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Title: Temperature, discharge, and development shape the larval diets of threatened green sturgeon in a highly managed section of the Sacramento River

Authors: Liam J. Zarri[1], Eric P. Palkovacs[1]

1) Department of Ecology and Evolutionary Biology,
University of California, Santa Cruz,
CA, USA

Corresponding author:
Liam J. Zarri
Department of Ecology and Evolutionary Biology
University of California, Santa Cruz
Coastal Biology Building
130 McAllister Way
Santa Cruz, CA 95060
Phone: (510) 325-4536
Email: ljz27@cornell.edu

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Abstract: Feeding at early fish life stages is a key determinant of survival to recruitment. To understand the environmental and developmental determinants of early life-stage feeding in ESA-threatened green sturgeon (*Acipenser medirostris*) we performed a diet study in a highly managed section of California's Sacramento River, where temperature and discharge are controlled by dam releases. Utilizing field collections from 2012-2016, we assessed the impacts of temperature, discharge, and morphological development on the composition and number of prey items in larval green sturgeon diets. Results show that there are more empty stomachs at colder temperatures. Higher discharge conditions decreased prey taxon richness and counts, especially the abundance of cyclopoid copepods in diets. Fish smaller than 30 mm had teeth on the oral jaws and showed a strong reliance on zooplankton prey. The developmental loss of teeth in fish greater than 30 mm was associated with decreased zooplankton consumption and increased richness of benthic macroinvertebrates in diets. Our results show that river management through dam releases has the potential to impact the earliest life stage of green sturgeon by reducing the prevalence of favored zooplankton prey in diets.

INTRODUCTION

Natural river dynamics, which support native fish species, are altered by dam releases and water diversions. These anthropogenic alterations can impact the scale, regularity, duration, and timing of river temperature and river discharge (Poff et al. 1997, Steel et al. 2017). Early life stage fishes are particularly sensitive to altered environment at the critical stage of initial feeding, and survival at this stage is a driver of fish recruitment (Hjort 1914, Sifa & Mathias 1987, Pepin 1991, Sanford et al. 2006). Therefore, it is crucial to understand the anthropogenic impact of altered river regimes on larval fish to better manage fish populations.

The early life stages of sturgeon have been studied extensively in the lab over the last 20 years, focusing on growth, behavior, and development (Gisbert & Williot 1997, Kynard & Horgan 2002, Deng et al. 2003, Kynard et al. 2005, Werner et al. 2007). Despite the breadth of these lab studies, information on the ecological role of early life stage sturgeons is lacking because there are relatively few studies of larval sturgeon in the wild. It is therefore important to understand how the physical river environment may be altering larval sturgeon diets, especially in reference to the ontogeny of key morphological traits. Sturgeon are opportunistic foragers, utilizing highly specialized sensory structures and jaw mechanisms to feed on a variety of prey types (Carroll & Wainwright 2003, Miller 2004). Here we explore the ecology of early life stage larval green sturgeon (*Acipenser medirostris*, Ayres 1854) in a highly managed section of the Sacramento River, California.

The southern genetically distinct population of green sturgeon has been in decline because of lost and altered habitat and is listed as threatened under the US Endangered Species Act (National Marine Fisheries Service 2006, Adams et al. 2007, Mora et al. 2009). Spawning and early life stage development of this population takes place in the Sacramento River, which has a watershed encompassing California’s northern Central Valley. The present upper extent of anadromy for mainstream spawning fish such as green sturgeon is Keswick Dam, which regulates the hydropeaking outflow from Shasta Reservoir, a critical source of water for agriculture and urban use for much of California. The hydrological management regime of this region involves controlling the temperature and discharge of the river habitat (USFWS 1999, MacDiarmid 1975). Spawning habitat of green sturgeon is characterized by deep, turbulent pools with cobble, gravel, or sand substrate, and water velocity of 1.0-1.1 m/s (Poytress et al. 2009, Wyman et al. 2017). Laboratory studies suggest optimal egg development temperatures range from 13°C-15.5°C (Van Eenennaam et al. 2001). Embryos hatch approximately 8 days after fertilization and hide in interstitial spaces between gravel and cobble while digesting the yolk sac, then larvae emerge at 10-15 days post hatch (DPH) to begin exogenous feeding and downstream nocturnal migration (Kynard et al. 2005). Larvae have 4-5 days to find food before starvation, and this critical period is one of the primary drivers of sturgeon population growth rate (Gross et al. 2002). We define larvae as those individuals which have not yet taken on juvenile phenotypes (Balon 1975), measured by scute count. Optimal growth of early life-stage green sturgeon has been found to occur between temperatures of 15-19°C (Mayfield & Cech, 2004). Studies on other sturgeon species, such as shortnose sturgeon (*Acipenser brevirostrum*) and white sturgeon (*Acipenser transmontanous*), have found that larvae consume primarily drifting prey (Buckley & Kynard 1981, Kynard et al. 2014, Kynard et al. 2016) while juveniles shift to benthic prey (Radtke 1966). However, the diet of larval green sturgeon in the Sacramento River is not known. The composition of larval diets has been identified as a priority area of research in recent management reports on green sturgeon (Moser et al. 2016, Heublein et al. 2017).

