# INCREASED TEMPERATURE EFFECTS ON FISH-MEDIATED NUTRIENT 

 CYCLING IN AN EAST TEXAS STREAM
## A Thesis

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# INCREASED TEMPERATURE EFFECTS ON FISH-MEDIATED NUTRIENT 

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#### Abstract

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The unprecedented rate of global warming is an inevitable outcome of anthropogenic $\mathrm{CO}_{2}$ release into the atmosphere and complex climatic feedbacks. In ectotherms, increasing temperature may increase metabolic rates, which could enhance the energy demands of individuals and should accelerate resource acquisition. Population size and fish biomass were measured seasonally in a small second order stream over a 10year period to examine seasonal variation in these parameters. I examined effects of increased temperature on nitrogen and phosphorus excretion in the four most abundant fish in this stream system. These fishes represent three functional feeding guilds common to many temperate stream ecosystems and comprise approximately $80-90 \%$ of the fish community. I developed temperature dependent nitrogen and phosphorus excretion models for fishes and applied these models to daily average temperatures in the stream. I then simulated climate warming $\left(+2,+4, \&+6^{\circ} \mathrm{C}\right)$ to examine the potential effects of increased temperature on fish-mediated nutrient dynamics in a southern temperate stream ecosystem. I found that increased temperature does increase nutrient cycling and nutrient flux within aquatic ecosystems; however, these effects appear to be tied to population size, biomass in addition to seasonal temperature. With increased temperature effects in spring and autumn having the greatest effect, when temperatures are cool and fish abundance and biomass is also greatest.

KEY WORDS: Global warming, Nutrient cycling, Metabolism, Temperature, Excretion, Fish, Nitrogen, Phosphorus.


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## CHAPTER I

## Introduction

Over the last century, global warming has become an unavoidable result of increasing anthropogenic $\mathrm{CO}_{2}$ emissions and other complex climatic feedbacks (IPCC 2014). The consequences of a warmer climate are countless; but ecologically speaking, the distribution and abundance of organisms will shift, altering community composition both locally and regionally (Walther et al. 2002; Gaston 2003; Parmesan and Yohe 2003; Krajick 2004; Perry et al. 2005; Rosenzweig et al. 2008; Farrell 2009). This could affect food webs and the consumer interactions that regulate ecosystem structure and function (Petchey et al. 2010; Woodward et al. 2010). The overwhelming evidence amassed over the past $\sim 50$ years that conceptually illustrates the direct and indirect regulation of ecosystems may lose predictive power for future climate scenarios if the mechanisms supporting these generalized theories do not scale proportionately with increasing ecosystem temperature. Adjustments to this framework that begin with organismal-based theory and then extend to populations, communities and ecosystems could provide a means for predicting potential impacts of climate change on consumer roles in ecosystems (e.g., Berlow et al. 2009).

For example, metabolic theory of ecology (MTE, Brown et al. 2004), could provide a valuable framework for predicting potential effects of increased temperature on food webs and the associated consumer-mediated effects to ecosystem structure and function (Kleiber 1932; Wood and McDonald 1997; Allen and Gillooly 2009; AndersonTeixeira et al. 2009; Kraemer et al. 2016). In ectotherms, increasing temperature could increase metabolic rates, which may enhance the energy demands of individuals and
accelerate resource acquisition (Brett and Groves 1979; Gillooly et al. 2001). If resources are not limiting in the ecosystem, then population growth rates, nutrient turnover and biomass storage may also increase in response to climate warming (Woodward et al.2010). Therefore, consumer-mediated effects of ectotherms on ecosystems should be magnified in a warmer climate because of increased interaction rates and effect size linked to increased metabolism and greater population density, respectfully (Woodward et al. 2005; Petchey et al. 2008). However, elevated metabolic rates in response to increasing temperature also may shift elemental demands of individuals at the cellular level as the abundance of phosphorus-rich subcellular components (ribosomes, RNA, ATP) needed for greater metabolic activity increase with rising temperature (Elser et al. 1996). This may alter nutrient ratios.

Some fish taxa can directly alter elemental composition and reduce nutrient limitation at local ecosystem scales by enhancing the flux of materials across ecosystem boundaries (Polis et al. 1997). These consumer-mediated subsidies are widely documented, affecting nutrient ratios (e.g., reducing nutrient limitation) in terrestrial, marine, and freshwater ecosystems (Marczak et al.2007). In streams, surface feeding fishes can link terrestrial nutrients to the primary producers and decomposers by foraging on the water surface and excreting terrestrial-derived nutrients into the stream ecosystem (Gido and Matthews 2001; Vanni 2002; Hargrave 2006; Hargrave et al. 2010). In net autotrophic streams, fish-mediated terrestrial nutrient subsidies can stimulate benthic algae production, increase invertebrate grazers and enhance growth of predatory fishes (Nakano and Murakami 2001; Hargrave 2006). In net heterotrophic streams, fishmediated terrestrial nutrient subsidies have similar bottom-up effects that increase
productivity of leaf litter microbes and increase the densities of leaf litter invertebrates that consume microbes (Hargrave et al. 2010).

