Experimental evaluation of the effects of bigmouth buffalo (*Ictiobus cyprinellus*) density on shallow lake ecosystems

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Abstract

Bigmouth buffalo (*Ictiobus cyprinellus*) is a large-bodied planktivore inhabiting shallow waterways in North America and subjected to unregulated harvest throughout much of their native range. Despite high harvest pressure on some populations, we know little about the ecosystem-level effects of lowering bigmouth buffalo densities. To evaluate the effect of bigmouth buffalo density on lower trophic levels we added fish in ambient and harvested densities to a set of ponds and compared plankton dynamics to reference, fishless ponds. Zooplankton biomass declined in ambient density ponds after the fish addition while chlorophyll-a concentrations increased. In the harvested density treatment chlorophyll-a concentrations were similar to the reference ponds despite a decline in zooplankton biomass, likely due to larger zooplankton community size in the harvested ponds exerting greater grazing pressure. This experimental manipulation revealed density-dependent top-down control on lower trophic levels by bigmouth buffalo and the potential for cascading trophic interactions with the harvest of this species. These results point to the need for ecosystem-level studies of the effects of intensive harvest of bigmouth buffalo on water quality.

Keywords: trophic cascade, bigmouth buffalo, commercial harvest, food web

INTRODUCTION

In the United States, commercial harvest of inland waters is estimated to exceed 41,000 metric tons annually (Murray et al. 2020). While the practice of harvesting freshwater fishes provides a source of dietary protein and contributes to food security (Lynch et al. 2016), targeted commercial harvest is also used as a management tool to control populations of invasive species or endemic species that are deemed undesirable for recreational fisheries. These endemic fishes are often disparagingly categorized as “rough fish”, grouped together with invasive species for the purposes of defining harvest regulations (Rypel et al. 2021). In some jurisdictions, the harvest of rough fish, whether commercially or recreationally, remains unregulated and encouraged in some locations.

One species commonly categorized as a “rough fish” and subject to targeted commercial and recreational harvest is the bigmouth buffalo (*Ictiobus cyprinellus*). Bigmouth buffalo are endemic to the Mississippi River and Hudson Bay drainages and are considered the longest-lived freshwater teleost (Goodchild 1990; Lackmann et al. 2019). They are a culturally and economically important species in North America (Lackmann et al. 2019), with a fishery valued at approximately $1.2 million USD annually for the Upper Mississippi River basin (U.S. Army Corps of Engineers 2012). Throughout most of their range in the United States, bigmouth buffalo harvest is unregulated (Lackmann et al. 2021) and some populations have been in decline (Bennett and Kozak 2016), leading to a designation of “special concern” in some regions of Canada and endangered status in Pennsylvania (USA) (Goodchild 1990; Scarnecchia and

Schooley 2020). The cause of this decline is likely a combination of overharvest from commercial and unmanaged bowfishing exploitation (Scarnecchia and Schooley 2020), competition with invasive species, and habitat loss (Welker and Scarnecchia 2003). Despite the economic value of bigmouth buffalo, numerous anthropogenic pressures, and declining populations, we know surprisingly little about the ecosystem-scale effects of harvesting this species.

Bigmouth buffalo are large-bodied planktivores from the family *Catostomidae* (order *Cypriniformes*). They are found in eutrophic and turbid shallow lakes and slow-moving stretches of rivers (Johnson 1963; Miranda and Lucas 2004). Although they are a member of the sucker family, bigmouth buffalo do not consume benthic organisms in large quantities (Johnson 1963; Hansen et al. 2020). Instead, their diet is dominated by zooplankton that they filter out of the water through their fine gill rakers (McComish 1967; Walleser et al. 2014), mainly consuming copepods and large-bodied cladocerans such as *Daphnia* (Starostka and Applegate 1970; Adámek et al. 2003). Due to their reliance on zooplankton, bigmouth buffalo have a high dietary overlap with invasive carp which has resulted in deteriorated body condition in some buffalo populations (Sampson et al. 2009; Phelps et al. 2017; Pendleton et al. 2017; Wang et al. 2018). While bigmouth buffalo diet, habitat use (Bouska and Whitledge 2014; Enders et al. 2019; Finger et al. 2020), and life history (Johnson 1963; Lackmann et al. 2019, 2021) have been documented to a limited degree, there have not been any investigations into the food web and ecosystem-level changes that may occur when bigmouth buffalo densities are altered through commercial harvest.

As bigmouth buffalo are planktivores, temporarily lower densities through commercial harvest is likely to result in cascading top-down trophic interactions (Carpenter et al. 1985).

Predation pressure on zooplankton decreases when planktivorous fish are removed in large quantities, resulting in increased predation pressure by zooplankton on phytoplankton. This will, in turn, decrease the standing stock of phytoplankton, an effect which may be amplified in nutrient-rich waterbodies that bigmouth buffalo often inhabit (Carpenter et al. 2001). Lower fish densities due to harvest could also result in a shift in the zooplankton community size structure (Brooks and Dodson 1965; Shapiro and Wright 1984; Pace et al. 2013) as bigmouth buffalo are thought to selectively consume large-bodied grazers such as *Daphnia* (Starostka and Applegate 1970). However, the strength of these food web interactions will be mediated by the magnitude of population changes in bigmouth buffalo with harvest. While the degree of commercial harvest varies annually and depends on market value (Rose 1949) (Higham 1974), when aggressive removal of bigmouth buffalo is undertaken, populations may be reduced by up to 94% in a given year (Rose 1949). Given the possibility that large portions of the population can be harvested annually, we hypothesized that low bigmouth buffalo densities brought on by commercial harvest in the spring in shallow temperate lakes would result in increased zooplankton biomass and decreased phytoplankton biomass.

To test this hypothesis, we added bigmouth buffalo to a set of fishless experimental ponds at densities typical of ambient and harvested populations, with two additional fishless ponds serving as a reference. We then compared the biomass of zooplankton and phytoplankton, and nutrient concentrations among bigmouth buffalo density treatments. Additionally, we evaluated changes in the zooplankton community and size structure with the addition of fish and compared these metrics among density treatments. This study provides the first experimental evidence of the top-down control in shallow lakes that may be altered by the harvest of bigmouth buffalo.

