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**Development of a foraging model framework to reliably
estimate daily food consumption by young fishes**

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1   **Development of a foraging model framework to reliably estimate daily food**
2   **consumption by young fishes**

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17   Running head: Age-0 Pallid Sturgeon Foraging Model

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24 Abstract

25 We developed a foraging model for young fishes that incorporates handling and
26 digestion rate to estimate daily food consumption. Feeding trials were used to
27 quantify functional feeding response, satiation, and gut evacuation rate. Once
28 parameterized, the foraging model was then applied to evaluate effects of prey type,
29 prey density, water temperature and fish size on daily feeding rate by age-0 pallid
30 sturgeon (19-70 mm)(*Scaphirhynchus albus*). Prey consumption was positively
31 related to prey density (for fish >30 mm) and water temperature, but negatively
32 related to prey size and the presence of sand substrate. Model evaluation results
33 revealed good agreement between observed estimates of daily consumption and
34 those predicted by the model ($r^2 = 0.95$). Model simulations showed that fish
35 feeding on Chironomidae or Ephemeroptera larvae were able to gain weight,
36 whereas fish feeding solely on zooplankton lost weight under most conditions. By
37 accounting for satiation and digestive processes in addition to handling time and
38 prey density, the model provides realistic estimates of daily food consumption that
39 can prove useful for evaluating rearing conditions for age-0 fishes.

40

41 Introduction

42 Factors affecting growth and survival of fishes during their early life history
43 can have an important influence on recruitment dynamics (Madenjian and
44 Carpenter 1991; Fulford et al. 2006). Yet in natural environments, quantifying food
45 consumption for young fishes poses a challenge owing to their small size, fast
46 growth rates, and the heterogeneity of habitats in which they live in (Karjalainen et
47 al. 1996; Paradis et al. 2008). Modeling approaches provide an alternative means to
48 quantify foraging dynamics of fishes and have been particularly useful in studies of
49 larval and(or) endangered fishes (e.g., individual-based models; Winkle et al. 1997;
50 Nes et al. 2002; Morita and Yokota 2002; Bestgen et al. 2006).

51 The application of functional feeding models (Holling 1959) has proven
52 useful for quantifying food consumption of larval fishes in the natural environment
53 (Houde and Schekter 1980; Alanis et al. 2009; Peña-Aguado et al. 2009). Foraging
54 models of this type have been used to document predator-prey interactions that can
55 affect short (e.g., growth) and long (e.g., fitness) term population dynamics of the
56 species involved (Moustahfid et al. 2010; Hunsicker et al. 2011; Rall et al. 2012).
57 Functional feeding models pertaining to fish predators are most commonly modeled
58 as a type II functional response where intake rate declines as prey density increases
59 owing to handling time limitation of the predator (Holling 1959). The functional
60 response of predators has been shown to be species specific (Miller et al. 1992),
61 temperature dependent (Lefébure et al. 2014; Watz et al. 2014), and strongly
62 influenced by prey type and predator size (Galarowicz and Wahl 2005). Functional
63 feeding responses have been used to address a range of questions that include the

64 impact of invasive species (Alexander et al. 2014), competitive interactions between
65 two predators (Persson 1987), and effect of refugia on prey consumption (Buckel et
66 al. 2000; Anderson 2001). Although the scaling-up of model outputs from
67 individuals to populations should be used with caution (Hunsicker et al. 2011),
68 strong inferences can be made if the functional feeding model is applied correctly
69 and the appropriate assumptions are made (Rose et al. 1999). For example, studies
70 looking to quantify functional feeding responses often rely on short-term (<1 h)
71 feeding trials to prevent predators from becoming satiated and(or) prey from
72 becoming depleted. As a result, extrapolation of short-term feeding response to
73 estimate daily food consumption can be misleading because the effect of gut
74 residence time is usually not taken into account (Jeschke and Hohberg 2008). Thus,
75 it is often unknown if the predator is limited by its prey handling time or by the time
76 it takes to clear the gut (i.e., gut residence-time limited; Jeschke et al. 2002). An
77 additional concern pertains to the amount of time a predator can spend feeding on a
78 daily basis. This will often depend on the life stage (i.e., young fish tend to eat more)
79 and the foraging strategy of the predator (e.g., benthic vs. pelagic; visual vs.
80 sensory). For example, benthic predators such as species found in the Acipenseridae
81 family (i.e., sturgeons) rely on sensory barbels to detect prey and can thus feed
82 throughout the day and night (Taverny et al. 2002; Kynard et al. 2005; Ware et al.
83 2006) whereas visual predators (e.g., Salmonidae family) are limited by the absence
84 of daylight or increased turbidity (Mazur and Beauchamp 2003; Jönsson et al. 2013).

85   Limited reproduction associated with the endangered species status often
86 precludes efforts to study the feeding and growth of age-0 fish in their natural

environment (Hrabik et al. 2007). Thus, development of a reliable foraging and growth model can provide an important tool to evaluate conditions favorable towards the recovery of endangered species (Rose et al. 2013). The pallid sturgeon (*Scaphirhynchus albus*) is a large, riverine fish endemic to the Missouri and Mississippi rivers that was listed as endangered under the Endangered Species Act in 1990 (Dryer and Sandvol 1993; Wildhaber et al. 2011). As a result of ongoing recovery efforts, hatchery propagation programs routinely produce young pallid sturgeon for stocking and research (Webb et al. 2005), providing an opportunity to develop a foraging model for age-0 pallid sturgeon. Previous research has shown that prey type, predator size (Rapp 2015), and water temperature (Chipps et al. 2009; Heironimus 2015) affect ontogenetic feeding and growth patterns of age-0 pallid sturgeon. In the wild, age-0 pallid sturgeon and the closely related shovelnose sturgeon (*Scaphirhynchus platyrhynchus*) feed primarily on Chironomidae larvae or pupae and Ephemeroptera larvae (Braaten et al. 2012; Sechler et al. 2012). Although the diets of first-feeding *Scaphirhynchus spp.* have yet to be observed in the wild, laboratory experiments have shown that while zooplankton might act as a transitional food at the onset of exogenous feeding they do not represent a main energy source past the initial stages of feeding (Harrison et al. 2014; Rapp 2015). While diet observations are important in understanding the foraging ecology of young *Scaphirhynchus spp.*, they only provide a snapshot in time and cannot be extrapolated to a daily time-scale or throughout the growing season. Understanding the mechanisms that regulate prey consumption by age-0 fishes makes it possible to evaluate the impact that biotic and abiotic conditions have on energy return (Cowan

et al., 2000). The ability to quantify food consumption for age-0 pallid sturgeon could be used to evaluate habitat quality in the Missouri River.

