with water temperature and ranged from 0.49 g/d at 13 °C to 7.01 g/d at 28 °C.   Mean specific consumption rates ranged from 0.007 at 13 °C to 0.12 g/g/d at 25 and 28 °C (Table 1). Because specific consumption rate declines with increasing body mass, and average size of pallid sturgeon was larger at 28 °C (58 g) than at 25 °C (42 g), we used 28°C to represent the optimal feeding temperature. The relationship between maximum food consumption C_{max} (g/g/d) and body mass (g) at 28°C was estimated as,

$$C_{max} = 0.553W^{-0.326}$$

(log-log linear regression, n=24, r^2 = 0.72, P < 0.001; Table 2).

Respiration

Oxygen consumption varied with water temperature and body size of pallid sturgeon and ranged from 0.00002 g O_2/d (0.03 g fish at 17 °C) to 3.42 g O_2/d (268 g

fish at 24 °C).   Water temperature and body size influenced respiration rate and
were used to predict daily oxygen consumption (M) as,

$$M (\log_e g \ O_2/d) = -6.041 + 0.852B + 0.065T,$$

where B is the natural logarithm of body mass ($\log_e$ g wet wt) and T is water
temperature in degrees Celsius (multiple regression analysis, $F_{2,213} = 2543$, $R^2=0.96$,
P<0.0001; Figure 2). Using this equation to estimate oxygen consumption for a 1-g
fish, we obtained values that ranged from 0.003 g O_2/d at 4 °C to 0.017 g O_2/d at 30
°C. Specific respiration rate (R, g/g/d), in turn, was estimated using an intercept
value of 0.017 for a 1-g fish and expressed as,

$$R = 0.017W^{-0.15},$$

where W is body mass in g wet weight (Table 2).

Lethal Temperatures

   Four day survival of juvenile pallid sturgeon was 100% at 29 °C, congruent
with feeding observations that showed optimal water temperatures close to this
value (i.e., 28 °C).   At 33°C, 4-d survival of pallid sturgeon was 83%. However, after
increasing water temperature to 35 °C, all fish quickly lost equilibrium (<30 s) and
survival declined to 0% within 2 h (Figure 3). Although tolerant of warm water
temperatures (<30 °C), we observed a narrow threshold from 33 to 35 °C where
survival declined sharply -- a pattern similar to that observed in other fishes (Selong
et al. 2001).

Model Evaluation

Effects of Variable Water Temperature

Growth rate of pallid sturgeon varied with water temperature and ranged from -0.12 to 1.3%/d at mean temperatures of 18.8 and 26.4 °C (Table 3). Bioenergetics estimates of total food consumption ($\bar{x}$ =197.4 g) agreed well with observed values ($\bar{x}$ =183.7 g) across the range of water temperatures examined ($t_{0.05,46}$ = 2.01, P=0.15; Table 3). Decomposition of MSE revealed that an appreciable amount of variation between total observed and predicted food consumption was due to random error (R=45%); combined error due to differences between means (Z=28%) and slope (S=27%) was 55%. However, regression of observed values on predicted values revealed that the 95% joint confidence region did not include an intercept of 0 and a slope of 1 ($F_{0.05;2,22}$=3.44, P<0.05). Separate tests of the slope (β_1, 95% CI = 0.53-1.06) and intercept (β_o, 95% CI = 15.8-100.2) values revealed that the intercept did not include a value of zero. This systematic error is likely due to model overestimation of food consumption at low water temperatures. At mean water temperatures of 18.8 and 13.5 °C, the model overestimated food consumption by 50 to 145% (Table 3).

Effects of Variable Ration Level

Mean food consumption by juvenile pallid sturgeon increased with ration level and ranged from 0.014 to 0.049 g/g/d at feeding rates of 1 to 5%/d. Similarly, mean specific growth rate increased with ration level and ranged from 0.04 to 1.58%/d (Table 4). Bioenergetics estimates of food consumption ranged from 0.034

to 0.042 g/g/d; on the average, model estimates of total food consumption (g) were higher than observed values at ration levels of 1, 2 and 3%/d (paired t-test, P<0.05; Table 4). Percent difference between observed and predicted values decreased with increasing ration level. Model estimates were 143, 78, or 37% higher than observed values at ration levels of 1, 2, or 3%/d, but were within -15% of observed values at the highest ration (5%/d; Figure 4). Decomposition of MSE revealed that most of the variation between observed and predicted food consumption was due to difference between means, particularly for rations <5%/d (Table 4). Similarly, regression of observed values on predicted values revealed that 95% confidence intervals did not include an intercept value of 0 at lower ration levels (1 and 2%/d; Table 4), implying that most variation was attributed to model overestimation at low ration levels (Figure 4).