METHODS

Six experimental ponds at the Iowa State University Horticulture Research Station (42.110005, -93.580454) were used for the experiment during the summer of 2019. The surface area of the ponds is 550 m^2, approximate volume of 450 m^3, and a maximum depth of 1.75 m. The ponds are lined with a mixture of natural sediment and bentonite. During mid-April the ponds were drained and any remaining fish were removed. The ponds were then refilled on day of year (DOY) 114 with water from the reservoir located at the research station. This seeded each pond with natural phytoplankton and zooplankton assemblages. Additionally, beds of longleaf pondweed (*Potamogeton nodosus*) and leafy pondweed (*Potamogeton foliosus*) were already established in each of the ponds.

Bigmouth buffalo were added to four of the six experimental ponds to create ambient density, harvested density, and reference (no fish) treatments. The fish were harvested through electroshocking from South Twin Lake (42.460459, -94.651639) which is a natural, shallow hypereutrophic lake in central Iowa, USA. The ambient density treatment ponds (n=2) received approximately 450 kg ha^{-1} of adult bigmouth buffalo, which is consistent with natural densities of bigmouth buffalo in nutrient-rich shallow lakes in the region (Simonson et al. 2022). The harvested density treatment ponds (n=2) received 150 kg ha^{-1} of fish, which is consistent with the biomass remaining in lakes in the region after harvesting occurs (Simonson et al. 2022). Finally, two ponds did not receive any fish (“reference” treatment) and served as a reference during the experiment. Fish were added on two dates to the ambient and harvested density treatment ponds, DOY 124 and 128, due to the low number of fish caught during the first electrofishing campaign. However, fish were added to the ponds on DOY 124 in proportion to the density difference between the treatments (3:1) and augmented to their target densities on DOY 128. The bigmouth buffalo added to the ponds were an average (± standard deviation, s.d.) of 463 mm (± 37 mm) in length and weighed an average (±s.d.) of 1934 g (± 579 g).

On DOY 125, prior to adding buffalo to the experimental ponds, ten fish were held separately in 40L tanks of unfiltered lake water to estimate the rate of ammonium+ammonia (NH_X) and soluble reactive phosphorus (SRP) excretion. Water samples from each holding tank were taken prior to the addition of a fish and filtered prior to preservation. After one hour, fish were removed from the tanks and another water sample was filtered and preserved for later analysis. A control tank was similarly sampled but no fish were added.

Routine monitoring of chlorophyll *a*, total nutrient concentrations, and zooplankton biomass in each pond began on DOY 115, prior to the addition of fish, and continued through DOY 168. Chlorophyll-a concentrations, an index of algal biomass, were measured in each pond daily with the Total Algae sensor as a part of the YSI ProDSS handheld sonde (Yellow Springs Instruments, Yellow Springs, Ohio USA). The sensor was suspended at 0.25 m depth in the water and measurements were recorded once the value was stable. The sensor was calibrated against laboratory standards regularly according to manufacturer specifications to minimize drift. Approximately every 2-3 days, a water sample was also collected from 0.25 m depth and was used to measure the concentrations of total phosphorus (TP) and total nitrogen (TN). An additional aliquot of water was filtered in the field and used to measure the concentration of nitrate+nitrate (NOx) and SRP. Water samples were stored on ice in a cooler for transport to the laboratory where samples were preserved with concentrated sulfuric acid and stored at 4°C until analysis. The ascorbic acid method was used to measure SRP while the same method was used following persulfate digestion to quantify TP. The concentration of TN was quantified using second-derivative spectroscopy following digestion with sodium hydroxide (Crumpton et al.

1992). All three analyses were performed using an Agilent Cary 8454 UV-VIS spectrophotometer (Agilent Technologies Inc., Santa Clara, CA, USA). The concentration of NO_X (following cadmium-reduction) and NH_X were measured using an AQ2 discrete analyzer (Seal Analytical, Mequon, WI, USA).

Zooplankton were sampled by vertically towing a Wisconsin net with 63 µm mesh from a depth of 1 m approximately every 2-3 days. Zooplankton samples were concentrated to approximately 60 mL using a 63 µm mesh cup and then 60 mL of 10% formalin sucrose solution was added to preserve the organisms. After 5 days in the formalin solution, the sample was transferred to 70% ethanol for storage prior to identification. For each sample, all zooplankton in a 1 mL subsample were identified and enumerated. Using a stereomicroscope, zooplankton were identified to genus for cladocerans and rotifers and family for copepods. If 60 organisms were not identified in the first 1 mL subsample, an additional 1 mL subsample was enumerated. Up to 25 individuals from each taxa were also measured for length to calculate biomass using length-mass relationships (Dumont et al. 1975; Mccauley 1984). Additionally, the mean length of the zooplankton community on each sampling date and each pond was calculated, using the relative abundance of each organism in the sample to weight the estimate of mean community length.

Statistical Analysis

To test our hypothesis that there was an effect of bigmouth buffalo on chlorophyll-a concentrations, zooplankton biomass, and zooplankton length, we constructed a set of general additive models (GAMs). GAMs are a regression method used to estimate smoothed, non-linear trends, in this case, over time (Simpson 2018). We used GAMs to determine if there was an identifiable difference in the trends of response variables among treatments (reference, harvested density, and ambient density) without imposing a linear model on the noisy environmental data. The observational data from both reference ponds were combined to fit smooths for each response variable (e.g., chlorophyll-a concentration) over time (DOY) and difference smooths of the other two treatment levels (harvested and ambient density fish). Similarly, the observations from both ponds in a treatment level (ambient or harvested density) were used to fit the difference smooth for that level. Difference smooths model the difference between the smooth estimated for the reference treatment and the other two levels of treatment. The difference smooths allow us to test the hypothesis there are different trends in the response variable over time among the two treatments separate from the day-to-day variability that all the ponds may be experiencing due to factors such as weather. If there is not an identifiably different trend in the response variable over time for the two treatments, the difference smooth for that treatment will be linear (effective degrees of freedom; edf = 1.00). However, if the difference smooths are significant (p-value < 0.01) and non-linear (edf > 1.00), then there is strong evidence that there are different trends in the response variable for a fish density treatment over time compared to the reference. The models also included a parametric comparison of the effect of harvested and ambient treatments in relation to the reference treatment.