We examined the impact of larval sturgeon development and river environment (temperature and discharge) on larval green sturgeon diets, including the most abundant diet items by weight and count, total number of food items (diet counts), the number of taxa (richness), and proportion of taxa by count (composition). Food web impacts of river temperature and discharge were not specifically evaluated, as invertebrate samples were not collected from the Sacramento River. Thus, any diet shifts we detect may reflect changes in green sturgeon foraging behavior, changes in metabolic rate, or changes in prey availability. We examined aspects of larval sturgeon development including total length, jaw articulation angle, and the presence of teeth. Although hatchling sturgeon do not have teeth, larvae develop fine, hairlike teeth on the dentary, dermopalatines, and palatopterygoid before losing teeth as juveniles (Hilton et al. 2011, Laumann 2016). Jaw articulation angle has been shown to alter diet in other fishes (Higgins & Horn 2014) as well as other sturgeon species, where piscivorous sturgeon have forward-opening jaws while benthically foraging sturgeon have downward-opening jaws (Bemis et al. 1997). However, the timing of this shift in mouth opening direction has not been documented with ontogeny. Based on diet findings with ontogeny in white sturgeon and shortnose sturgeon (Radtke 1966, Buckley & Kynard 1981, Kynard et al. 2014, Kynard et al. 2016), we hypothesize that as larval green sturgeons increase in total length, they shift from zooplankton to benthic macroinvertebrates (BMI). We predict that this shift coincides with the development of benthic feeding morphology, including the loss of teeth and the shift from a forward-opening mouth to a downward-opening mouth. We assessed whether larval green sturgeon consume larger diet items with increasing fish size (indicating gape-limitation at small sizes) and whether diet richness increased with increasing fish size (indicating expanding niche breadth). Further, we examined the role of water temperature and discharge in shaping the number and composition of dietary prey items. Given the optimal growth at warmer temperatures observed in early life-stage green sturgeon, we hypothesize that the low temperature conditions created by Shasta Dam negatively impact diet metrics such as diet count and proportion of empty stomachs. The highly managed release of water from Keswick Dam during the summer has the effect of increasing discharge and decreasing water temperature, which may impact the diets of larval green sturgeon during this key developmental stage.

MATERIALS AND METHODS

Field Collections

Field collections for this study came from rotary screw traps at Red Bluff Diversion Dam (latitude 40.153627, longitude -122.202324), which continuously capture a range of vertebrates, including larval green sturgeon and salmonid fry, and are checked one to two times per day. Given that samples could be in the trap for variable amounts of time, from minutes to just under 24 hours, there is the possibility of a post-capture digestion trap effect (Haywood 1995). Nonetheless, this sampling method is the only reliable method to collect larval green sturgeon in this part of the Sacramento River. Screw traps are maintained and monitored by the US Fish and Wildlife Service, which preserved trap mortalities in 95% ethanol after total length was recorded. 314 larval green sturgeon samples were collected from 2012 to 2016. All collected fish were less than 100 grams and did not require formalin injection to the gut area for preservation of diet contents (Gelwick & Matthews 2017). Temperature and discharge measurements for this region came from the River Assessment for Forecasting Temperature, a heat budget model which integrates Keswick Dam output and meteorological forcings (Pike et al. 2013, Daniels et al. 2018).

Diet analysis

Using a protocol adapted from Gelwick and Matthwes (2017), we extracted diet items from the digestive system and stored them in 70% ethanol. If the stomach tissue appeared to be compromised, that individual's diet was removed from analysis to prevent post-mortality loss of stomach contents from altering results. As the study was focused on the larval life stage, we removed individuals from analysis that had the juvenile phenotype, leaving 314 samples. Juveniles were identified as individuals having less than 7 dorsal scutes, 22 lateral scutes, or 5 ventral scutes (North et al. 2002). Analyses which used important diet items removed individuals which did not have those diet items, leaving 265 individuals in the sample. We used a dissecting microscope to identify individual diet items to Order (for zooplankton) and Family (for BMI) and measured major axis length. We found primarily hard-bodied diet items and counted head capsules to avoid bias caused by potential differences in rates of digestion among prey items. The mass of each diet item was estimated using length-mass relationships from literature values (Malley et al. 1989, Benke et al. 1999). We used counts as a measure of prey choice and weight data as a measure of the relative importance of prey items. Proportion by count of diet items per fish were used to assess how diet shifts with environment and fish development. Lab experiments have estimated diet passage time of larval sturgeon as less than 1 day (Silas Hung, *unpublished data)*; therefore, we compared stomach contents to temperature and discharge on the day the fish was caught.