The objective of this study was to develop a foraging model for pallid sturgeon that encompasses foraging theory and physiological processes. As a basis for our model, we used a framework developed for a terrestrial predator-prey system that incorporates the handling and digestion of prey, where hunger level (and associated feeding rate) is driven by digestive processes (Jeschke and Hohberg 2008). The model was designed to allow for the estimation of prey consumption under different temperature, prey type, prey density, prey size, and fish size conditions. Once parameterized, the model was then evaluated using a series of 24 h feeding trials across a range of age-0 pallid sturgeon sizes, where model predictions were compared to observed values of prey consumption. Finally, simulations were conducted to evaluate the effect of prey type, prey density and water temperature on daily energy acquisition by age-0 sturgeon.

Materials and methods

Foraging model framework

The foraging model for age-0 pallid sturgeon is comprised of three main components that includes (1) the functional feeding response, (2) a satiation index and (3) gut residence time (Jeschke et al. 2002; Jeschke and Hohnberg 2008). The first component is the functional feeding response that allows for the estimation of prey handling time (T_h , in min) and an associated attack coefficient (a , in m^2/min) based on initial prey density (no. prey/ m^2 or L). Handling time (T_h), in this case,

incorporates the amount of time spent on the full predatory sequence, which includes pursuing, capturing, and consuming a prey before resuming the search for the next prey. The type II functional feeding response (Holling 1959) is represented as

$$N = \frac{a \cdot T_f \cdot x}{(1 + a \cdot T_h \cdot x)} \quad (1)$$

where N is the amount of prey consumed per unit time, a is the attack coefficient, T_f is the duration of a feeding trial (i.e., 15 min), x is prey density, and T_h is handling time. Using estimates of N from equation 1, we developed a multiple regression model to predict prey consumption (N') as a function of pallid sturgeon length (L), prey type (Prey), water temperature (Temp), and prey density (Density) as

$$N' = a_0 + a_1 L + a_2 \text{Prey} + a_3 \text{Temp} + a_4 \text{Density} \quad (2)$$

where a_0 is the intercept value, and a_1 - a_4 are regression coefficients. Prey consumption (N') can then be integrated over time as

$$\frac{dy(t)}{dt} = N' \cdot 4 \cdot h(t) \quad (3)$$

where N' is feeding over a 15-min interval, given by equation 2 (multiplied by 4 to estimate hourly consumption), and the hunger level at time t ($h(t)$). The hunger level varies between 0 and 1, with a value of 1 indicative of a hungry fish (i.e., empty gut) and a value of 0 corresponding to a fully satiated fish. As prey are consumed (given by y in equation 3) by the predator, h is affected as

$$\frac{dh(t)}{dt} = \frac{1-h(t)}{t_g} - S \cdot y(t) \quad (4)$$

where S is the satiation index that specifies the proportion an individual prey item constitutes of a fish's stomach fullness (see below; 2. Satiation). The gut retention

time (t_g) is used to adjust h based on the time it takes to generate space in the gut to allow for the ingestion of additional prey. Finally, prey density decreases with time and can be calculated as

$$x(t) = x_0 - y(t) \quad (5)$$

where prey density at a given time, $x(t)$, is dependent on the initial prey density (i.e., before the beginning of the feeding trial; x_0) and the number of prey eaten at time t ($y(t)$ given by equation 3). The full foraging model consists of the coupled equations 3, 4, and 5 (Jeschke et al. 2002; Jeschke and Hohberg 2008). Depending on the prey taxa, handling time or gut residence time can limit prey ingestion by predators. Once fully parameterized (see methods below), the model can then be used to calculate daily prey consumption by integrating the three state variables (y , h and x) on an hourly basis (24 time steps per day) using the deSolve package in R (Soetaert et al. 2010). It is important to mention here that 24 hour time steps were used for the pallid sturgeon foraging model as preliminary experiments did not show diurnal effects on consumption rate. Integration time steps of the model should be reduced to accommodate species with shorter feeding periods. All statistical and modeling implementations were performed using R (R Core Team 2014) and values were found to be significant when $\alpha = 0.05$.

Model parameterization

Fish Rearing

Larval pallid sturgeon were the progeny of captive broodstock held at the U.S. Fish & Wildlife Service Gavin's Point National Fish Hatchery (Yankton, South

Dakota). Fish used in the experiments were produced in June of 2012 and 2013 and came from multiple family strains. During both years, one-day post-hatch larvae were transported to South Dakota State University (Brookings, South Dakota) in oxygenated water (~50 individuals/L) from the hatchery. Upon arrival, larvae were placed in 38 L aquaria at 16 °C (similar as hatchery temperature) and acclimated to 14, 18, or 24 ± 1 °C at a rate of 1°C/h. Fish were acclimated at these temperatures for at least 5 days prior to any experimentation. Once the fish were able to feed exogenously (~18-19 mm), they were fed a mixture of dry food (70% Otohime and 30% Cyclopeeze; Kappenman et al. 2011) and thawed Chironomidae larvae. In addition, live prey items (*Daphnia* spp., Ephemeroptera and Chironomidae larvae) were fed in small quantities to the fish to avoid a naïve behavior during the feeding trials that used live prey. Dry food was removed from the diet once the fish had reached 30 mm in total length. Fish were fasted for 24 h prior to any trials to ensure gut clearance. Fish from the same cohort (both in 2012 and 2013) were used as they grew to accommodate experimentation on different size classes. Finally, fish were never used more than once for any given trial.

1. *Functional feeding response*

We quantified the functional feeding response of pallid sturgeon larvae (19, 20, 30, 40, 50, and 70 mm total length) fed three prey types at water temperatures of 14, 18 and 24 °C. Prey types fed to pallid sturgeon included either *Daphnia* spp., Ephemeroptera larvae or Chironomidae larvae. Larger pallid Sturgeon (70 mm) were only fed Chironomidae larvae, because previous work showed nearly exclusive

feeding on this prey by fish > 50 mm (Rapp 2015). Feeding trials were conducted in aquaria (900 mL with area of 0.095 m² for 18-30 mm size classes; 2600 mL with area of 0.0345 m² for 40-70 mm size classes) that were placed in a water bath (450 L raceways) where water temperature was controlled using either a bayonet heater (1700W; Process Technology, Mentor, OH) or a chiller unit (Frigid Units, model D1-33, Toledo, OH) set to maintain target temperatures of 14, 18, or 24°C. Small pumps were placed at either end of the raceways to ensure a uniform temperature was maintained. The size of the aquaria was large enough to allow fish to swim a minimum of 3 body lengths in one direction regardless of fish size.