Fish-mediated nutrient effects are linked to foraging and excretion, which are both controlled tightly by metabolic rate. Because fishes are ectotherms, metabolic rate is a function of body size and temperature (e.g., Gillooly et al. 2001). Therefore, increased water temperatures resulting from global warming should stimulate rates of foraging and subsequent nitrogen $(\mathrm{N})$ and phosphorus $(\mathrm{P})$ nutrient excretion (C. W. Hargrave unpublished data). With trends for climate warming, fishes may experience higher N and P excretion rates, which may enhance fish-mediated nutrient cycling in stream ecosystems. This would therefore stimulate primary and secondary production in autotrophic streams and accelerate respiration and decomposition in heterotrophic streams across the landscape (e.g., Yvon-Durocher et al. 2010; Boyero et al. 2011). Therefore, I hypothesize that fish-mediated nutrient cycling will increase with increases in temperature.

I investigated this hypothesis in fishes through population size and biomass estimate data and laboratory experiments; using these data to develop temperaturedependent excretion models to predict nutrient excretion effects under elevated temperature scenarios. Population size and average individual biomass were estimated for all species within the community at three seasonal periods (Autumn, Spring, Summer) over a 10-year span in a small second order stream to examine seasonal variation within these population parameters. I tested the effects of increased temperature on N and P excretion in four common freshwater fish species, representing three functional feeding guilds (i.e., two surface-feeding insectivores, a watercolumn drift-feeding omnivore, and
a benthic omnivore) common to many temperate stream ecosystems. Finally, I developed temperature-dependent excretion models for P and N based on the above data and applied these models to daily average ambient temperatures from a natural stream as well as these temperatures increased by $+2^{\circ} \mathrm{C},+4^{\circ} \mathrm{C}$, and $+6^{\circ} \mathrm{C}$ to examine effects of increased temperature on fish-mediated nutrient dynamics across seasons in a second order Gulf Coast stream ecosystem.

## CHAPTER II

## Materials and Methods

## Study Site

Harmon Creek is a small, heavily forested, second order, north-flowing, headwater stream located within the Sam Houston State University's Center for Biological Field Studies in Huntsville, Texas. The 1000 meter stretch of this creek that was sampled over a 10-year span resembles typical second order headwater streams of East Texas. Harmon Creek has an average width of 3.5 m and average depth of 12.2 cm and is characterized by densely vegetated banks and overhanging canopy, and predominately sandy bottom runs with microhabitats including shallow riffles and deeper pools (Dent and Lutterschmidt 2001; Hargrave et al. 2009).

## Population size and biomass estimates

Using the sample-plot method, fishes were collected from sites along Harmon Creek, within the SHSU CBFS seasonally (Autumn, Spring, Summer) from October 2006 to March 2016 by the Hargrave research lab. Sites were selected to include multiple habitat characteristics (e.g., sandy runs, shallow riffles, and deep pools) in order to obtain diverse species, respectively. Fishes were anesthetized in MS-222 and preserved in 10\% formaldehyde and stored in archival storage in the Sam Houston State University Vertebrate Museum (SHSUVM). For this fish collection, I verified all species identifications; then I counted, massed to the nearest 0.01 g and measured standard length to the nearest 0.01 mm for all individuals in order to estimate population size and biomass for all fish species in all seasons collected over this 10 -year period. I then
transferred all fishes to $70 \% \mathrm{EtOH}$ and returned them to archival storage in the

## SHSUVM.

## Temperature-dependent excretion

Using nylon seines ( $1.2 \mathrm{~m} \times 3.05 \mathrm{~m}, 1.2 \mathrm{~m} \times 6.1 \mathrm{~m}$, with 3.2 mm mesh) I collected fifty individuals of each of the following fish species from Harmon Creek at the SHSU CBFS: Blacktail Shiner (Cyprinella venusta), Blackstripe Topminnow (Fundulus notatus), Western Mosquitofish (Gambusia affinis), and Bullhead Minnow (Pimephales vigilax). All individuals of non-targeted fish species were released unharmed back into the creek; study fishes were maintained in a cooler with stream water and transported to the CBFS aquatics facility.