Morphological development

Jaw opening direction and teeth presence were assayed for a subset of 46 individuals from 2016, which were double-stained using a protocol adapted from Dingerkus and Uhler (1977). For detailed information on double-staining techniques, see *Supplementary Information*. Following methods in Higgins and Horn (2014), we photographed double-stained individuals with jaws articulated. We calculated jaw articulation angle as the difference between the articulated jaw line and the main body axis line (Figure 1). The articulated jaw line was digitized by placing points at the distal end of the upper jaw and lower jaw, digitizing a line connecting these points, then digitizing a perpendicular line (the articulated jaw line). Each jaw was articulated and imaged three times to calculate mean and standard deviation of jaw articulation angle. Sampling standard deviation of jaw articulation angle was calculated using the mean of all standard deviations, and individuals were categorized as having either downward-opening mouths (within 2 standard deviations of 90°) or forward-opening mouths (greater than 2 standard deviations from 90°). Teeth presence or absence was determined by searching for the hair-like teeth on the oral jaws using high-resolution jaw articulation images.

Statistical analysis

First, we analyzed whether development in total length, jaw opening direction (forward or downward), or presence of teeth altered diets. To determine whether total length impacts the maximum prey size found in the diet, we used a linear mixed model. The impact of total length on the presence of any diet items (gut empty versus at least one diet item present) was assessed using a generalized linear mixed model (GLMM), binomial family**.** We used a GLMM of Poisson family to examine whether sturgeon length is related to diet richness. To determine whether teeth presence or mouth opening direction altered proportion of zooplankton in diet, we used a nonparametric t-test (Wilcoxon rank sum test) and calculated effect size using Hedge's g correction to account for small sample sizes. We included year as a random effect for all development analyses.

Next, we assessed the impact of river temperature and discharge on green sturgeon diets. Temperature and discharge measurements were scaled to standard deviations from the mean prior to model fitting. To determine if river temperature or discharge impacted the presence of important diet items we used corrected Akaike Information Criterion (AICc, Hurvich & Tsai 1989) to select the best binomial generalized linear model (GLM). Important diet items were identified as those which composed greater than 1% of the diet by count. To determine if empty vs non-empty stomachs were associated with temperature or discharge, we used AICc to select the best logistic GLM. To determine if nonzero diet count was impacted by temperature or discharge, we used AICc to select the best negative binomial GLM. To determine if diet richness was altered by river environment, we used AICc to select the best Poisson GLM. We did not include year as a random effect for environment analyses because much of the temperature variance is between years and doing so would reduce our ability to detect diet shifts resulting from temperature. All statistical analyses were conducted using R statistical language (R Core Team 2017, version 3.4.2).

RESULTS

Individuals were analyzed across 5 years which represented a range in temperature and discharge regimes (Table 1). The most common diet items were cyclopoid copepods (Copepoda: Cyclopoida), baetid mayflies (Ephemeroptera: Baetidae), chironomids (Diptera: Chironomidae), and simulids (Diptera: Simuliidae; Table 2). Larval green sturgeon developmental features were associated with zooplankton consumption while total length was associated with diet richness. Although jaw articulation angle was not a significant predictor of diet composition, both total length and teeth presence significantly impacted diets. Total length was positively correlated with maximum diet item length (mixed linear regression: df = 259, t = 2.8, marginal $r^2 = 0.03$, p = 0.005), non-empty stomachs (GLMM binomial family: residual df = 302, z = 3.3, marginal $r^2 = 0.36$, $p < 0.001$), and diet richness (GLMM poisson family: residual df = 302, z = 3.0, marginal $r^2 = 0.02$, p = 0.002). Larval green sturgeon consumed equal numbers of BMI and zooplankton until ~30 mm total length, when BMI consumption increased but zooplankton consumption remained constant (Figure 2). Although fish consumed greater biomass of BMI through the larval life stage, zooplankton biomass peaked at ~30 mm total length (TL) before decreasing (Figure 3). Teeth were found on smaller individuals and lost at approximately 30 mm (logistic regression prediction: 8.2% error). Larval green sturgeon with teeth consumed a greater proportion of zooplankton than sturgeon without teeth (Figure 4; Wilcoxon rank sum test: n = 46, p = 0.05; Hedge's g effect size: n = 46, g = 0.64 (medium effect), 95% confidence = 0.62).