The range of prey densities used in the feeding trials was chosen based on values reported for the Missouri River (Grohs 2009; Rapp 2015). *Daphnia spp.* densities ranged from 15 to 90/L, whereas Chironomidae and Ephemeroptera densities ranged from approximately 150 to 900/m² (Grohs 2009). Chironomidae larvae were collected in a local pond and transported to the laboratory where they were sorted using 250, 500 and 750 µm sieves. Mean size of prey (length in mm) used on the day a feeding trial was completed was quantified from digital pictures (n=3) of 10 individual prey items taken from a stock tank. The invertebrates used for the pictures were not used in the feeding trials. Pictures were imported into Image J (Abràmoff et al. 2004), and mean prey lengths were calculated. Because Chironomidae represent an important component of young pallid sturgeon diets (Braaten et al. 2012; Sechler et al. 2012; Harrison et al. 2014), we conducted feeding trials using four size groups of chironomids that included small (6.07 mm ± 1.52 S.D.; 0.002 g ± 0.001 S.D.), medium (9.17 mm ± 1.49 S.D.; 0.005 g ± 0.001 S.D.), large

(11.49 mm $\pm$ 1.63 S.D.; 0.010 g $\pm$ 0.002 S.D.) or mixed (9.38 mm $\pm$ 2.71 S.D.) size classes. The use of different chironomid groups was intended to document size-dependent capture rates by sturgeon and provide consumption estimates that were representative of what would be found in the wild. No substrate (i.e., bare tank) was used during these feeding trials, although in feeding trials using the “mixed” size chironomids, we quantified sturgeon consumption in aquaria with or without sand substrate. These additional trials were conducted because pilot studies indicated that chironomids build sand casings within the first 30 min of being introduced to the aquaria, and we hypothesized that this behavior could negatively affect the foraging efficiency by pallid sturgeon. Fine silica sand (Granusil Silica) was used as a substrate to facilitate the burrowing behavior of chironomid larvae and was placed to cover a depth of $\sim$ 1 cm off the bottom of the containers. Trials using small, medium or large size classes of Chironomidae were performed in aquaria without sand substrate. In the “mixed” size group, chironomids were released into the aquaria to allow them to bury if sand was present. Then, the sturgeon were placed on a fine meshed screen that was installed midway through the water column of the aquaria. This allowed the sturgeon to acclimate to the aquaria without having access to the prey. After a 30-min period had elapsed, the screen was removed and the fish could begin foraging on the prey.

We collected Ephemeroptera larvae (Baetidae, Ephemeridae, and Heptageniidae) in a local stream using a kick net. In the laboratory, Ephemeroptera larvae were carefully removed from the samples but were not sorted since the range of sizes (2 to 6 mm) was small. Methods for Ephemeroptera larvae feeding trials

were similar to those for chironomids; however sand substrate was not used because pilot studies showed that mayflies did not display a burrowing behavior. Ephemeroptera larvae averaged $3.83 \text{ mm} \pm 1.55 \text{ S.D.}$ in length and $0.006 \text{ g} \pm 0.010 \text{ S.D.}$ in weight. *Daphnia spp.* ($1.90 \text{ mm} \pm 0.58 \text{ S.D.}$; $0.125 \text{ mg} \pm 0.100 \text{ S.D.}$) were collected in a local pond and sifted through a 2 mm sieve to remove large individuals ($>2 \text{ mm}$) that exceeded the gape dimensions of the first-feeding sturgeon size-class (Snyder 2002). *Daphnia spp.* were introduced after the sturgeon had acclimated to the container.

Feeding trials were always performed using a single fish per aquarium and were replicated five times for each combination of fish size, water temperature, prey density, prey type, and(or) prey size (i.e., Chironomidae). In addition, we used a total of six prey density treatments for fish $\leq 40 \text{ mm}$ while five prey density treatments were used for the 50 and 70 mm size classes. Thus, for 20 mm pallid sturgeon maintained at 14°C , a total of 30 fish were used to evaluate predation rates on *Daphnia* at densities of 15 to 90/L (i.e., five fish per density; Table 1). Similarly, for 50 mm pallid sturgeon feeding at 24°C on small Chironomidae (180 to 900 individuals/ m^2), a total of 25 fish were used (Table 1). After being transferred to aquaria, fish were acclimated for 30 min before allowed to feed for 15 min. At the end of each trial, we removed fish from the aquaria and remaining prey items were counted. Consumption rates (number of prey eaten/15 min) were used to generate parameter estimates for equation 1 for each feeding trial. Parameters for T_h and a were estimated using the nlsLM function in R for non-linear regression (Elzhov et al. 2013). Prey depletion was taken into account using the Lambert W function from

the emdbook package (Bolker 2013). In some cases, small pallid sturgeon (≤ 30 mm) had difficulty capturing prey items resulting in the absence of a significant effect of prey density on the number of prey consumed. In these cases, the mean number of prey eaten (N_m) across all prey density trials was used instead of estimating N .

Using estimates of N or N_m , we developed a multiple regression model for predicting prey consumption (N') as a function of pallid sturgeon size (L), prey type (Prey), water temperature (Temp), and prey density (Density) (see equation 2). Both N' and L were transformed using a natural logarithmic transformation to meet assumptions of normality and homogeneity of variance. Prey types (Prey) were analyzed as a categorical variable and included small, medium, mixed or large chironomids on bare substrate, mixed chironomids on a sandy substrate, Ephemeroptera larvae, or zooplankton treatments (total of 7 prey treatments). Estimates of N' for each prey type were calculated by adding or subtracting their parameter estimates from the intercept value based on the reference prey type (i.e., large chironomids). Because zooplankton and benthic invertebrate densities are presented in different units (individuals per L or per m^2), prey density (Density) was expressed as a proportion of maximum prey density (i.e., maximum density = 90 for *Daphnia* and 900 for Chironomidae/Ephemeroptera larvae) to explain the variability associated with prey abundance. For example, a prey proportion value of 0.5 was equivalent to 45 *Daphnia*/L or 450 chironomids/ m^2 .

2. Satiatiati

Satiatiati was calculated using short term (90-180 minute) feeding trials that quantified the maximum amount of food a fish could eat when offered an *ad-libitum* ration. Trials were performed using four size groups of age-0 pallid sturgeon that were acclimated to 24°C (optimum feeding temperature; Heironimus, 2015); mean length of each size group was 19 (± 0.48 S.D.), 25 (± 3.29 S.D.), 68 (± 7.14 S.D.), or 122 (± 12.66 S.D.) mm. The range in size groups was intended to quantify the effects of fish size on satiatiati throughout the first growing season. Individual fish were placed in 900 mL aquaria and allowed to acclimate for 24 h without being fed. Following the acclimation period, smaller pallid sturgeon (19 and 25 mm) were fed 10 live Chironomidae larvae (0.001 and 0.005 g wet weight/chironomid) whereas larger sturgeon (68 and 122 mm) were fed thawed Chironomidae larvae (Hikari Bio-Pure) representing ~5 % of their body weight. The smaller groups of fish (19 and 25 mm) were allowed to feed for 30, 60, 90, 120, 150, or 180 min while the larger group of fish (68 and 122 mm) were allowed to feed for 15, 30, 45, 60, 75, or 90 min. The difference in time intervals between the small and large fish groups was necessary due to significantly longer handling times for smaller fish feeding on live prey. A total of 5 replicates per foraging time were used for each size class of fish. After each feeding trial had ended, the remaining chironomids were quantified and converted to biomass. To account for the change in thawed chironomid weight that might occur over time, control trials without fish (n=5 at each temperature) were performed and prey weight loss was added to the weight of the recovered food. At

the end of the trial, the fish were weighed wet (ingested food weight was subtracted) and measured for total length.