I acclimatized 10 individuals of each species to each of 5 temperatures $(15,20$, $25,30,35^{\circ} \mathrm{C}$ ), with a $12 \mathrm{Hr}: 12 \mathrm{Hr} \mathrm{L}: \mathrm{D}$ for a two week period. Temperature of the lab facility was maintained at $15^{\circ} \mathrm{C}$; aquaria at higher temperatures were controlled with aquaria heaters and monitored twice daily using a YSI 85 meter. Feeding consisted of frozen bloodworms given once daily; however, fishes were fasted 48 hours prior to experimentation. After the fasting period, an individual was randomly selected from an acclimatization tank and placed into an experimental chamber with 500 mL spring water and maintained at the temperature treatment from which the individual was selected (15, $20,25,30,35^{\circ} \mathrm{C}$ ) for a two hour period. Three water samples were taken from the experimental chamber over the two hours. The first water sample was taken prior to placing the fish in the chamber. The second water sample was taken one hour after the fish was placed, and the third water sample was taken two hours after the fish was placed. All water samples were immediately put on ice to prevent nutrient degradation. This
method was repeated for a total of ten replicates per species at each of the temperature treatments. At the conclusion of each replicate, individuals were anesthetized in MS-222, massed to the nearest 0.001 g , preserved in $10 \%$ formaldehyde then placed in archival storage at the SHSUVM. P and N excreted in each water sample were measured using the ascorbic acid and phenate methods, respectively (APHA 1998). I first calculated an ANCOVA (with and without interactions) to test for differences among fish species in total and mass-specific P and N excretion, respectively. As there were no speciesspecific differences in P or N excretion, I chose to perform all subsequent analyses and analyzed effects of temperature on all fish species combined. I then calculated an ANCOVA with an interaction to determine whether mass-specific excretion rates of P and N for all fishes combined varied across the five temperature treatments.

## Predicted excretion

To predict P and N excretion (E), I developed the following generalized model:

$$
\begin{equation*}
\mathrm{E}=\sum \mathrm{M}_{i} \mathrm{rr}_{\mathrm{r}} \mathrm{~N}_{i} \tag{1}
\end{equation*}
$$

where $E$ for fishes is based on the total excretion of all taxa in the community, $M$ is average individual mass of species i for a season, $\mathrm{r}_{\mathrm{T}}$ is temperature-dependent excretion rate, and N is estimated population size of species i for a season. To determine the $\mathrm{r}_{\mathrm{T}}, \mathrm{I}$ regressed the slopes from the actual excretion rate regressions (Table 2) against the temperature treatments from the excretion experiment (Table 3). I then generated the temperature-dependent excretion models for nitrogen and phosphorus based on Eq. 1. I ran these models with daily average ambient temperatures in the stream for each species population over the 10 -year period to estimate predicted excretion of P and N . I summed all predicted excretion for all species in a single season to estimate total fish excretion of
both P and N for that season. I then simulated climate warming by increasing average daily ambient temperatures in the stream by $+2^{\circ} \mathrm{C},+4^{\circ} \mathrm{C}$, and $+6^{\circ} \mathrm{C}$, and running the models for each species in each season at these elevated temperatures to examine potential effects of increased temperature on fish-mediated nutrient dynamics in a second order Gulf Coast stream ecosystem. I chose these temperature increases based on the predicted range of temperature increase of aquatic ecosystems for the next 100 years (IPCC 2014). After running the model, I used the N and P excretion data to calculate the percent change per degree increase in excretion to determine the magnitude of change in excretion at elevated temperatures relative to ambient temperatures. I then calculated predicted average $\mathrm{N}: \mathrm{P}$ based on the predicted excretion data at both ambient and elevated temperatures.

## CHAPTER III

## Results

## Population size and biomass estimates

Over a 10-year sampling period (C. W. Hargrave unpublished data), 18 fish species were collected from Harmon Creek (Table 1). Population size, density and average individual biomass varied across seasons. The most consistently abundant species included surface feeding species Blackstripe Topminnow (F. notatus) and Western Mosquitofish (G. affinis), watercolumn feeding species Blacktail Shiner (C. venusta), and benthic feeding species Bullhead Minnow ( $P$. vigilax), respectively. These four species comprised approximately $80-90 \%$ of the fish collected over the ten year sample period (Table 1). Abundance of most species decreased from Autumn to Spring (Fig. 8). Fish population size was largest in Spring and Autumn seasons and smallest in Summer seasons. Average individual biomass was largest in Autumn seasons followed by Spring seasons and then Summer seasons (Fig. 7).