River environment (discharge and temperature) was associated with a shift in larval green sturgeon diets. Because of a temperature control device installed on Shasta Dam in 1996, river discharge and temperature are not collinear at Red Bluff Diversion Dam (variance inflation factor = 1.5). Therefore, we ran models with both temperature and discharge. We found more empty stomachs at colder temperatures (GLM, binomial family: residual df = 303, z = 2.069, Nagelkerke pseudo-$r^2 = 0.03$, $p = 0.04$). Using AICc to select the best GLM of binomial family, we found that temperature and discharge impacted the presence of cyclopoid copepods and simulids in diets (Table 3). Then, we used AICc to determine the impact of river environment on nonzero diet count, finding that count decreased with discharge (GLM, negative binomial family: residual df = 272, z = -6.5, Nagelkerke pseudo-$r^2 = 0.11$, p-value < 0.001). We calculated the effect of river environment on diet richness with corrected AIC, finding that taxon richness decreased with discharge (GLM, Poisson family: residual df = 303, z = -3.9, Nagelkerke pseudo-$r^2 = 0.14$, p-value < 0.001).

DISCUSSION

Summer management of dam releases on the Sacramento River is aimed at providing discharge for downstream water users and cold water for winter-run Chinook egg survival (Yates et al. 2008), yet other native species, including threatened green sturgeon, rely on habitat in this highly altered section of river. We examined the effects of morphological development, temperature, and discharge on larval diets of threatened green sturgeon. Our results show that green sturgeon decrease zooplankton consumption when teeth are lost and increase diet richness with total length. Mouth width in larval green sturgeon increases non-linearly with length, with an inflection point from rapid to slowed growth just before 30 mm TL, which is the same size that an inflection point indicating decreased barbel growth occurs (Gisbert & Doroshov 2006). In support of our first hypothesis, we detected a loss of teeth on the oral jaws at 30 mm, which was also the approximate size at which zooplankton counts in diets decreased and BMI counts increased (Figure 2). However, contrary to our hypothesis, mouth opening direction was not associated with a shift in diet.

The decrease in zooplankton and increase in BMI at 30 mm TL may indicate a shift in the optimal prey for larval green sturgeon. Predators may shift prey items based on prey size (Werner & Gilliam 1984, Scharf et al. 2000) and/or foraging efficiency of capturing different prey items (Mittelbach 1981). Cyclopoid copepods represent 40% of larval green sturgeon diets by count but form only 0.6% of diet weight (Table 2). Other sturgeon species have been shown to shift from zooplankton to BMI (Buckley & Kynard 1981, Dadswell et al. 1984) and diet analyses indicate gape-limitation in early life stages (Muir et al. 2000). Larval green sturgeon diet richness increased with total length, indicating that they widen their niche with increasing size. Although larval green sturgeon increase BMI consumption beginning at approximately 30 mm, zooplankton remain in the diet throughout the larval life stage (Figure 2). Our study identifies a replacement of zooplankton with BMI at 30 mm in larval sturgeons, and finds this shift associated with the ontogenetic loss of teeth on the oral jaws.

River temperature and discharge were found to strongly impact diets of larval green sturgeon. Cold temperatures significantly increased the proportion of larval sturgeon with empty stomachs. However, diets were more closely associated with river discharge than temperature. This has important management implications because the discharge of the Sacramento River above Red Bluff is driven by Shasta Dam releases. More empty stomachs were found at colder temperatures, indicating that foraging activity or food availability may be increased at warmer temperatures. Food consumption, growth, and metabolism has been previously demonstrated to increase with temperature in early life stage green sturgeon (Mayfield & Cech 2004). Increasing discharge significantly decreased the total number of prey items in the diets and significantly reduced the presence of cyclopoid copepods in diets. Cyclopoid copepods were an important prey item for green sturgeon below 30 mm, suggesting that fish in this critical life stage may be adversely impacted by dam releases. Density of copepods in the Sacramento River has been found to be inversely associated with discharge (Sommer et al. 2004), so decreased prey availability may be driving the reduced presence of copepods observed in larval sturgeon diets under high flow. Temperature and discharge had a positive association with simulid presence in diets and a negative association with chironomid presence. Future studies could profitably examine mechanisms by which dam releases impact larval sturgeon diet by simultaneously collecting information on both diets and invertebrate prey availability.

Understanding the dynamics of early life stage listed green sturgeon has been identified as an important management priority (Moser et al. 2016, Heublein et al. 2017). Our findings provide information which could be used to refine the current management of environmental flows in the Sacramento River. We found that temperature, discharge, and larval development shape green sturgeon diets in ways that may make the smallest larvae potentially vulnerable to the effects of dam releases. The current management regime downstream of Shasta Reservoir uses dam releases to decrease summer temperature for endangered salmonids and increase summer discharge for downstream water users. Our results suggest that this management regime may negatively impact the feeding of threatened green sturgeon in this section of the Sacramento River. Rivers are increasingly being put under pressure to provide water for human use and habitat to support aquatic biodiversity. However, knowledge of habitat requirements for the larval life stages of many fish species is lacking. Understanding the habitat needs of larval fishes and incorporating them into management plans is critical for balancing human water needs and the habitat requirements of native fish species.