Differences in zooplankton community composition among treatments and over time were visually assessed using non-metric multidimensional scaling (nMDS). The zooplankton biomass data were Hellinger-transformed to reduce the weight of rare taxa. Models of the zooplankton communities were fit using a Bray-Curtis dissimilarity matrix. We then performed an analysis of similarity (ANOSIM) test to quantify the degree of dissimilarity between zooplankton community composition across treatments and over time. The ANOSIM test produces the *R* statistic which varies from 0 – 1 with 1 indicating a high dissimilarity in communities among treatment and 0 indicating a high degree of similarity.

The rate of NH_X excretion was estimated for each of the ten fish. The concentrations of SRP were below the limit of detection for all but one tank preventing an estimate of P excretion. The change in NH_X concentration in a tank during the incubation was standardized to the volume of water in the tank and corrected for the incubation time; this resulted in an excretion rate per individual in units of $\mu g\ individual^{-1}\ h^{-1}$. We also standardized the rates by fish wet weight (w.w.), resulting in an estimate of mass-specific NH_X excretion in units of $\mu g\ g^{-1}\ w.w.\ h^{-1}$. The mean mass excretion rate for all ten fish was then multiplied by the mass of fish added to each pond and converted to concentration based on the pond's volume and extrapolated to a daily timescale. This resulted in a fish NH_X excretion rate for each pond in units of $\mu g\ L^{-1}\ d^{-1}$ to compare with the TN concentrations in $mg\ L^{-1}$ measured every 2-3 days during the experiment.

All data analysis was performed using R version 4.1.1 using the *mgcv* package for the GAM analysis and *vegan* package for the NMDS analysis (Wood 2017; Oksanen et al. 2020). All data and analysis scripts are available at https://github.com/goodgracious23/BigmouthBuffalo_TrophicCascades and will be archived upon acceptance.

RESULTS

Chlorophyll-a concentrations were high in all the ponds prior to the addition of bigmouth buffalo and rapidly decreased during the period of fish additions, even in the reference pond where no fish were added (Figure 1A, Figure 2A). However, after fish were added to the harvested and ambient treatment ponds, there was a significant divergence in the chlorophyll-a concentrations and trends among treatments. Both the ambient and harvest density ponds decreased in chlorophyll-a concentrations at a higher rate than the reference ponds immediately prior to the fish addition, which subsequently reversed these trends (Figure 2B). The ambient ponds rapidly increased in chlorophyll-a concentrations following the addition of fish, as did the harvested ponds, but to a lesser extent. After this period of rapid change following the addition of fish, concentrations in all ponds were steady with lower day-to-day variability. The GAM constructed for chlorophyll-a explained 90.1% of the deviance in observations.

Overall, the ambient density treatment had a significant positive effect on chlorophyll-a concentration compared to the reference ponds while the harvested density treatment had a significant negative effect on chlorophyll-a concentration compared to the reference (Figure 2C). However, this negative effect was driven by low chlorophyll-a concentrations in the harvested density ponds during the pre-fish and fish addition periods (DOY 115 – 128) (Figure 1A). If the pre-fish and fish addition periods were excluded from the GAM analysis, there was not a significant effect of the harvested density treatment on chlorophyll-a compared to the reference treatment, but the positive effect of the ambient density treatment remained (Figure S1).

Unlike the difference among treatments for chlorophyll-a, nutrient concentrations did not vary substantially throughout the experiment or among treatments (Figure 3). Total phosphorus concentrations were highest during the pre-fish addition period and decreased across all ponds beginning around DOY 150 (Figure 3A). Total nitrogen, on the other hand, remained variable with little trend throughout the experiment (Figure 3B). Based on the molar N:P using the total phosphorus and total nitrogen data, all ponds were phosphorus limited (N:P > 60 for all sampling dates and ponds). There were no significant differences in trends or parametric effects by treatment level for either nutrient (Figure S2). The mean concentrations of SRP among all ponds and sampling dates was 4.0 µg L^{-1} (±2.7 s.d.) and did not vary among treatments. Similarly, the mean concentration of NO_X for all ponds and sampling dates was low at 0.05 mg L^{-1} (±0.02 s.d.) and did not vary among treatments. For fish, the mean individual excretion rate was 5256 µg ind^{-1} h^{-1} (±2918; Figure S4) and the mass-specific mean excretion rate was 2.35 µg N g^{-1} w.w. h^{-1} (±1.14) for the ten fish assayed prior to addition to the experimental ponds. Using the mass-specific mean rate and the density of fish added to each pond, the estimated rate of N excretion in the harvested density ponds was 1.04 µg L^{-1} d^{-1} and 3.11 µg L^{-1} d^{-1} in the ambient density ponds.

During the experiment, zooplankton biomass spanned almost four orders of magnitude among the ponds (Figure 1B). There was a shallow, positive trend in zooplankton biomass in the reference ponds over time but not significantly different than a linear trend (Figure 2D, edf = 1.00). The difference between the reference and harvested ponds was also linear, but negative and only marginally significant (Figure 2E, edf = 1.00). However, there was a significantly different trend in the ambient density ponds compared to the reference ponds with a sharp decline in zooplankton biomass after the addition of fish followed by a shallow, steady increase for the rest of the experiment (Figure 2E, edf = 4.448). The GAM for zooplankton biomass only explained 32.9% of the deviance among observations. Overall, there was not a significant effect on zooplankton biomass for either of the fish treatments compared to the reference (Figure 2F); however, zooplankton biomass was lower in both fish treatments compared to the reference. With the pre-fish addition period excluded from the GAM analysis (DOY 115-128), the negative effect of fish treatment on zooplankton biomass was significant (Figure S1).

Mean zooplankton length increased in all ponds over the course of the experiment (Figure 1C), but the rate of increase differed by treatment. Throughout the experiment, abundance weighted mean zooplankton length significantly increased in the reference ponds (Figure 2G, edf = 5.004). The mean zooplankton length also increased over time in the harvest and ambient density ponds, but at a much slower rate, resulting in a negative trend in the difference smooths for both treatments (Figure 2H, harvest edf = 2.557, ambient edf = 2.784). The GAM for mean zooplankton length explained 63.9% of the deviance in observations. Overall, the harvested and ambient treatment ponds had a significantly lower mean zooplankton length compared to the reference ponds (Figure 2I) and this effect remained even with the pre-fish period excluded from the GAM analysis (Figure S1).