In an attempt to improve model performance, we used a regression-based approach that incorporated water temperature and growth rate (as a surrogate for feeding rate) to explain variation in model error (Bajer et al. 2004b). Although this approach does not address the mechanism(s) responsible for model error, it has been shown to improve the reliability of model output (Schoenebeck et al. 2008). Using information from each of the simulations (n=9), we found that an appreciable amount of variation in model error (E) could be explained as a function of water temperature (T) and growth rate (G) as,

$$E = 207 - 5.5(T) - 65.1(G),$$

where E is percent error in model output, calculated as (predicted-actual consumption)/(actual consumption) x 100, T is water temperature (°C), and G is

specific growth rate [(log$_e$ final mass)-(log$_e$ initial mass)]/days x 100 (multiple

regression analysis, R^2=0.73; F $_{2,6}$ = 7.7, P=0.05;). This correction factor can be used

to calculate adjusted consumption (C$_{ADJ}$, g) obtained from the model (C, g) as,

$$C_{ADJ} = \frac{C}{\left(\dfrac{E}{100}+1\right)}.$$

Application of this correction factor decreased the average observed error rate from

47.7% (n=9, SE=21.0) to -2.4% (n=9, SE=6.4), thus appreciably improving the

reliability of bioenergetic estimates.

Model Application

Application of the model to field-derived growth, diet and water

temperature data showed that total food consumption for a small pallid sturgeon

(200-400 mm) was about 37% of that predicted for larger (500-700 mm) juveniles

(336 g versus 908 g) from June-October, 2006. For a small fish, adjusted

consumption ranged from 21 kJ for plecoptera to 506 kJ for fish prey. Invertebrates,

primarily Ephemeroptera (44%), and fish (46%) represented important energy

sources for small pallid sturgeon, accounting for about 90% of consumed energy.

For larger juveniles (500-700 mm), consumption ranged from 54 kJ for Trichoptera

to 2,633 kJ for fish, where fish prey represented over 80% of consumed energy

(Table 5).

Discussion

The influence of water temperature on feeding and growth of juvenile pallid sturgeon is not well documented. We found that optimal water temperature for juvenile pallid sturgeon was 28°C based on maximum feeding rates. Growth and survival data showed that pallid sturgeon were well-adapted to temperatures of 25 to 28°C. Evidence that these temperatures encompass the optimal range for juvenile pallid sturgeon is also supported by lethal temperature experiments. In our study, the difference between the lethal and optimal temperatures (35-28° = 7°C), is consistent with that reported for many other fishes (mean=7.3°C, range=6-12°; Hanson et al. 1997). Throughout their range, pallid sturgeon likely experience temperatures ranging from 25-30°C during summer months. In the lower Mississippi River, water temperatures exceed 25°C from mid-June through mid-September, with maximum water temperatures near 30°C during much of August (J. Dean, USFWS, unpubl. data). Summer water temperatures in the upper Missouri River, near Springfield, South Dakota are generally lower, with maximum values of 25°C occurring for only 1-3 weeks each August (Klumb 2007). Large impoundments on the Missouri River can influence water temperatures downstream, owing to coldwater releases below dams. Although serial discontinuity in river water temperatures has been well-documented (Ward and Stanford 1983), the influence of this on growth dynamics of pallid sturgeon is not known. Nonetheless, optimal water temperatures documented here rarely (or only briefly) occur in the upper Missouri River, where a majority of the propagation and recovery efforts have been focused (Bergman et al 2008).

Energy allocation in juvenile pallid sturgeon is similar to that reported for other sturgeon species. Although approximate, energy acquisition by pallid sturgeon is partitioned into waste losses, metabolism and somatic growth as 13, 49 and 38% of consumed energy. Studies with Atlantic and shortnose (*A. brevirostrum*) sturgeon report similar findings (Niklitschek 2001). In juvenile Atlantic sturgeon, waste losses, metabolism and somatic growth are partitioned as 12, 56, and 32% of consumed energy and, for shortnose sturgeon, as 12, 53, and 35% (Niklitschek 2001). In white sturgeon, waste, metabolism and growth represents about 6, 61, and 33% of consumed energy (Cui et al. 1996). These approximations suggest that 30-35% of consumed energy is allocated to somatic growth in juvenile sturgeons, similar to that reported for other fishes (Hanson et al. 1997).