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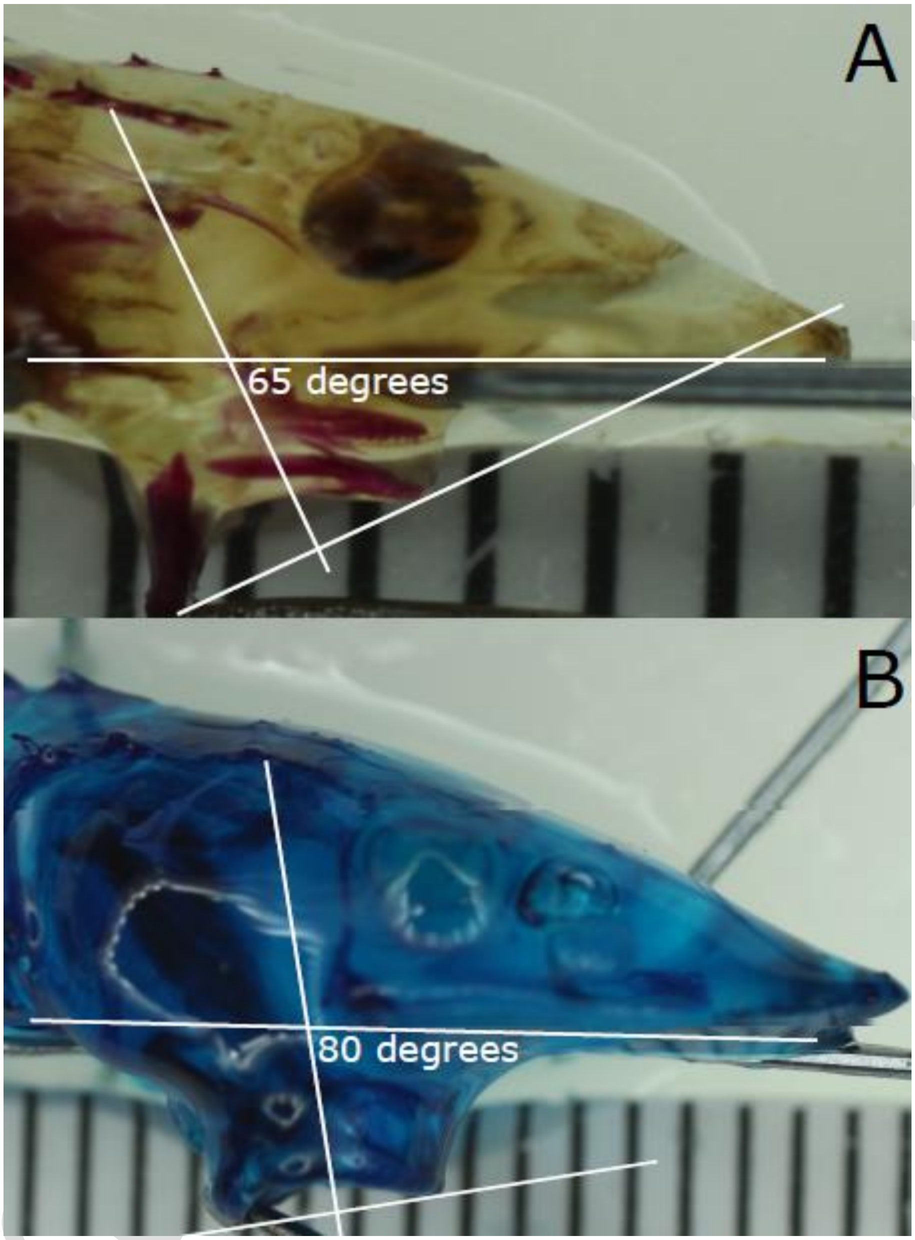

Figure 1. Jaw articulation angle is the angle between a line on the body axis and a line perpendicular to a line connecting the tips of both jaws. Panel A is a younger fish with forward-opening jaw, and panel B is an older fish with downward-opening jaw