Given the significant differences in mean zooplankton length and biomass in the treatments with fish, we used nMDS to evaluate if the community composition varied significantly among the ponds and over time. The stress for the nMDS was 0.15, indicating an adequate representation of the community compositions in reduced dimensions. Zooplankton community composition was significantly different among treatments ($p = 0.027$) and over time ($p = 0.001$). However, differences in the zooplankton assemblages among treatments was low ($R = 0.033$) whereas differences over time across all ponds were more pronounced ($R = 0.492$) (Figure 4). At the beginning of the study, the zooplankton communities in all ponds were dominated by cyclopoid copepods and small-bodied cladocerans such as *Bosmina* and were similar due to being seeded from the same source population. After the fish addition, small-bodied Cladocera and copepod nauplii contributed more to the overall biomass in the reference ponds, whereas large-bodied Cladocera and calanoid copepods contributed more to the zooplankton biomass in harvest density and reference ponds (Figure 5).

DISCUSSION

There were clear cascading trophic interactions that occurred with the addition of bigmouth buffalo to the experimental ponds that varied with fish density. The most pronounced response of phytoplankton and zooplankton biomass occurred in the ambient density ponds. Both zooplankton biomass and mean length quickly declined with the introduction of the planktivorous fish into the ambient density ponds. Congruent with the trophic cascade hypothesis, chlorophyll-a concentrations in the ambient density ponds increased and remained high after the fish addition. The chlorophyll-a dynamics slightly lagged the loss of zooplankton grazing pressure with the decline in biomass and body size, as would be expected for these cascading interactions (Carpenter et al. 1985). Based on these results, bigmouth buffalo may exert strong top-down control on phytoplankton biomass in shallow waterbodies when their populations are at ambient densities.

At harvested densities, the strength of the trophic cascade was dampened with no detectable difference in chlorophyll-a trends between the harvested and reference treatments after fish were added. The disparate response of chlorophyll-a in the harvested and ambient density ponds may be due to a difference in zooplankton grazing pressure driven by bigmouth buffalo predation altering the community size structure. Grazing pressure is generally the same among large- and small-bodied zooplankton communities when biomass differences are accounted for (Cyr and Pace 1992). In this case, the effect of fish on zooplankton biomass in the ambient and harvest density ponds was similar, but the mean zooplankton length was larger in the harvested density pond. There was also a modest divergence in community composition later in the experiment in the ponds with fish compared to the reference ponds. This difference in community and size structure may have allowed for greater grazing pressure in the harvested density ponds resulting in a lack of an effect on chlorophyll-a concentrations after the fish addition in comparison to the reference ponds. If so, bigmouth buffalo may exert weaker top-down control on phytoplankton biomass when populations are at harvested densities and their removal through harvesting could result in a weak trophic cascade until populations rebound.

A higher density of bigmouth buffalo could also lead to higher rates of nutrient recycling and availability through fish excretion (Vanni et al. 2013; Williamson et al. 2018), supporting phytoplankton growth. We estimated a daily excretion rate of bigmouth buffalo in each pond based on the excretion assays performed prior to the fish addition. Based on the rates measured, fish excretion was unlikely driving the pattern in chlorophyll-a concentrations among treatments. The daily contribution of N from fish excretion was three orders of magnitude less than the average total nitrogen pool. The excretion rates may have been underestimated due to incubation of the fish in unfiltered lake water, resulting in higher nitrification and uptake rates during the incubation. Additionally, the measurements were made in early spring when temperatures were low, potentially suppressing excretion rates (Vanni 2002). However, the conclusion that fish excretion did not contribute substantially to the patterns in chlorophyll-a is further supported by the lack of difference in total nitrogen and phosphorus dynamics among the fish treatments throughout the course of this experiment.

The timing of our experiment in the spring was aligned with a typical period for commercial harvest of bigmouth buffalo in this region of North America. Spring is also a dynamic period for plankton in temperate lakes, often characterized by a springtime phytoplankton bloom of diatoms after ice-out followed by a clear-water phase of low phytoplankton biomass as zooplankton populations increase in response to the spring bloom (Sommer et al. 2012). This typical phenology was also occurring in the experimental ponds;

however, the trajectory of plankton in these ecosystems was altered by the addition of fish in varying densities. As our experiment revealed, altering bigmouth buffalo densities during the spring bloom and clear-water phase had lasting effects on chlorophyll-a concentrations and zooplankton size structure. However, the experiment was terminated in mid-June prior to the typical onset of the later summer cyanobacteria-dominated bloom in temperate eutrophic waterbodies. As such, we cannot evaluate the effects of varying densities of bigmouth buffalo on late-summer blooms.

While the phytoplankton and zooplankton assemblages reflected natural communities, the fish communities in the experimental ponds were highly simplified with only bigmouth buffalo present. Eutrophic shallow lakes in this region have complex communities of planktivores, piscivores, and detritivores (Fischer and Quist 2019) that were not considered in this experiment. However, by only using bigmouth buffalo in this experiment, we were able to isolate and quantify the ecosystem-scale effects of ambient and harvested densities of this large-bodied planktivore. Based on our results, there is a need for future ecosystem-level studies of the effects of commercial harvest of bigmouth buffalo on water quality and food web structure to better understand these dynamics within the context of natural fish assemblages and population dynamics.

Our experimental manipulation of bigmouth buffalo densities revealed density-dependent top-down control on lower trophic levels and the potential for cascading trophic interactions with the harvest of this species. Given the paucity of ecological information for this exploited species, our experiment provided some of the first estimates of effect that varying bigmouth buffalo densities have on zooplankton and phytoplankton biomass. This information is useful when considering both harvest and water quality management in shallow lakes; however, we would caution against using the results of this controlled and simplified experiment to inform water quality management decisions at this time. What our results do support is the hypothesis that differences in bigmouth buffalo density can alter the biomass of lower trophic levels, suggesting the need for further study of the ecosystem-scale effects of intensive harvest of this species.