Evaluation of bioenergetics models represents an important phase in the model development and application process (Chipps and Wahl 2008). Here, we tested our model against laboratory observations and found that model estimates of total food consumption agreed well (+7.4%) with observed values across a range of water temperatures. However, at low water temperatures (mean = 13.3°C), model estimates of food consumption were over twice as high as observed values. Similar findings were reported for an esocid bioenergetics model, where error in model estimates was attributed to seasonal changes in fish metabolism, not accounted for in bioenergetics models (Chipps et al. 2000a). Subsequent work with juvenile muskellunge (*Esox masquinongy* x *E. lucius*) showed that metabolic rate varied seasonally, independent of water temperature. At a constant water temperature, metabolic rate was significantly lower during winter months compared to summer

and autumn (Chipps et al. 2000b). If true for sturgeons, this could explain model error at low water temperatures and the observation that model estimates are higher than actual values. To test this hypothesis, additional information is needed on seasonal metabolic rates of pallid sturgeon, reared under natural photoperiods and constant temperatures.

Feeding rate of fishes has been widely shown to influence the accuracy of model output (Chipps et al. 2000a; Bajer et al. 2004b) and presents a pragmatic problem in the application of bioenergetics models. Our evaluation showed that error in model estimates increased at low feeding rates. For fish fed higher rations of 3-5%/d, model estimates of food consumption agreed well with observed values (mean=+11%). Recent efforts to address the problem of consumption-dependent error (CDE) in bioenergetics models have focused on 1) correction of model output (cits) or 2) hypothesis testing to uncover the mechanism(s) of CDE (Ranney 2008). The first approach uses regression-based techniques to account for known model error; a corrective equation is then used to adjust consumption estimates obtained from the model (Bajer et al. 2004a; Schoenebeck et al. 2008).   This approach has been shown to reduce model error, but does not address the fundamental cause of CDE. Recent work with largemouth bass (*Micropterus salmoides*) has shown that sustained periods of reduced food intake can lower standard metabolic rate and influence the accuracy of bioenergetics output (Ranney 2008). This is a plausible hypothesis that could explain observed model error, although it has not been evaluated for pallid sturgeon.

Growth and diet composition for juvenile pallid sturgeon are known to vary in the Missouri River basin. Studies in Montana showed that diet composition of juvenile pallid sturgeon was composed of native cyprinids (90%), primarily sicklefin (*Macrhybopsis meeki*) and sturgeon chubs (*M. gelida*) (Gerrity et al. 2006). These species are generally absent in portions of the Missouri River in South Dakota, where invertebrates compose a larger portion of juvenile diets (34 to 62%; Wanner 2007; Berg 2008). Diet composition also varies with body size in juvenile pallid sturgeon (Berg 2008), and as demonstrated by our modeling efforts, has important implications for energy acquisition. Invertebrates represented an appreciable energy source (~45%) to young pallid sturgeon (200-400 mm FL), whereas the percent contribution of fish increased to over 80% for older juveniles (500-700 mm FL). These differences have important implications for stocking and habitat enhancement efforts in the Missouri River. Spatial distribution of juvenile pallid sturgeon is correlated with invertebrate densities (Ephemeroptera and Diptera) in South Dakota portions of the Missouri River (Spindler 2007). Hence, understanding the importance of prey composition and abundance on pallid sturgeon growth can enhance efforts in choosing appropriate stocking locations and/or construction of shallow water habitat. The model developed here provides a quantitative tool for assessing energy acquisition and growth dynamics for juvenile pallid sturgeon that should prove useful for addressing research and management questions, important to recovery efforts.

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Table 1. Temperature-dependent consumption estimates for juvenile pallid sturgeon fed *ad-libitum* rations of *E. foetida.* Consumption estimates were based on 5-d feeding trials at each water temperature and averaged for each fish (N=24). Values in parentheses represent 1 SE.