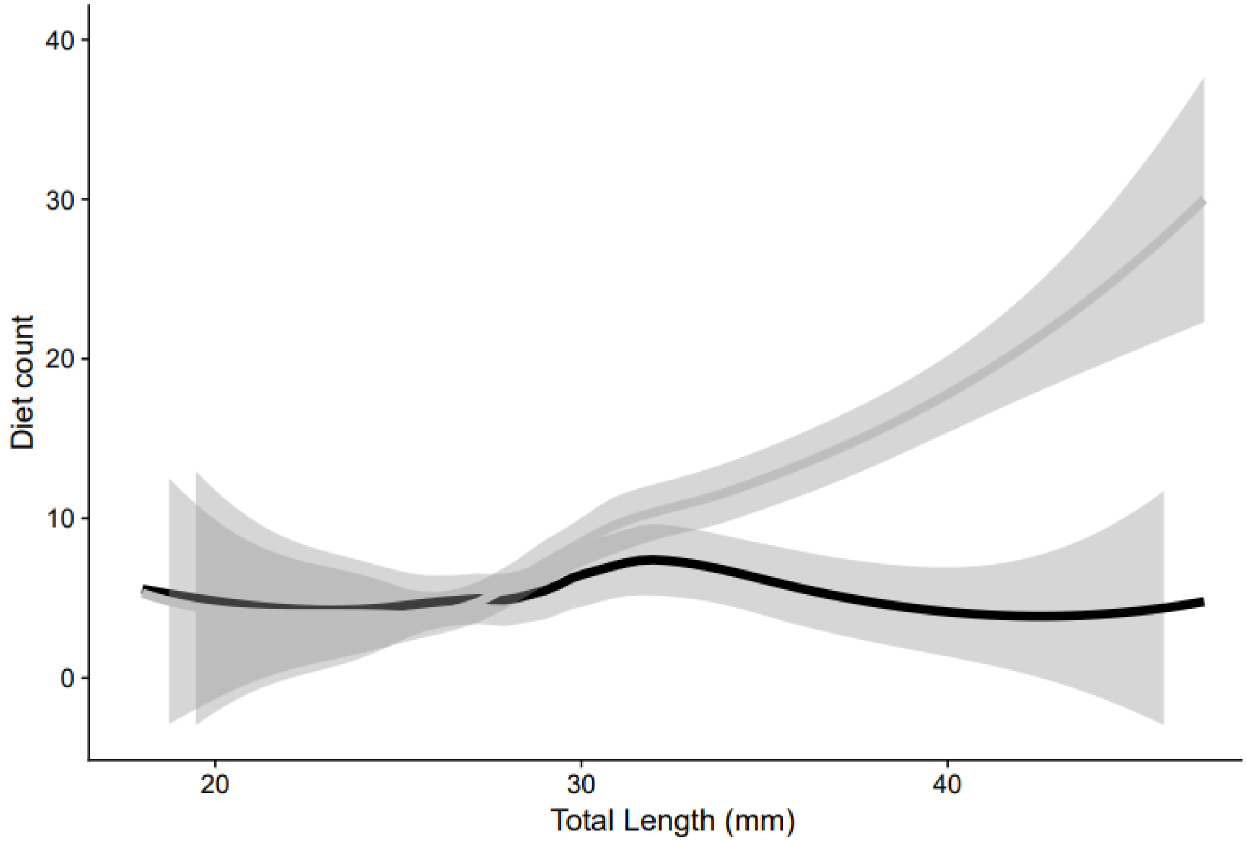

Figure 2. Association of larval green sturgeon total length with diet by count. Grey line is benthic macroinvertebrates while black line is zooplankton, fit with a spline of span 1.8. Shading represents standard error.