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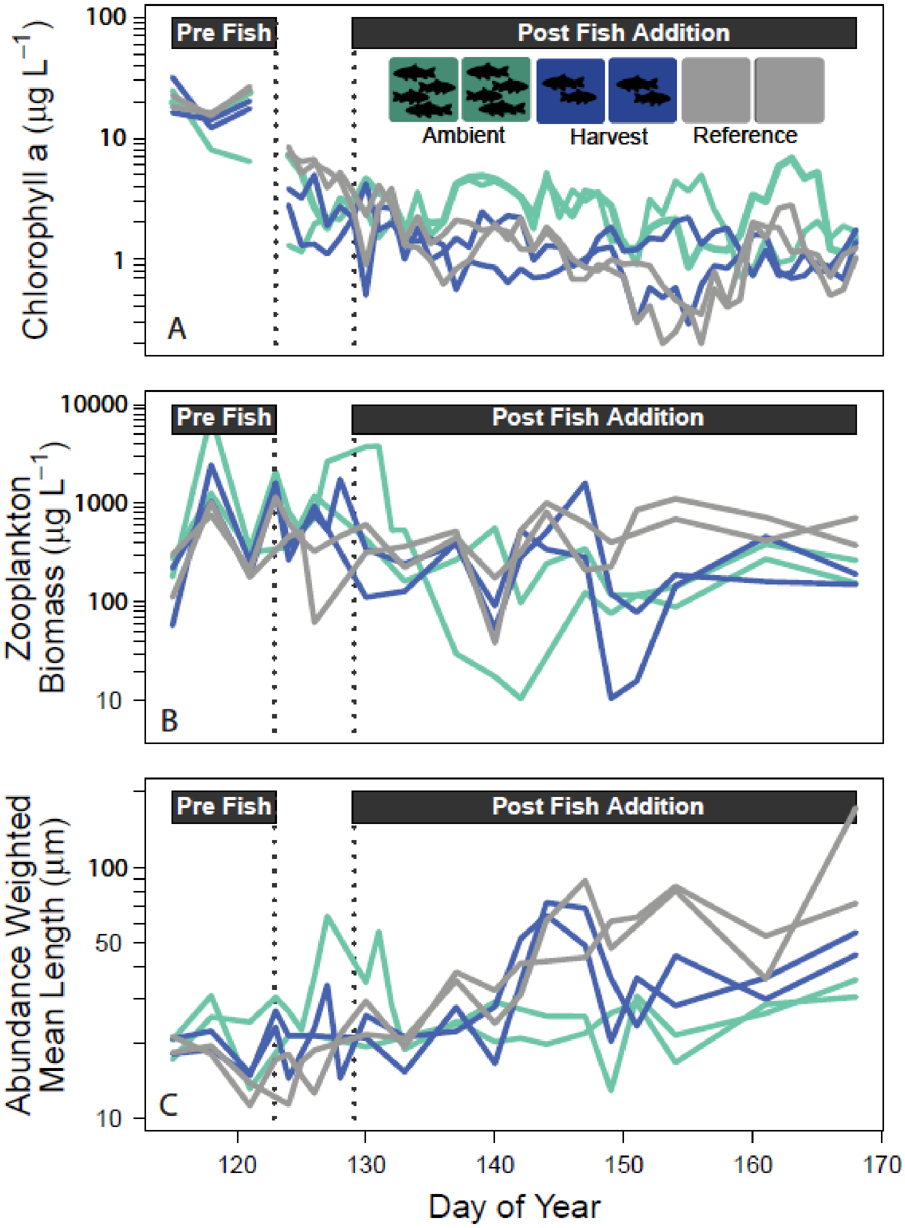

Figure 1. a) Chlorophyll-a concentrations, b) zooplankton biomass, and c) abundance-weighted mean zooplankton length from each of the ponds, color coded by treatment (see legend in panel a). The pre-fish addition and post-fish addition periods are denoted on each graph by the vertical dashed lines.