For each pallid sturgeon size group, a one-way ANOVA was performed with foraging time as the independent factor and food consumed (in g) as the dependent variable. Maximum stomach fullness was identified when there was no longer a significant increase in the mass of prey consumed with an increase in foraging time. The mean consumption value that corresponded to stomach fullness (i.e., when the fish could no longer ingest additional prey; S_{Full}) was expressed as

$$S_{Full} = S_0 e^{r \cdot L}, \tag{6}$$

where S_{Full} is the maximum amount of food a fish can eat (in g), S_0 and r are intercept and slope coefficients and L is fish length in mm. The satiation index (S) indicates the relative amount of a given prey that can be stored in the gut and was calculated as

$$S = 1/S_{Full}/prey_i \tag{7}$$

where $prey_i$ is the weight (g wet weight) associated with an average prey item (*Daphnia*, Ephemeroptera larvae or chironomid). Values for S vary positively with mean size of individual prey; small prey have lower S values whereas larger prey have greater S values. It is assumed that all invertebrate prey items have a similar specific gravity and thus a similar volume (Spaargaren 1979), implying that a fish of a given size can fit the same amount of weight in its gut regardless of the prey taxon.

3. Gut residence time

Because stomach fullness in fishes can affect the functional feeding response, we quantified gut residence time in pallid sturgeon as a function of body size and water temperature (14, 18, and 24°C). Trials lasted 24 hours while guts of fish were examined every 4 h. For each temperature treatment, fish were divided into groups of 5 for each 4-hour interval (0, 4, 8, 12, 16, 20 and 24 h) and placed individually in 900 mL aquaria. Fish (40-110 mm) were fed a known amount of thawed chironomids (~ 5% Body Weight) for 30 min and the amount of food consumed was calculated after correcting for uneaten chironomids (regurgitation was not observed), which were removed following the 30 min feeding period. This procedure ensured fish had a full stomach by the end of the feeding period. Fish were serially sacrificed using Tricaine-S (Western Chemical inc.; [200 mg/L]) over a 24 h period (4-hour time intervals) to examine evacuation rates. The stomach was cut open and food items were removed with forceps, blotted dry to remove excess water, and weighed to the nearest mg. Individual fish were also weighed and measured before the gut was removed. Gut residence time data followed an exponential decline over time (Bochdansky & Deibel, 2001) that could be described as

$$V_t = V_0 e^{-rt} \quad (8)$$

where V_t is the proportion of food left in the gut based on the amount of food ingested, V_0 is the intercept coefficient, r is the slope coefficient and t is the time interval. A multiple regression model was constructed using the slopes (r ;

dependent variable) generated from the different fish size (L) and temperature (Temp) combinations (N=9; 3 size categories x 3 temperatures) as

$$r = a_0 + a_1L + a_2Temp, \tag{9}$$

where a_0 , a_1 and a_2 are the intercept and respective slope coefficients. The model was then used to estimate t_g or the time to it takes to empty the gut as

$$t_g = \frac{\log(0.01)}{-r} \tag{10}$$

Model evaluation

To evaluate the performance of the model, we conducted a series of 24 h feeding trials using a range of fish sizes (19-130 mm), Chironomidae larvae density, and water temperatures (14, 18 and 24°C; Table 2). Each treatment was replicated 5 times. Fish were allowed to acclimate to their aquaria for 24h where food was not provided. Prey items were introduced following the acclimation period and given 30 min to burrow (fish were isolated from the ground using screened mesh mid-way through the water column) before fish were given 24 h to forage. Each aquarium contained a sand substrate to allow for the chironomids to burrow. After the 24 h period, the fish were removed and measured (total length in mm), and any prey not consumed were quantified.

Observed consumption values were compared to those predicted by the foraging model using linear regression analysis. To generate consumption estimates, integration of equations 3, 4, and 5 was performed over 24 hours (i.e., 24 iterations). The hunger level was set to 1 at the beginning of the model run to indicate that fish started with an empty gut. From the regression model, Bonferroni

joint confidence intervals for the intercept and slope coefficients (i.e., 97.5% joint confidence interval) were used to test the joint null hypothesis that the intercept and slope coefficients were equal to 0 and 1, respectively. Thus, deviation from the joint null hypothesis indicates divergence between the observation and model prediction. Additionally, the decomposition of mean square error (MSE) was used to partition the variance into error associated with differences in the means (observed and predicted), error associated with the slope differing from 1, and error linked to residual variation (Rice and Cochran 1984).

Daily energy return

Daily maximum energy return ($E_{\max}$) for each pallid sturgeon size group (19, 20, 30, 40, and 50 mm) was calculated as,

$$E_{\max} = y_{24} \cdot w_i \cdot ED_i \quad (11)$$

where y_{24} is the number of prey items consumed over a period of 24 h (see equations 3, 4 and 5), while w_i and ED_i represent average weight (in g) and energy density (in J/g), respectively, associated with prey i . Prey energy densities used were 2310, 2922 or 3368 J/g for zooplankton, Chironomidae, and Ephemeroptera larvae, respectively (James et al. 2012). For each prey taxon, $E_{\max}$ was calculated for all prey density (proportion of maximum density used in the functional feeding experiments ranging from 0 to 1; prey depletion was not allowed) and temperature combinations (14, 18 and 24°C). $E_{\max}$ outputs were compared to the minimal amount of energy required for a fish of a given size to maintain its weight over the course of a day (i.e., maintenance ration). This maintenance ration (MR) provides

sufficient energy for metabolic and waste processes, but does not allow for growth to occur. To do so, the bioenergetics model developed by Heironimus (2015) was used and can conceptually be written as

$$MR = (R + ACT + SDA) + (F + U) \tag{12}$$

where MR is balanced by respiratory demands (i.e., standard metabolism (R), active metabolism (ACT), and specific dynamic action (SDA)) and waste losses (i.e., egestion (F) and excretion (U)). Standard metabolism is regulated by fish weight and water temperature, ACT is dependent on water temperature, while SDA, F, and U costs are given as a proportion of energy consumed. All parameters and equations for the bioenergetics model can be found in Heironimus (2015) and Deslauriers et al. (2016). Because fish weight is used as input in the bioenergetics model, fish length was converted to weight using the equation,

$$\log_{10} W = \frac{(\log_{10} L - 1.865)}{0.367}, \tag{13}$$

where W is the weight of the fish (g) and L is the total length (mm; Heironimus 2015). The initial weight calculated for each size class was also used as the final weight value. We used a value of 2736 J/g as input for pallid sturgeon energy density (Heironimus 2015). Bioenergetics model simulations were used to generate a daily maintenance ration (in Joules/d), which was subtracted from $E_{\max}$ (equation 11) to calculate the net energy gain/loss of fish feeding on zooplankton, Chironomidae, or Ephemeroptera larvae.