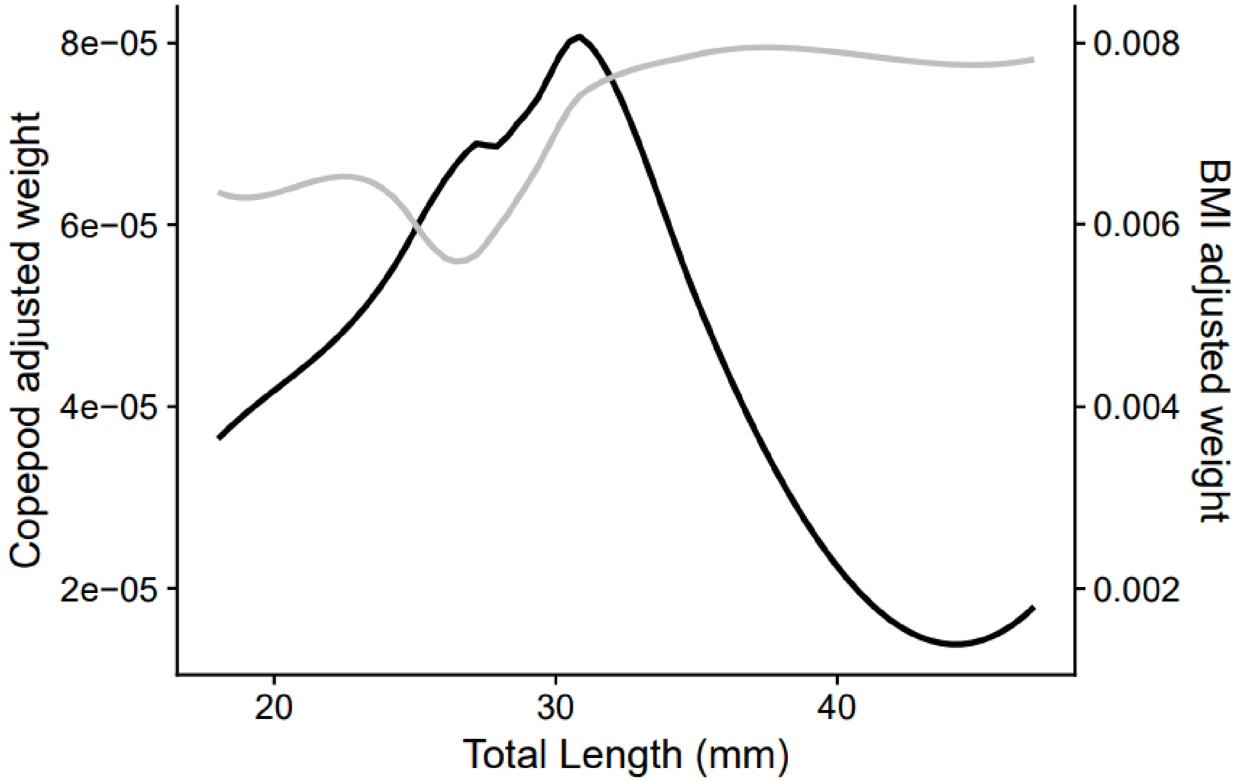

Figure 3. Association of total length and diet of larval green sturgeon by adjusted weight (diet / fish weight). Black line is zooplankton with axis on the left side while grey line is BMI with axis on the right side. Line is fit with a spline of span 1.8.

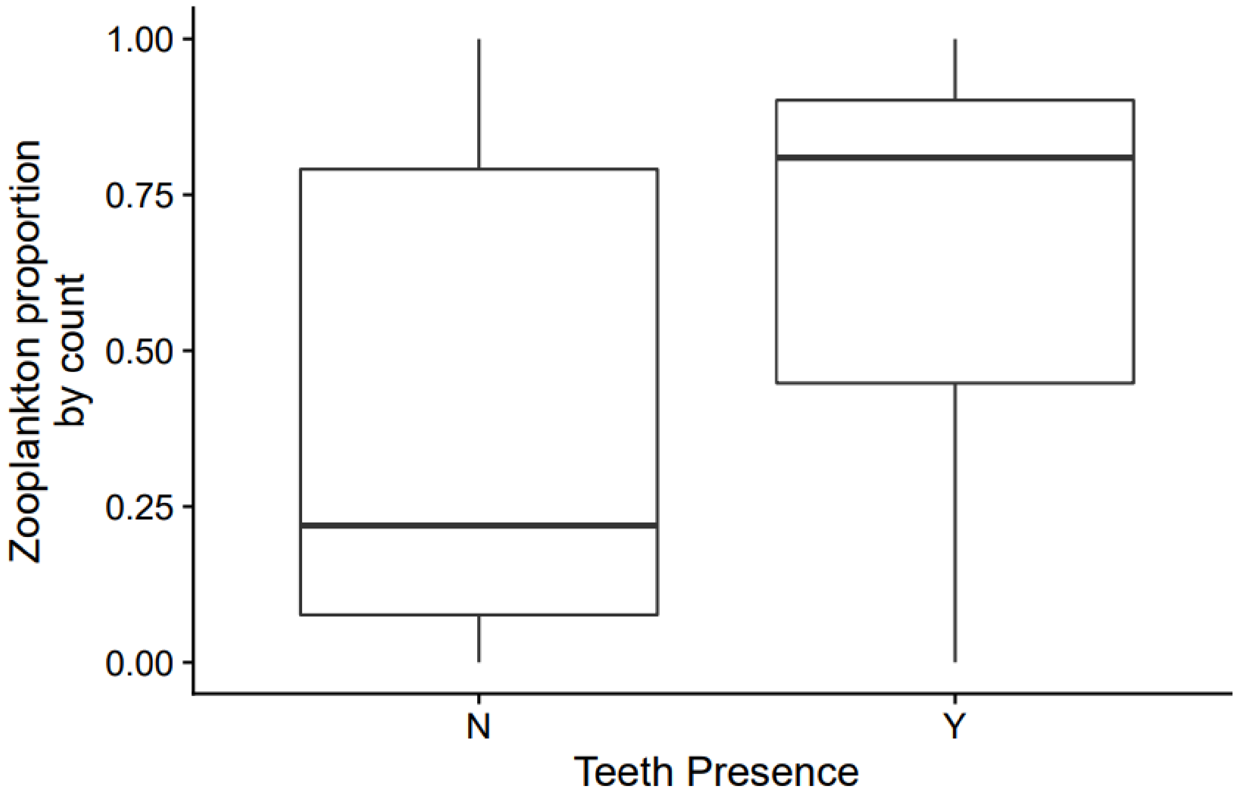

Figure 4. Association of teeth presence with zooplankton proportion by count in diet.