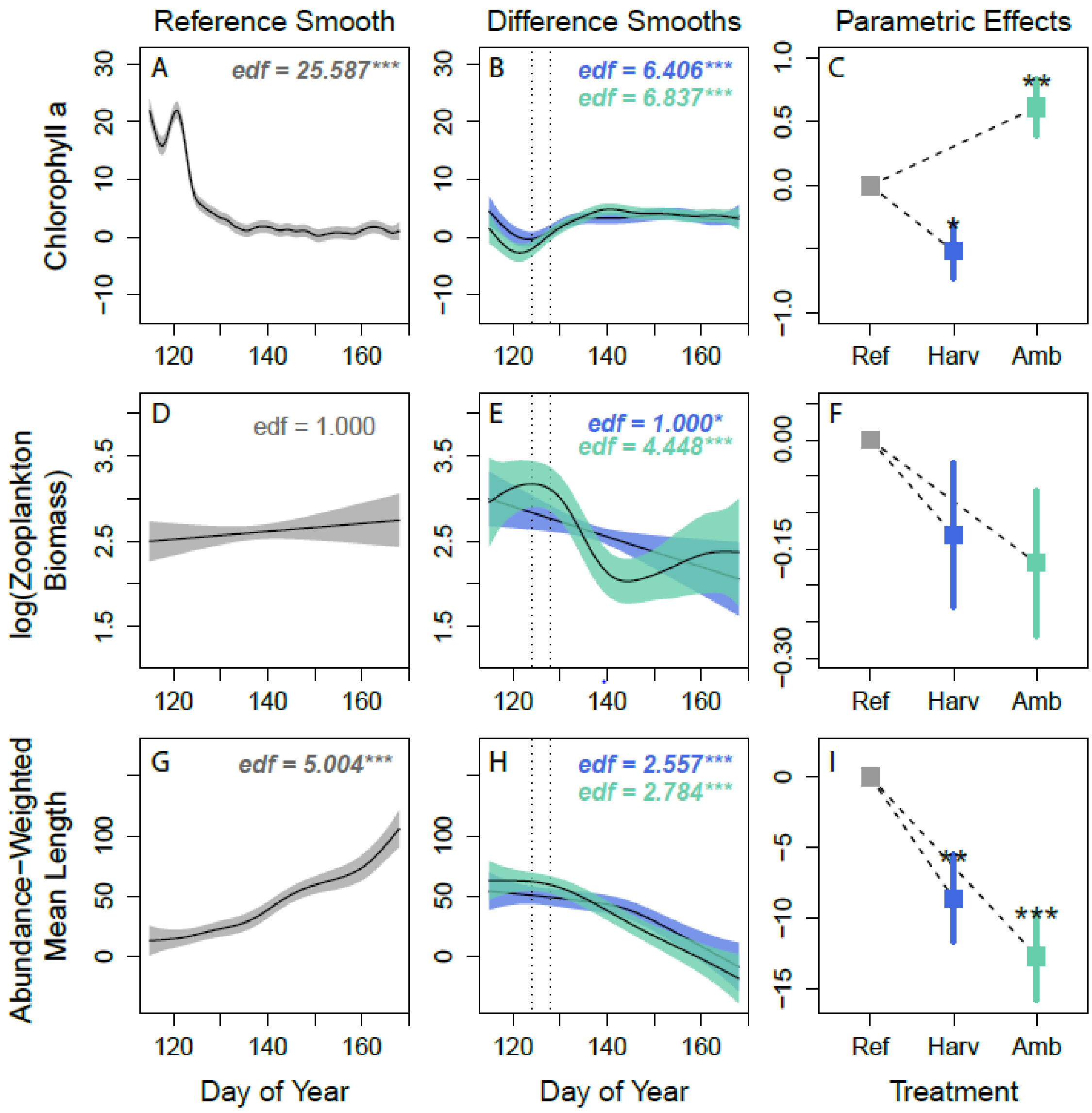

Figure 2. The results of the GAM analysis for a-c) chlorophyll-a, d-f) zooplankton biomass, and g-i) abundance weighted mean zooplankton length, including smooth fit to the reference pond observations (left column of panels), the difference smooths for the harvested (blue) and ambient (teal) treatments (middle column of panels), and the parametric effects estimated by the model (right column of panels). Color coding is the same as Figure 1. The vertical dashed lines in the panels with difference smooths indicate the DOY of the two fish additions. The asterisks next to the effective degrees of freedom (edf) values and above the parametric effects correspond to the estimated p-value, with * <0.05, ** <0.01, *** <0.001.

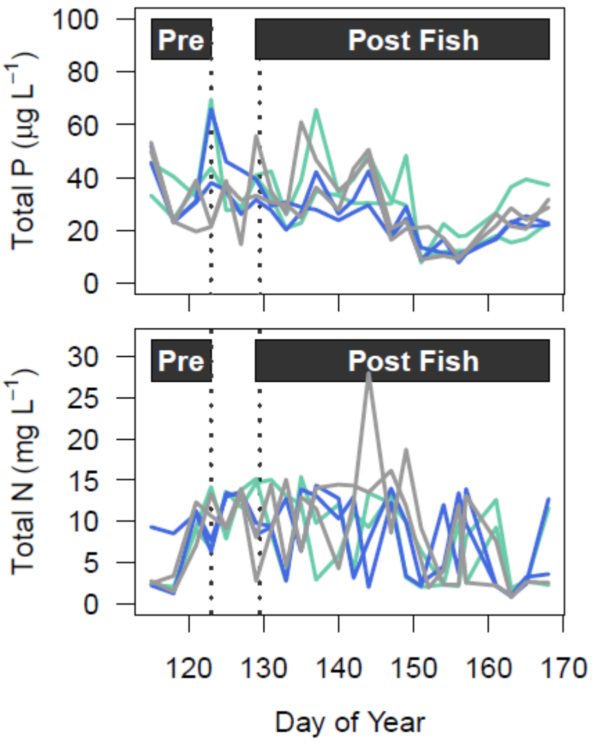

Figure 3. The a) total phosphorus, and b) total nitrogen concentrations in each pond over the course of the experiment. Color coding is the same as Figure 1. The pre-fish addition and post-fish addition periods are denoted on each graph by the vertical dashed lines.

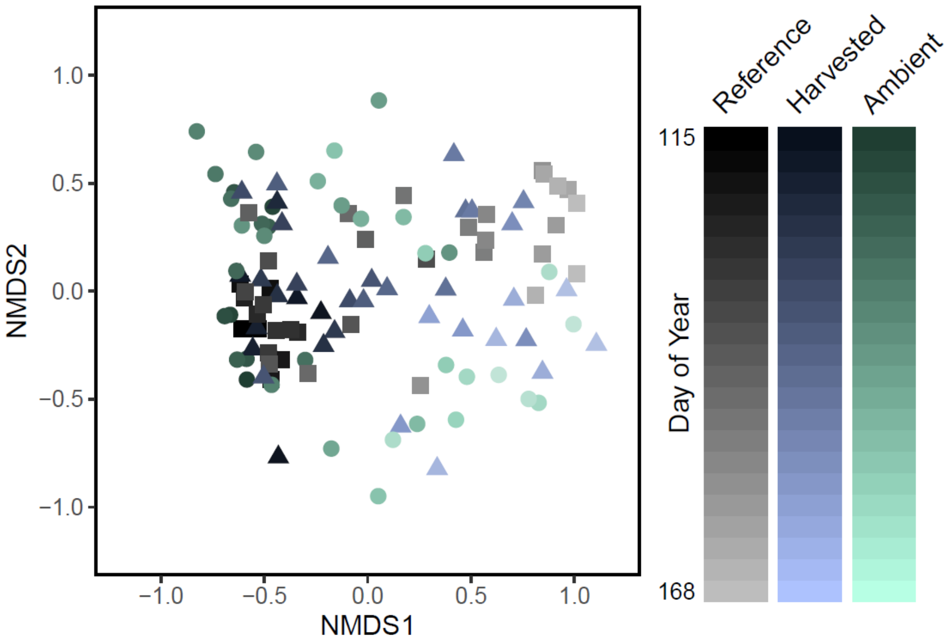

Figure 4. Zooplankton community composition visualized using nMDS (non-metric multidimensional scaling). The colors of the points correspond to the legend in Figure 1, with the reference ponds as gray squares, the harvested ponds as blue triangles, and the ambient density ponds as teal circles. The shading of the points corresponds to the DOY that the sample was taken (see scale at right).