Results

Functional feeding response

Age-0 pallid sturgeon (≥ 40 mm) displayed a type II functional response across all prey types and sizes. However, for fish < 40 mm, most predation rates did not vary with prey density, thus functional feeding coefficients were not generated. As fish grew in size, capture rates for all three prey types (zooplankton, Chironomidae and Ephemeroptera larvae) increased (Figure 1; see Table 3 for regression coefficients). On the average, fish were able to capture more Ephemeroptera larvae per unit of time, with 14% and 19% less zooplankton and Chironomidae larvae being consumed, respectively. The presence of sand substrate decreased foraging efficiency on chironomids by 86% compared to feeding off a bare substrate (Figure 1; Table 3). Prey size also influenced capture rates, with large (avg. 11 mm) and medium (avg. 9 mm) sized chironomids being captured 58% and 18% less often than small chironomids (Figure 2; Table 4 and 5). As a result, the maximum amount that could be ingested over a period of 15 min (N') was calculated for the different prey densities and a multiple regression was generated. The model ($F_{9,1160} = 425.1$; $R^2=0.77$; $p<0.001$) indicated that fish size, water temperature, prey density, prey type and the presence of sand substrate all played a significant role in determining the amount of prey that could be ingested over time (Table 5).

Satiation

Foraging time did not affect consumption for the 19 mm ($p = 0.206$), 25 mm ($p = 0.592$), or 68 mm ($p = 0.101$) size groups and they were thus satiated within 30,

30, or 15 min, respectively. Foraging time was found to significantly affect consumption for the larger size class of sturgeon (122.2 mm), that required 45 min to become fully satiated ($p = 0.002$). Stomach fullness (S_{Full} , in g) was positively related to fish size (L , in mm) as $S_{\text{Full}} = 0.016 \cdot e^{0.027 \cdot L}$ ($n = 20, p < 0.001$); size-dependent, stomach fullness estimates were then input into equation 7 to account for weights associated with individual prey taxa (Figure 3).

Gut residence time

Gut residence time was significantly affected by water temperature and followed an exponential decline over time (Figure 4). The slope coefficient (r ; equation 8; see materials and methods section) from each gut residence time trial was used to build a multiple regression model where the slope coefficients for both fish size (L) and water temperature (Temp) were found to be significant (Figure 5; $F_{2,6} = 28.5$; $R^2 = 0.87$; $p < 0.001$). The regression model can then be expressed as,

$$r = 0.25 - 0.06 \cdot \log_e(L) + 0.006 \cdot \text{Temp}$$

The model indicated that gut residence times were shortest for smaller fish at warmer temperatures and longer for larger fish at colder temperatures (Figure 5).

Model evaluation

Model predictions, on average, overestimated observed food consumption values by 19.6 % ($[1 - (\text{Predicted}/\text{Observed})] \times 100$). Observed food consumption was only slightly underestimated for the small (19 mm; $n=30$; -1.0%) and large (100 mm; $n=75$; -1.1%) size classes; however, for intermediate-sized fish (20 and 40 mm;

n=91) observed food consumption values were overestimated by 47.9% and 18.4%, respectively (Figure 6). Regression of observed versus predicted values for all feeding trials resulted in confidence intervals for the intercept and slope that included 0 and 1, respectively (Table 2). MSE of observed and predicted consumption values were influenced largely by the residual component (72—95%), while the mean and slope were associated with 4—20% and 1—14% of the variance, respectively (Table 2). These results indicate that the model predictions were able to capture relative differences between treatments and provide reasonable estimates for consumption.

Daily energy return

Model simulations of daily energy consumption showed that fish could maintain their weight and allocate energy towards growth when feeding on Chironomidae and Ephemeroptera larvae even at low prey densities (proportion = 0.1) or water temperatures (14°C; Figure 7). In contrast, fish feeding on zooplankton could not satisfy their daily energetic needs until they reached sizes of 40 mm and were provided ≥ 45 zooplankton/L (i.e., Density = 0.5). Additionally, the simulations demonstrated that fish smaller than 30 mm were limited by prey handling time while larger fish were limited by their gut residence time. Lastly, energy acquisition differences existing between fish feeding on Chironomidae compared to Ephemeroptera decreased as fish increased in size.

Discussion

The feeding dynamics of age-0 pallid sturgeon were strongly influenced by prey type, water temperature and sturgeon size. As reported with other fishes, age-0 pallid sturgeon were able to increase their search ability (i.e., attack coefficient) and decrease prey handling time as they became larger (Miller et al. 1992; Galarowicz and Wahl 2005; Gustafsson et al. 2010). Increases in foraging efficiency can be attributed to an increase in swimming ability (Hunter 1972; Brachvogel et al. 2012), a wider gape size (Wanzenböck 1995), and a larger detection span (Nunn et al. 2011; Watz et al. 2014). Furthermore, larger individuals are able to access a greater number of prey that may be inaccessible to smaller fish (Anderson 2001), such as the case building chironomid larvae. Oppositely, smaller fish with limited swimming abilities might be at an advantage in laboratory feeding studies, as the area to explore is much more limited than it would be in a natural setting. However, linking empirical data from diet studies (Grohs et al. 2009; Braaten et al. 2012; Winders et al. 2014) and prey selectivity experiments (Rapp 2015) to our modeling framework, allowed us to generate reliable estimates of prey consumption under controlled conditions.

Digestion rates and satiation indices were both important parameters in regulating the amount of food consumed over the course of a day (Gill and Hart 1994; Munk 1995; Jeschke and Hohberg 2008). However, a sensitivity analysis of the foraging model combined with a bioenergetics model (Heironimus 2015) found that prey consumption estimates were more sensitive to satiation rather than evacuation (Deslauriers et al. 2016). This observation does not appear to be

applicable to smaller sturgeon as the ability to rapidly evacuate food at higher water temperatures ensured that small sturgeon (19-30 mm) never became satiated. As a result, smaller sturgeon continuously searched for food because they were not able to capture food at a rate fast enough to satiate the gut, regardless of water temperature. On the other hand, modeling results showed that larger sturgeon could become satiated when feeding on Chironomidae or Ephemeroptera larvae because of a the combination of short handling times and slower gut evacuation rates. Only when simulations involved fish feeding on zooplankton was satiation not observed, even if feeding rates were high. Thus, zooplankton may not provide sufficient net energy return to age-0 pallid sturgeon, supporting related studies that show generally low prey selectivity for zooplankton by age-0 sturgeon (Rapp 2015).