Water Temperature (°C)	N	Mean fish mass (g)	Mean daily Consumption (g/d)	Mean specific Consumption (g/g/d)
13	24	63.4 (1.2)	0.5 (0.04)	0.007 (0.001)
17	24	37.9 (0.8)	0.8 (0.07)	0.02 (0.001)
21	24	37.2 (0.8)	2.4 (0.09)	0.06 (0.002)
25	24	42.6 (0.7)	5.1 (0.17)	0.12 (0.003)
28	24	58.1 (1.1)	7.0 (0.20)	0.12 (0.003)

Table 2. Equations and parameter values used in the juvenile pallid sturgeon bioenergetics model. All terms in the first column are described in Hanson et al. (1997). W represents wet weight of fish in g. For the temperature rate multiplier, the parameters V, X, Z, and Y are fitted with CQ, CTM, and CTO (as shown) or with RQ, RTM, and RTO.

Symbol	Description	Value
Consumption, C	$C = P_{Cmax} \cdot aW^b \cdot f(T)$	
P_{Cmax}	Proportion of maximum consumption ($C_{max} = aW^b$)	
a	Parameter in C_{max} equation	0.553
b	Parameter in C_{max} equation	-0.326
CQ	Q_{10} rate at low temperatures	5.9
CTO	Optimum feeding temperature	28
CTM	Maximum feeding temperature	33
Metabolism, R	$R = aW^b \cdot f(T) \cdot ACT$	
a	Parameter in R equation	0.017
b	Parameter in R equation	-0.15
RQ	Q_{10} rate at low temperatures	1.92
RTO	Optimum temperature for respiration	30
RTM	Maximum (lethal) water temperature	35
ACT	Activity multiplier, <20°C	1.0[a]
	Activity multiplier, >20°C	1.5[a]
Energy losses	$F = FA \cdot C$; $U = UA \cdot (C-F)$; $S = SDA \cdot (C-F)$	
FA	Proportion of energy egested (F)	0.1[a]
UA	Proportion of energy excreted (U)	0.04[a]
SDA	Specific dynamic action (S)	0.13[a]
Temperature rate multiplier, $f(T)$	$f(T) = V^x e^{(x(1-V))}$	
(T)	Observed water temperature (°C)	
(V)	(CTM-T)/(CTM-CTO)	
(X)	$(Z^2(1+(1+40/Y)^{0.5})^2)/400$	
(Z)	$Log_e(CQ)(CTM-CTO)$	
(Y)	$Log_e(CQ)(CTM-CTO+2)$	

[a] Niklitschek 2001

Table 3. Mean growth and food consumption for juvenile pallid sturgeon reared at water temperatures from 13 to 28 °C. Observed food consumption was measured in the laboratory; predicted consumption was estimated using the bioenergetics model for each of six simulation periods over the 86 day feeding trial (see Figure 1). The last column shows percent error between actual (observed) and predicted (model) estimates of food consumption, where negative or positive values indicate model estimates that under- or overestimate observed values, respectively. Values in parentheses represent 1 SE.

Simulation days	Mean water Temperature (°C)	Mean specific growth rate (%/d)	Mean observed Consumption (total g)	Mean predicted Consumption (total g)	Percent error $\left(\dfrac{\text{predicted - observed}}{\text{observed}}\right)\times 100$
1 to 12	18.8	-0.12 (0.006)	7.2 (0.6)	10.8 (0.5)	50
12 to 25	22.6	1.04 (0.05)	26.6 (1.3)	22.0 (0.9)	- 17.3
25 to 49	26.4	1.29 (0.06)	86.6 (2.1)	80.6 (2.9)	- 6.9
49 to 66	25.6	0.54 (0.02)	54.2 (2.7)	61.7 (2.3)	13.8
66 to 86	13.5	0.007 (0.0003)	9.1 (0.8)	22.3 (0.7)	145.1
Total		0.62 (0.02)	183.7 (5.7)	197.4 (7.2)	7.4

Table 4. Analytical results comparing observed to predicted food consumption for juvenile pallid sturgeon (N=24) fed one of four ration levels at 20°C. Analyses included paired t-test, decomposition of mean square error, and tests of intercept and slope coefficients. Significance levels are indicated as * P<0.05 or ** P<0.001 for paired t-tests comparing observed to predicted food consumption, where predicted values were estimated using a bioenergetics model. † indicates that confidence intervals on intercept or slope values do not include 0 or 1. Values in parentheses represent 1 SE.