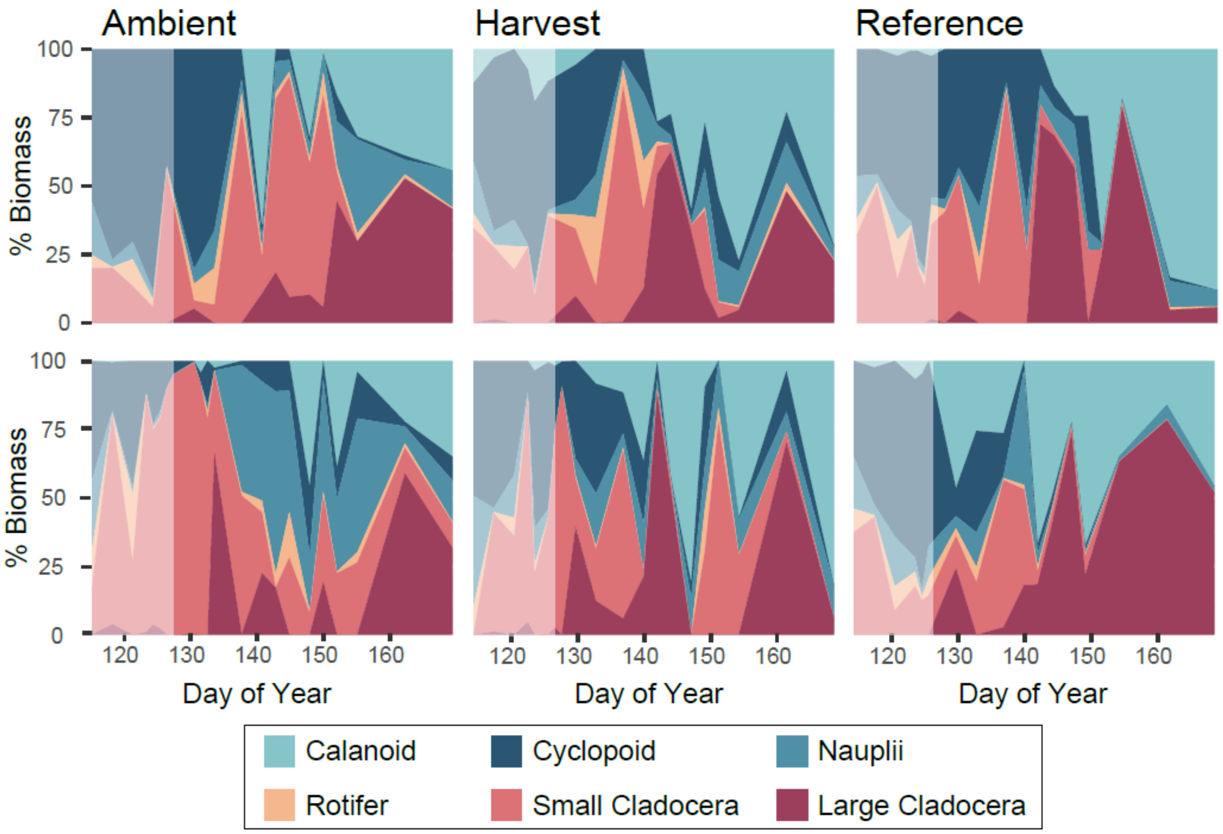

Figure 5. Zooplankton community composition as a percent of total biomass in all ponds over the course of the experiment. The columns are the different fish treatments and the rows are the two pond replicates. The opaque white box at the beginning of each time series denotes the period before the second fish addition on DOY 128.

Supplemental Information

The effects of bigmouth buffalo (*Ictiobus cyprinellus*) density on shallow lake ecosystems

Grace M. Wilkinson, Tyler J. Butts, Elena Sandry, Martin Simonson, Michael J. Weber