Sturgeon <40mm were found to be very inefficient predators as indicated by the lack of a functional relationship for most treatments. They appeared able to detect prey items but they could not capture the prey or if they did, they would rapidly swim upwards and often end up losing the prey they had captured. While this behavior was observed for all prey types, separate experiments provided the opportunity to observe unique behaviors. For example, small zooplankton were rarely captured in the water column but were captured when located at the bottom of the tank, or by the pressing of the prey against the side of the tank before ingesting. This behavior indicates that the capture efficiency would likely be reduced in a natural setting, thus leading us to speculate that zooplankton consumption provides a very negligible source of energy. Interestingly, the capture efficiency of zooplankton increased with fish size indicating that larger pallid

543 sturgeon could forage on these prey types if given no other choice. However, these
544 predators discriminate against such prey in the presence of other, more easily
545 captured prey with higher energy densities (Rapp 2015). In addition, most fish <50
546 mm were not able to break through the sand casings built by Chironomid larvae.
547 The fish would often be able to detect a buried prey and would attack it repeatedly,
548 but would fail in capturing the prey. Ingestion thus came from chironomids that had
549 not buried, or that had been forced out of their casings by the pressure applied by
550 the sturgeon. Once the fish reached ~50 mm, they were able to create a small
551 opening in the casing and strip the prey from it. Fish >70 mm were often seen
552 swallowing the prey along with its casing, and expelling sand from the mouth and
553 gill slits before ingesting the prey. Interestingly, energy return was very similar
554 across all chironomid treatments, indicating that the fish are able to compensate
555 high handling times with higher energy returns. Pallid sturgeon <50mm, however,
556 were not able to capture a significantly larger amount of Chironomidae larvae
557 compared to Ephemeroptera larvae despite greater mobility associated with the
558 latter prey type. This result might have differed if trials had been performed under
559 varied water velocities, in larger foraging arenas, or by using different substrata (e.g.
560 gravel, cobble, vegetation) where Ephemeroptera larvae would have been more
561 likely to cling to the substrate or escape. Based on daily energy estimates, larger fish
562 would be able to gain about twice the energy feeding on mayflies while spending the
563 same amount of time foraging on Chironomidae larvae. This result agrees with
564 empirical diet data from pallid sturgeon captured in the Missouri River, where the

fraction of Ephemeroptera larvae in guts has been shown to increase with fish size (Grohs et al. 2009).

Optimal foraging theory predicts that predators will seek to minimize prey handling time while maximizing energy return associated with available prey items (Pyke 2003). By extension, age-0 pallid sturgeon would likely benefit from foraging on Ephemeroptera larvae. However, when faced with the choice between Chironomidae and Ephemeroptera larvae, age-0 pallid sturgeon will almost exclusively select chironomids (Rapp 2015), indicating that prey selection might not always be dictated by energy return (Marcotte and Browman 1985). One of the problems associated with calculating energy returns in this case is that it does not take fish activity levels into consideration (Giacomini et al. 2013). It is very likely that age-0 sturgeon spend more energy (e.g., swimming) trying to capture Ephemeroptera larvae than they would for Chironomidae larvae, thus negating the higher energy contribution of mayflies. In turn, activity levels would be expected to decrease as the fish get larger, thus rendering Ephemeroptera larvae an appealing prey for juvenile pallid sturgeon prior to switching to piscivory (Sherwood et al. 2002; Grohs et al. 2009).

As with all models, a thorough evaluation process requires confronting model output with independent data before it can be applied to test hypotheses (Hilborn 1997). In the current study, the evaluation process focused on the ability of age-0 pallid sturgeon to forage on Chironomidae larvae since it has been shown that these taxa are highly preferred in a riverine setting. The model slightly overestimates consumption at higher prey densities for the intermediary size

classes (i.e., 20 and 40 mm), mirroring results that have employed this modeling strategy in the past (Jeschke and Hohberg 2008). Reasons for overestimation might be attributed to an accumulation of indigestible components (e.g., sand, chitinous body parts) in the gut of the fish resulting in a higher degree of satiation not accounted for in the S and t_g parameters. In addition, chironomid larvae were sometimes difficult to access if they had settled close to the walls of the containers. This problem became increasingly apparent as fish size increased and contact between the fish's rostrum and the side of the aquaria prevented them from capturing some prey. Such a restriction often resulted in remaining prey at the outer edges of the container. This tank effect was more likely to occur during the 24h feeding trials than in the short-term 15-min trials. This is another example where tank restrictions might have affected the foraging behavior of the fish and is something to consider when looking to apply any foraging model. Lastly, the model did not consider predator and(or) prey diel effects (Nunn et al. 2011) or prey tax-dependent gut residence time (Jobling 1987), which have been shown to affect other fish species.

The use of laboratory-derived models to address questions in the natural environment has often been criticized because factors that affect prey encounter rates are difficult to replicate in a captive setting (MacKenzie et al. 1990). Caution should always be taken in the application of models developed in a laboratory setting because observed behaviors, as seen in this study, likely differ from those fish experience in their natural environment. It is also important to account for the ecology and biology of the fish under study, as those are likely to differ between taxa

and will influence the study design. These challenges notwithstanding, the model framework presented here can provide a reasonable approach for comparing relative differences in food consumption among age-0 pallid sturgeon in the natural environment as a function of sturgeon size, prey type, prey density, and water temperatures. Specifically, early life forms of pallid sturgeon are believed to inhabit a wide range of habitats that vary in water temperature and velocity (Wildhaber et al. 2011), prey type and density (Troelstrup and Hergenrader 1989; Hay et al. 2007) and substrates (Gerrity et al. 2008). In this study, we have shown that age-0 pallid sturgeon can sustain growth at low Ephemeroptera and Chironomidae larvae densities (~ 10 ind./m²) and cannot rely solely on zooplankton to develop. The behavioral and physiological constraints accounted for by the model help provide conservative estimates of food consumption, and facilitates the hypothesis testing (e.g., diet switch under sub-optimal conditions to confer greater energy gain) given reliable, *in situ* prey energy density estimates. Applications of the model could use the consumption estimates in combination with a bioenergetics model to simulate growth associated with different river regulation scenarios involving water temperature fluctuations. Similarly, the model could be applied to evaluate conditions found in shallow water habitats (water depth < 1.5 m and water velocity < 0.6 m/s) currently being constructed to enhance recovery of the species (Gemeinhardt et al. 2016).