Ration	Mean initial fish mass	Mean specific growth	Tests of Observed versus Predicted Food Consumption						
			Paired t-test		Decomposition of mean square error (% MSE)			Intercept (β_o) and Slope (β_1)	
(%/d)	(g)	(%/d)	N	T	Mean (Z)	Slope (S)	Residual (R)	$\beta_o \pm$ 95% CI	$\beta_1 \pm$ 95% CI
1	17.8 (3.2)	0.04 (0.05)	6	8.7**	0.92	0.02	0.06	-6.6 ± 5.8†	0.79 ± 0.44
2	11.3 (3.2)	0.54 (0.08)	6	3.1*	0.63	0.35	0.02	1.9 ± 0.8†	0.41 ± 0.07†
3	15.7 (2.1)	0.84 (0.28)	6	7.1**	0.83	0.03	0.14	- 5.6 ± 9.6	1.01 ± 0.64
5	16.7 (2.4)	1.58 (0.22)	6	-1.6	0.27	0.32	0.41	20.6 ± 30.1	0.38 ± 1.52

Table 5. Prey-specific consumption for two size-classes of juvenile pallid sturgeon in the Missouri River, South Dakota. A bioenergetics model was used to estimate total food consumption for an average juvenile pallid sturgeon from June-October, 2006. Consumption estimates were then adjusted to account for model error associated with water temperature and feeding rate (see text). Energetic contribution for each prey taxon was calculated as energy of prey$_i$ consumed divided by total consumption (in J). Fish prey consisted primarily (92%) of johnny darters (*Etheostoma nigrum*). Diet data were obtained from Berg (2008).

Prey taxon	Prey energy density[a]	Juvenile pallid sturgeon consumption			
		Small (105 to 158 g)		Large (598 to 620 g)	
	($J g^{-1}$ wet wt)	Total	Energetic contribution	Total	Energetic contribution
		(g)	(%)	(g)	(%)
Ephemeroptera	3016	158	44	163	15
Diptera	2536	27	6	27	2
Fish	3756	134	46	699	81
Trichoptera	2964	10	3	18	2
Plecoptera	1781	7	1	0	0

[a] Cummins and Wuycheck (1971)

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Figure 1. Growth (solid line) and water temperatures (dashed line) experienced by juvenile pallid sturgeon fed *ad-libitum* rations of *E. foetida*. Temperature dependent feeding rates were determined at 17, 21, 25, 28 and 13°C, indicated by 5-7 d acclimation periods followed by 5-d feeding trials (horizontal dashed lines).

Figure 2. Routine metabolic rate for pallid sturgeon as a function of water temperature and body size. Multiple regression was used to derive relationships among oxygen consumption (M), water temperature (T, °C), and body mass (B, $\log_e$ g wet wt) as M ($\log_e$ g O_2/d) = -6.041 + 0.852B +0.065T; $F_{2,213}$ = 2543, R^2=0.96, P<0.0001).

Figure 3. Influence of water temperature on 4-d survival of juvenile pallid sturgeon (n=6/treatment). Sturgeon (N=18, 18 to 38 g) were acclimated to 26°C, and water temperature was increased at 1°C/h until target temperatures of 29, 33 or 35 °C were achieved.