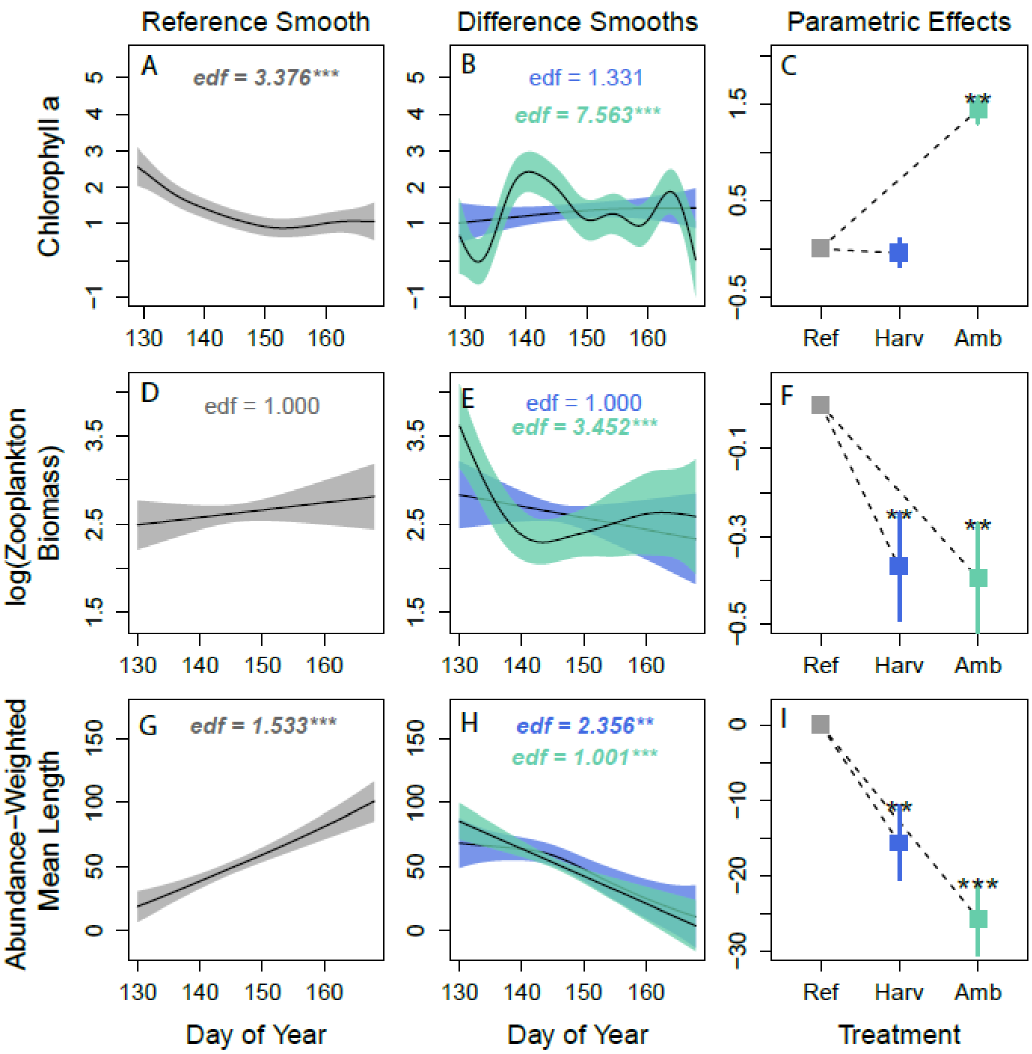

Figure S1. The results of the GAM analysis for a-c) chlorophyll-a (53.4% of deviance explained), d-f) zooplankton biomass (37.2% of deviance explained), and g-i) abundance weighted mean zooplankton weight (56.7% of deviance explained) during the post-fish addition period only (after DOY 128). Smooth fit to the reference pond observations (left column of panels), the difference smooths for the harvested (blue) and ambient (teal) treatments (middle column of panels), and the parametric effects estimated by the model (right column of panels). Color coding is the same as Figure 1. The asterisks next to the effective degrees of freedom (edf) values and above the parametric effects correspond to the estimated p-value, with * <0.05, ** <0.01, *** <0.001.

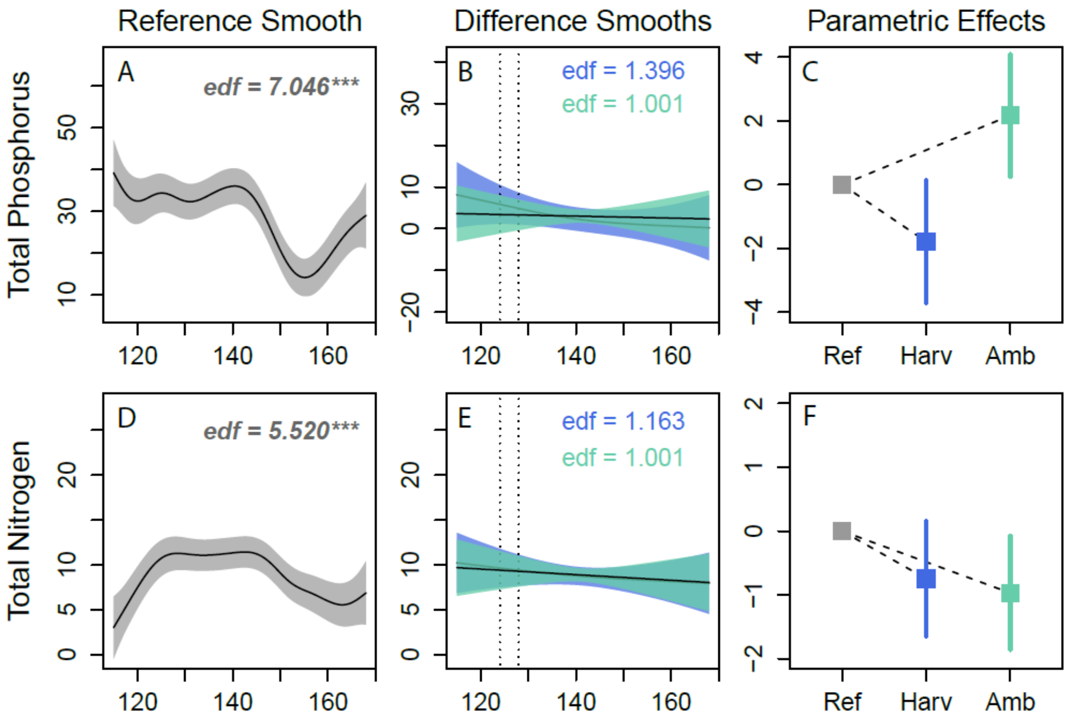

Figure S2. The results of the GAM analysis for a-c) total phosphorus (48.6% of deviance explained), and d-f) total nitrogen (31.6% of deviance explained). Smooth fit to the reference pond observations (left column of panels), the difference smooths for the harvested (blue) and ambient (teal) treatments (middle column of panels), and the parametric effects estimated by the model (right column of panels). Color coding is the same as Figure 1. The asterisks next to the effective degrees of freedom (edf) values and above the parametric effects correspond to the estimated p-value, with * <0.05, ** <0.01, *** <0.001.

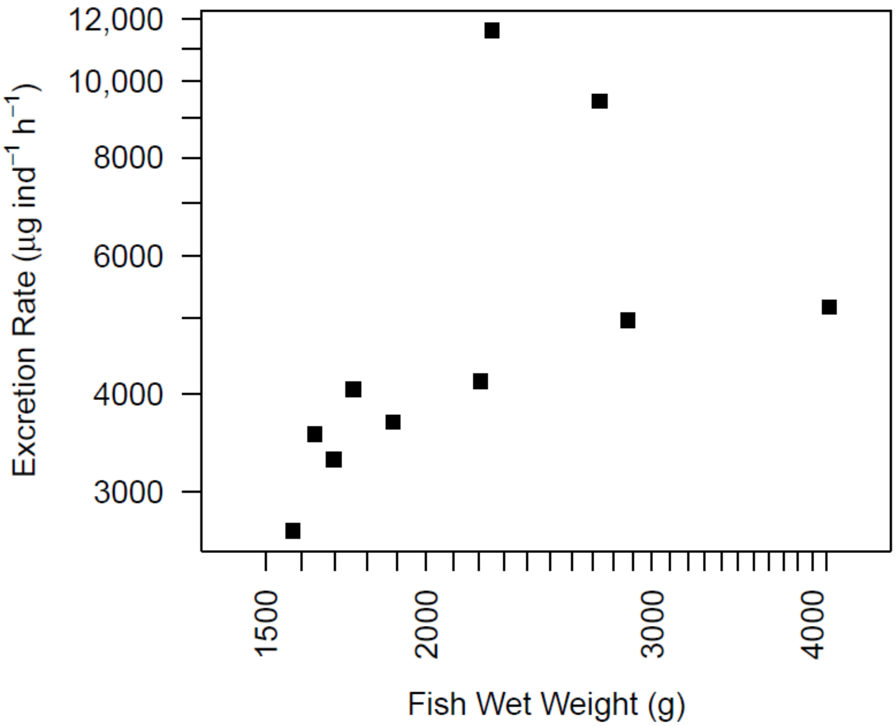

Figure S3. The excretion rate of NH_X for each individual fish (µmol ind^{-1} h^{-1}) and their wet weight (grams).