Table 1: Fish count, temperature, and discharge throughout the five years of this study separated by month. Fish count is n, mean temperature in Celsius is μT, temperature standard deviation is σT, mean discharge in cubic meters per second is μD, and standard deviation of discharge is σD.

Year	Month	n	μT (C)	σT (C)	μD (CMS)	σD (CMS)
2012	May	7	13	0.3	314.7	5.1
2012	June	11	12.6	0.7	322.9	12.9
2013	May	9	13.7	0.4	344.1	6.2
2013	June	17	13.7	0.7	391.9	39.2
2013	July	6	14	0.3	419.7	7.4
2013	August	1	13.9	-	336.4	-
2014	May	8	13.7	0.7	224.4	14.6
2015	April	12	14.5	0.5	188.6	25.5
2015	May	17	14.4	0.4	224.7	3.3
2015	June	7	16.4	0.3	210.5	2.4
2015	July	1	16.6	-	211.3	-
2016	April	1	14.3	-	182.7	-
2016	May	150	14.7	0.5	216.1	6.2
2016	June	16	14.4	0.5	253.7	16.3
2016	July	1	13.6	-	296.7	-
2016	Sep.	1	12.9	-	256.8	-

Table 2: Proportion of diet items by weight and count, averaged across all individuals. Life stages are larval (L), pupal (P), adult (A), or unknown (U). Group is zooplankton (Zoop) or benthic macroinvertebrate (BMI).

Diet item	Life stage	Group	Diet item proportion by count	Diet item proportion by weight
Cyclopoida	A	Zoop	0.42	<0.01
Baetidae	L	BMI	0.30	0.71
Chironomidae	L	BMI	0.22	0.16
Simuliidae	L	BMI	0.03	0.06
Chironomidae	P	BMI	<0.01	<0.01
Tricoptera	L	BMI	<0.01	<0.01
Chironomidae	A	BMI	<0.01	<0.01
Coleoptera	L	BMI	<0.01	<0.01
Heptageniidae	L	BMI	<0.01	<0.01
Nematoda	U	BMI	<0.01	<0.01
Herpacticoida	L	BMI	<0.01	<0.01
Acari	U	BMI	<0.01	<0.01

Table 3: Presence of 4 main diet items as impacted by river environment. In the 'Environmental model terms' column, (+) means a positive correlation and (-) means a negative correlation. Predictors standardized, models fit with binomial GLM, best model chosen with corrected AIC. Nagelkerke r^2 fit with MuMIn package in r (Barton 2017).

Response	Environmental model terms	df	LogLik	Weight	Marginal r^2
Copepod presence	Discharge (-)	2	-149.792	0.696	0.22
Baetid presence	No impact	-	-	-	-
Chironomid presence	Temperature (-) & discharge (-)	3	-153.982	0.714	0.06
Simulid presence	Temperature (+) & discharge (+)	3	-147.629	0.747	0.05

Supporting Information

Double-staining was conducted under a fume hood and individual sample vials were taken through the process because different sized specimens absorbed chemicals at different rates. Formalin-fixed larval sturgeon specimens were soaked in distilled water for 24 hours before evisceration, which allows better penetration of chemicals. Samples were then submerged for up to two days in blue stain, which was 8:2 absolute ethanol to glacial acetic acid with 20mg of alcian blue 8GX for every 100ml of solution. Specimens remained in blue stain until entire body appeared blue. Specimens were then placed in 95% ethanol solution for 48 hours with one ethanol change halfway through. After the alcohol no longer retained blue dye, specimens were put in 50:50 solution of ethanol and distilled water until they sank to the bottom of the vial, at which point solution was replaced with distilled water. Tissue digestion was done with a solution of 3:7 Borax to distilled water, with 1g of trypsin powder for every 100ml of solution. Samples remained in trypsin until solution turned blue (at which point trypsin was replaced), or tissues were sufficiently macerated. Specimens were then transferred to 0.5% KOH solution for two hours, then moved to red stain to stain bones. Red stain was 0.5% KOH solution with enough alizarin red to turn the solution bright purple. Specimens remained in red stain for up to two days until they appeared dark red before being moved to a decolorizing solution consisting of 0.5% KOH and a few drops of H_2O_2. Specimens were then placed in 1:1 0.5% KOH to vegetable glycerin solution for two days, then vegetable glycerin with a few phenol crystals to preserve and prevent mold growth.