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Table 1. Conditions used to generate the functional feeding responses of age-0 pallid sturgeon. All trials lasted 15 min.

Total Length	Temp.	<i>Daphnia</i> Density	Chironomidae/Mayfly Density	Chironomidae size ^{1,2}
mm	°C	inds/L	inds/m ²	class
19	14, 18, 24	15,30,45,60,75,90	150,300,450,600,750,900	Small,Medium,Mixed,Large
20	14, 18, 24	15,30,45,60,75,90	150,300,450,600,750,900	Small,Medium,Mixed,Large
30	14, 18, 24	15,30,45,60,75,90	150,300,450,600,750,900	Small,Medium,Mixed,Large
40	14, 18, 24	18,36,54,72,90	180,360,540,720,900	Small,Medium,Mixed,Large
50	14, 18, 24	18,36,54,72,90	180,360,540,720,900	Small,Medium,Mixed,Large
70	14, 18, 24	NA	180,360,540,720,900 ²	Mixed

¹: Only mixed size classes for chironomids were tested with and without a sand substrate

²: Only chironomids were tested for 70 mm sturgeon

Table 2. Conditions used to evaluate the age-0 pallid sturgeon foraging model along with their respective evaluation metrics. All trials (n=5 per combination) lasted 24h and were performed using a sand substrate. Mixed sizes of chironomids (9.38 mm $\pm$ 2.71 S.D.) were used for all trials. A total of 210 fish was used to evaluate the model. Values in parentheses represent 1 S.D., C.I. indicates the 97.5% confidence intervals while MSE symbolizes the mean square error components.

Experimental Conditions				Model Evaluation				
Size mm	Temperature °C	Prey given individuals	Container Area m ²	Intercept C.I. 1.25—98.75%	Slope C.I. 1.25—98.75%	MSE mean %	MSE slope %	MSE residual %
18.90 (0.10)	14, 18, 24	2, 4, 6	0.0095	-1.68—0.26	1.00—1.66	4	14	81
20.81 (0.42)	14, 18, 24	3, 6, 9	0.0095	-0.83—2.61	-0.08—1.01	18	10	72
44.42 (1.09)	14, 18, 24	3, 6, 9	0.0095	-0.74—1.67	0.61—1.01	20	8	72
108.27 (1.08)	14, 18, 24	25, 50, 75, 100, 125	0.125	-8.10—9.16	0.90—1.17	5	1	95

Table 3. Functional feeding response coefficients for age-0 pallid sturgeon of different sizes feeding on zooplankton, Chironomidae (mixed treatment) or Ephemeroptera larvae. All trials were performed on a bare and sand substrate for chironomids. Values in parentheses represent the standard error. Temp represents water temperature, L is fish total length, a is the attack coefficient, T_h is the handling time, and N_m is the mean number of prey consumed by a fish over a 15 min period. N_m was only calculated in the absence of a significant functional feeding response. Data used to generate the coefficients can be seen in Figure 1.

Zooplankton					Ephemeroptera			Chironomidae w/o sand			Chironomidae w/ sand		
L	Temp	a	T_h	N_m	a	T_h	N_m	a	T_h	N_m	a	T_h	N_m
mm	°C	L/min	min	eaten/15 min	m ² /min	min	eaten/15 min	m ² /min	min	eaten/15 min	m ² /min	min	eaten/15 min
19	14	NA	NA	0.03 (0.03)	NA	NA	0.10 (0.07)	NA	NA	0.03 (0.03)	NA	NA	0.003 (0.001)
	18	NA	NA	0.10 (0.06)	NA	NA	0.27 (0.10)	NA	NA	0.03 (0.03)	NA	NA	0.003 (0.001)
	24	NA	NA	0.17 (0.07)	NA	NA	0.27 (0.08)	NA	NA	0.37 (0.11)	NA	NA	0.006 (0.002)
20	14	NA	NA	0.10 (0.07)	NA	NA	0.10 (0.06)	NA	NA	0.23 (0.09)	NA	NA	0.07 (0.05)
	18	NA	NA	0.07 (0.05)	NA	NA	0.93 (0.22)	NA	NA	0.57 (0.11)	NA	NA	0.13 (0.06)
	24	NA	NA	0.53 (0.14)	NA	NA	0.10 (0.07)	NA	NA	0.20 (0.07)	NA	NA	0.17 (0.11)
30	14	NA	NA	0.30 (0.10)	0.07 (0.05)	2.41 (1.50)	NA	0.03 (0.04)	11.84 (6.69)	NA	NA	NA	0.03 (0.03)
	18	0.06 (0.09)	9.16 (4.57)	NA	NA	NA	0.40 (0.15)	0.05 (0.03)	3.51 (1.83)	NA	NA	NA	0.47 (0.14)
	24	0.10 (0.16)	7.25 (3.41)	NA	NA	NA	0.17 (0.10)	NA	NA	0.27 (0.17)	NA	NA	0.17 (0.10)
40	14	0.01 (0.00)	1.47 (0.64)	NA	0.04 (0.05)	5.91 (2.56)	NA	0.11 (0.10)	2.66 (0.83)	NA	0.02 (0.02)	6.11 (2.86)	NA
	18	0.05 (0.03)	1.72 (0.37)	NA	0.02 (0.02)	2.06 (3.25)	NA	0.05 (0.04)	1.59 (1.21)	NA	0.14 (0.29)	8.59 (2.39)	NA
	24	0.03 (0.03)	1.22 (0.60)	NA	0.32 (0.53)	5.15 (0.84)	NA	0.18 (0.13)	2.24 (0.42)	NA	0.14 (0.22)	6.46 (1.52)	NA
50	14	0.02 (0.01)	2.36 (0.60)	NA	0.01 (0.01)	0.50 (3.05)	NA	0.10 (0.05)	1.78 (0.38)	NA	0.18 (0.16)	3.15 (0.58)	NA
	18	0.05 (0.02)	0.83 (0.21)	Na	0.07 (0.05)	1.36 (0.73)	NA	0.32 (0.20)	1.26 (0.21)	NA	0.11 (0.06)	1.20 (0.46)	NA
	24	0.04 (0.02)	0.53 (0.25)	NA	0.04 (0.03)	2.61 (1.75)	NA	0.02 (0.02)	0.60 (2.14)	NA	0.18 (0.25)	3.59 (0.90)	NA

Table 3 continued

70	14	NA	NA	NA	NA	NA	NA	0.14 (0.13)	0.44 (0.64)	NA	0.29 (0.41)	2.19 (0.58)	NA
	18	NA	NA	NA	NA	NA	NA	0.39 (0.20)	1.13 (0.17)	NA	0.30 (0.28)	1.44 (0.32)	NA
	24	NA	NA	NA	NA	NA	NA	0.41 (0.45)	0.99 (0.30)	NA	0.20 (0.11)	1.20 (0.28)	NA

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Table 4. Functional feeding response coefficients for fish of different sizes of pallid sturgeon feeding on small, medium and large size classes of Chironomidae larvae. All trials were performed on a bare substrate. Values in () representing the standard error. a is the attack coefficient, T_h is the handling time, and N_m is the mean number of prey consumed by a fish over a 15 min period. N_m was only calculated in the absence of a significant functional feeding response. Data used to generate the coefficients can be seen in Figure 2.