Figure 4. Mean observed (solid line) and predicted (dashed line) cumulative food consumption by juvenile pallid sturgeon fed four ration levels (1 to 5%/d) of *E. foetida* at 20°C. Predicted consumption was estimated using a bioenergetics model. Error bars represent 1 SE (N=6).
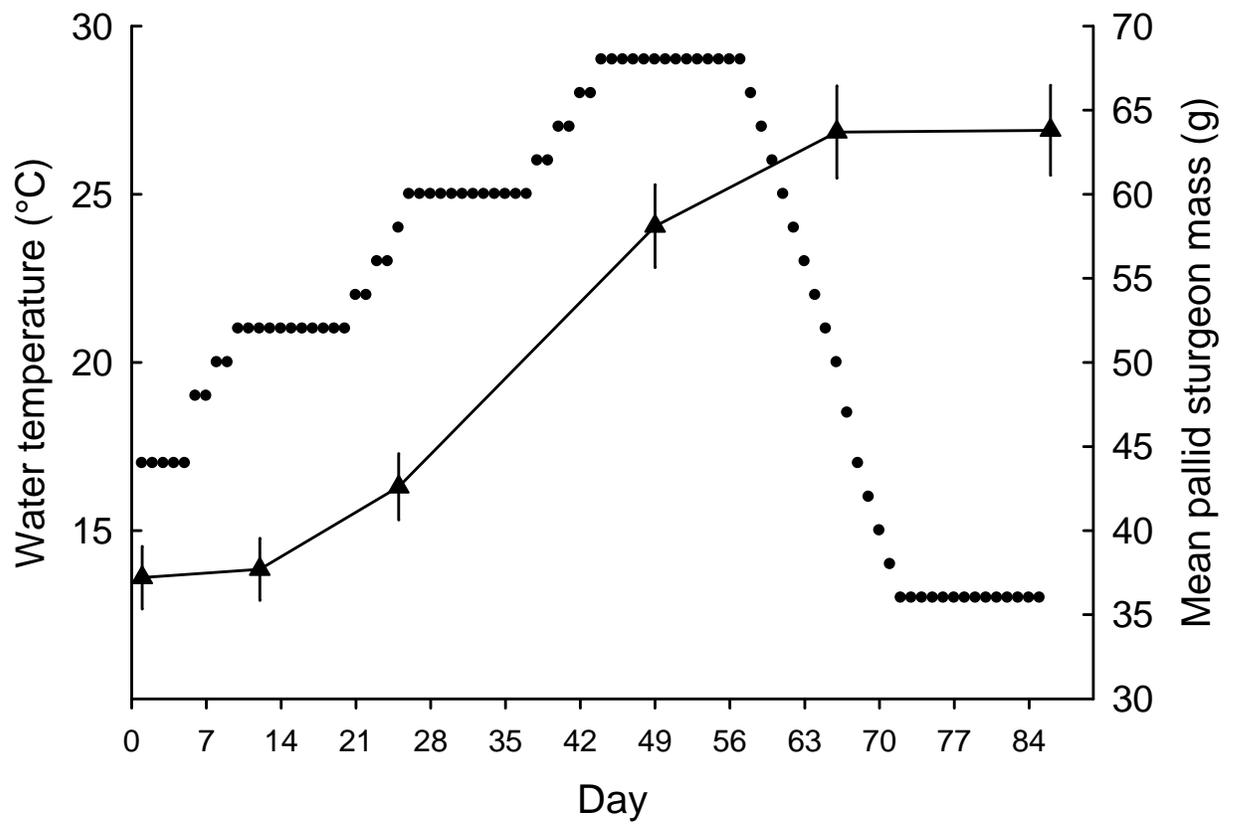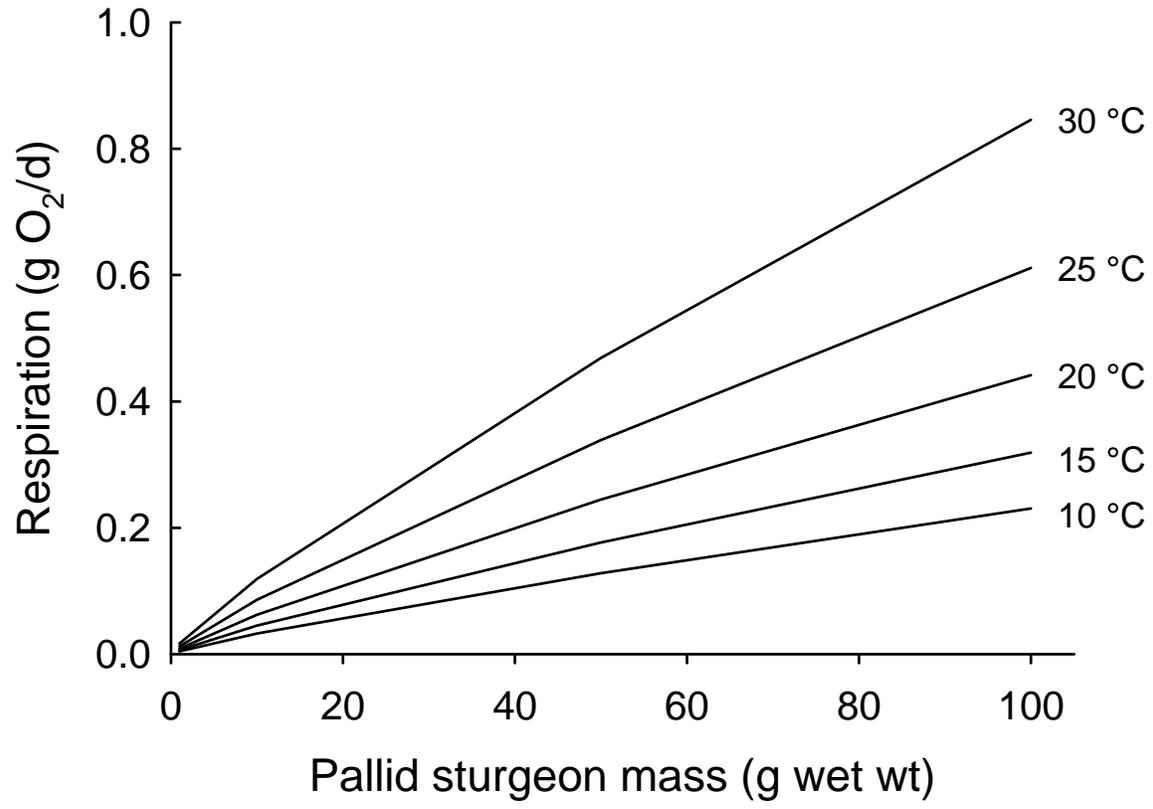