Total Length mm	Temperature °C	Small chironomids			Medium chironomids			Large chironomids		
		a m ² /min	T_h min	N_m eaten/15 min	a m ² /min	T_h min	N_m eaten/15 min	a m ² /min	T_h min	N_m eaten/15 min
19	14	NA	NA	0.017 (0.002)	NA	NA	NA	NA	NA	NA
	18	NA	NA	0.017 (0.003)	NA	NA	NA	NA	NA	NA
	24	NA	NA	0.041 (0.006)	NA	NA	NA	NA	NA	NA
20	14	NA	NA	0.53 (0.12)	NA	NA	0.03 (0.03)	NA	NA	NA
	18	NA	NA	0.83 (0.14)	NA	NA	0.13 (0.06)	NA	NA	NA
	24	NA	NA	0.30 (0.11)	NA	NA	0.03 (0.03)	NA	NA	NA
30	14	0.14 (0.22)	4.32 (2.06)	NA	0.02 (0.02)	7.37 (9.39)	0	NA	NA	0.27 (0.15)
	18	0.28 (0.20)	1.40 (0.54)	NA	0.19 (0.16)	1.74 (0.88)	0	NA	NA	0.57 (0.12)
	24	0.52 (0.73)	1.57 (0.59)	NA	0.07 (0.06)	1.50 (1.68)	0	0.05 (0.06)	8.03 (3.63)	NA
40	14	0.05 (0.03)	0.92 (0.90)	NA	0.14 (0.17)	2.19 (0.82)	0	0.03 (0.03)	3.38 (1.93)	NA
	18	0.09 (0.04)	0.77 (0.37)	NA	0.04 (0.05)	0.98 (1.75)	0	0.03 (0.03)	9.87 (2.29)	NA
	24	0.89 (1.62)	1.26 (0.24)	NA	0.73 (1.16)	1.91 (0.29)	0	0.19 (0.25)	4.53 (0.87)	NA
50	14	0.10 (0.06)	0.63 (0.48)	NA	0.09 (0.03)	1.00 (0.32)	0	0.07 (0.03)	2.47 (0.65)	NA
	18	0.08 (0.04)	0.33 (0.46)	NA	0.14 (0.07)	0.36 (0.35)	0	0.49 (0.60)	1.58 (0.30)	NA
	24	0.09 (0.04)	0.31 (0.50)	NA	0.10 (0.07)	1.34 (0.68)	0	0.31 (0.58)	4.91 (0.91)	NA

Table 5. Multiple regression coefficient estimates and standard errors (SE) for $\log_e(N')$ (equation 2). As the most common prey type for age-0 pallid sturgeon, the Mixed Chironomidae treatment was used as the reference prey type. To estimate consumption ($\log_e N'$) for other prey types that were coded as dummy variables, their parameter estimates are added (or subtracted) to the intercept value.

Parameter	Estimate	SE	t-value	P-value
Intercept ^a	-17.75	0.31	-57.27	< 0.001
$\log_e(\text{Length})$	4.3	0.07	57.874	< 0.001
Temperature (°C)	0.03	0.01	4.272	< 0.001
Prey density ^b	1.4	0.1	13.559	< 0.001
Large Chironomidae	0.779	0.131	5.936	< 0.001
Medium Chironomidae	1.711	0.119	14.324	< 0.001
Mixed Chironomidae Bare	1.365	0.094	14.517	< 0.001
Small Chironomidae	2.134	0.113	18.969	< 0.001
Mayfly	1.502	0.113	13.349	< 0.001
Zooplankton	1.399	0.112	12.437	< 0.001

^a Intercept value based on Mixed Chironomidae with sand substrate

^b Proportion of maximum value

Figure 1. Functional relationships depicting the number of prey consumed based on the initial prey densities for different pallid sturgeon size classes feeding on different prey taxa. Trials at different temperatures are indicated by (—▼—) for 14°C, (---●---) for 18°C and (··▲··) for 24°C. Trials with a missing regression line indicate a lack of prey density effect. Regression coefficients can be seen in Table 3. **Note:** y-axes scales differ depending on treatment.

Figure 2. Functional relationships depicting the number of prey consumed based on the initial prey densities for different pallid sturgeon size classes feeding on different Chironomidae larvae size classes. Trials at different temperatures are indicated by (—▼—) for 14°C, (--●--) for 18°C and (·▲·) for 24°C. Trials with a missing regression line indicate a lack of prey density effect. Regression coefficients can be seen in Table 4. **Note:** y-axes scales differ depending on treatment.

Figure 3. Variation of the satiation index (S ; equation 7) with fish total length (in mm) and prey type. An S value of 0.1 indicates that 10 prey items can fit in the gut at a given time.

Figure 4. Changes in gut fullness for three sizes of pallid sturgeon a) 41.2 mm b) 69.5 mm, or c) 107.6 at 14°C (—▼—), 18°C (--●--) or 24°C (··▲··). Symbols from the same time interval were separated to avoid overlap. Curves depict the proportion of gut fullness (0-1) as it decreases over time.

Figure 5. Multiple regression model displaying how the gut evacuation slope coefficients vary with age-0 pallid sturgeon length ($\log_e(\text{length})$) and water temperature ($^{\circ}\text{C}$). Temperatures are indicated by (—▼—) for 14 $^{\circ}\text{C}$, (--●--) for 18 $^{\circ}\text{C}$ and (..▲..) for 24 $^{\circ}\text{C}$.

Figure 6. Plots displaying the observed number of prey eaten against the model predictions for the 24 h feeding trials for each size class. The solid line represents the 1 to 1 line whereas the dashed line represents the fitted regression line through the observed and predicted data. The grey area around the regression line represents the 95% confidence interval. Temperatures are indicated by (∇) for 14°C, ($\bullet$) for 18°C and ($\blacktriangle$) for 24°C.

Figure 7. Plots demonstrating the effect of temperature, prey density, prey type and predator size on daily net energy return. The minimum proportion of maximum prey density is set to 0.01. The number in bold represents the minimum energy needed for the fish to maintain its weight for a day. Fish feeding on zooplankton, Chironomidae or Ephemeroptera larvae, are indicated by (---), (—), or (···), respectively.