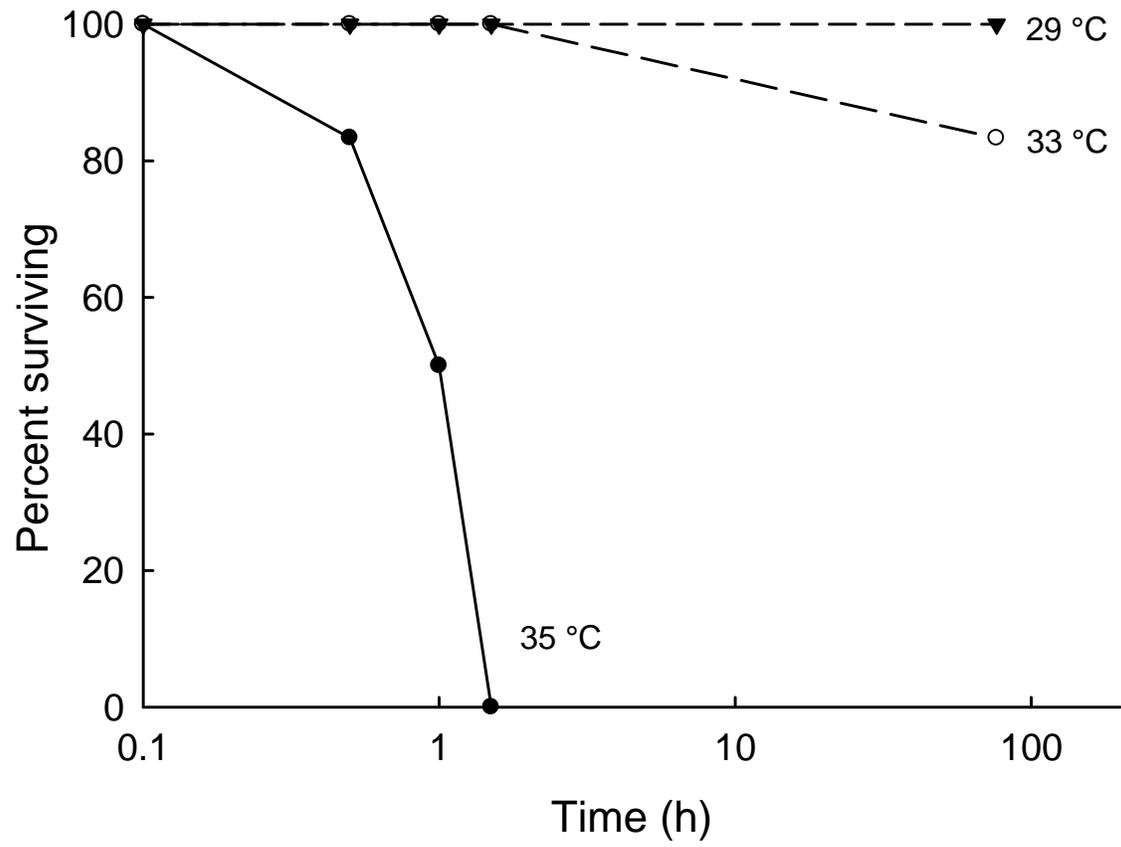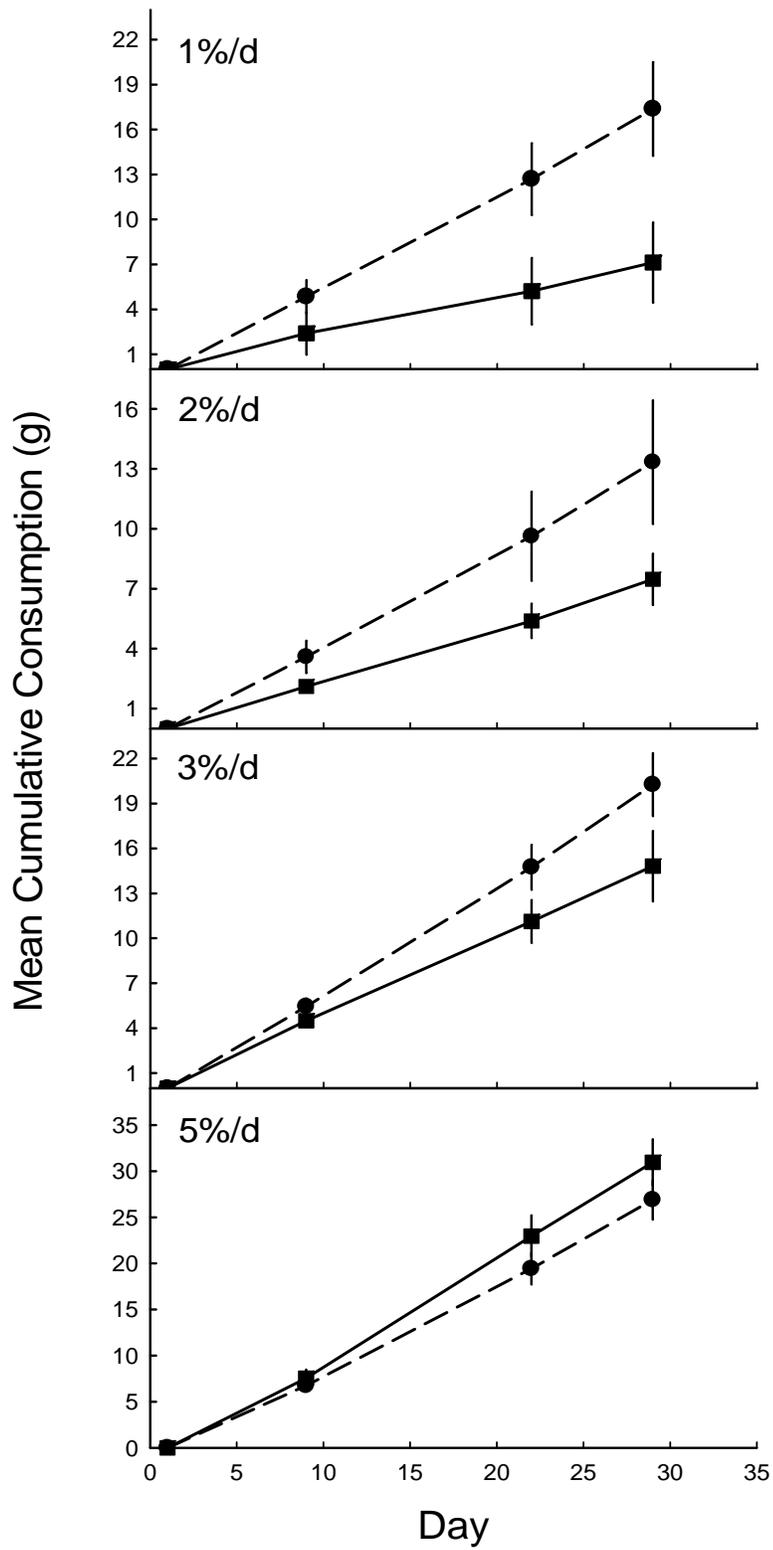
Figure 1

Figure 2

Figure 3

Figure 4

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