## Temperature-dependent excretion

There were no significant differences in total P and N excretion among species based on the ANCOVA models (without or with interaction). For P excretion without an interaction: (Overall Model: $\mathrm{F}=3.46, \mathrm{P}=0.01$; Mass: $\mathrm{F}=5.37, \mathrm{P}=0.59$; Species: $\mathrm{F}=$ $1.50, \mathrm{P}=0.22$ ), and with an interaction term: (Overall Model: $\mathrm{F}=2.12, \mathrm{P}=0.046$; Mass: $\mathrm{F}=0.00, \mathrm{P}=0.95$; Species: $\mathrm{F}=0.38, \mathrm{P}=0.77$; Interaction: $\mathrm{F}=0.40, \mathrm{P}=0.76$ ). For N excretion without an interaction: (Overall Model: $\mathrm{F}=27.01, \mathrm{P}<0.0001$; Mass: $\mathrm{F}=$ 41.39, $\mathrm{P}<0.0001$; Species $\mathrm{F}=1.50, \mathrm{P}=0.22$ ), and with an interaction term: (Overall

Model: $\mathrm{F}=15.21, \mathrm{P}<0.0002$; Mass: $\mathrm{F}=5.74, \mathrm{P}=0.02$; Species: $\mathrm{F}=0.51, \mathrm{P}=0.68$; Interaction: $\mathrm{F}=0.09, \mathrm{P}=0.97$ ).

I found that for fishes as a group, mass-specific P and N excretion rate varied significantly among temperature treatments: for P excretion rate: (Overall Model: $\mathrm{F}=$ $0.540 ; \mathrm{P}<0.001$; Mass: $\mathrm{F}=14.43, \mathrm{P}=0.0002$; Temperature: $\mathrm{F}=3.38, \mathrm{P}=0.012$; Interaction: $\mathrm{F}=5.16, \mathrm{P}=0.0007$ ) and for N excretion rate: treatments (Overall Model: F $=12.59 ; \mathrm{P}<0.001 ;$ Mass: $\mathrm{F}=82.29, \mathrm{P}<0.0001$; Temperature: $\mathrm{F}=2.56, \mathrm{P}=0.082$; Interaction: $\mathrm{F}=7.16, \mathrm{P}=0.03$ ). Mass-specific excretion rates for P and N increased as a linear function of wet fish mass and these relationships were found to be significant for all temperature treatments in the laboratory study (Table 2). The $\mathrm{x}, \mathrm{y}$ relationships for N excretion rate at each temperature treatment were as follows: $\left(y=0.0196 x ; R^{2}=0.6393\right.$; $\mathrm{p}<0.0001)\left(15^{\circ} \mathrm{C}\right),\left(\mathrm{y}=0.0217 \mathrm{x} ; \mathrm{R}^{2}=0.7163 ; \mathrm{P}<0.001\right)\left(20^{\circ} \mathrm{C}\right),\left(\mathrm{y}=0.03 \mathrm{x} ; \mathrm{R}^{2}=\right.$ $0.4950 ; \mathrm{P}<0.0001)\left(25^{\circ} \mathrm{C}\right),\left(\mathrm{y}=0.0277 \mathrm{x} ; \mathrm{R}^{2}=0.7473 ; \mathrm{P}<0.0001\right)\left(30^{\circ} \mathrm{C}\right)$, and $(\mathrm{y}=$ $\left.0.0317 \mathrm{x} ; \mathrm{R}^{2}=0.7170 ; \mathrm{P}<0.0001\right)\left(35^{\circ} \mathrm{C}\right)$. The $\mathrm{x}, \mathrm{y}$ relationships for P excretion rate at each temperature treatment were as follows: $\left(y=2.2091 x ; R^{2}=0.3615 ; P=0.0004\right)$ $\left(15^{\circ} \mathrm{C}\right),\left(\mathrm{y}=2.5504 \mathrm{x} ; \mathrm{R}^{2}=0.3603 ; \mathrm{P}=0.0015\right)\left(20^{\circ} \mathrm{C}\right),\left(\mathrm{y}=5.3014 \mathrm{x} ; \mathrm{R}^{2}=0.6777 ; \mathrm{P}<\right.$ $0.0001)\left(25^{\circ} \mathrm{C}\right),\left(\mathrm{y}=6.4504 \mathrm{x} ; \mathrm{R}^{2}=0.6396 ; \mathrm{P}<0.0001\right)\left(30^{\circ} \mathrm{C}\right)$, and $\left(\mathrm{y}=5.4751 \mathrm{x} ; \mathrm{R}^{2}=\right.$ 0.3029; $\mathrm{P}=0.0044)\left(35^{\circ} \mathrm{C}\right)($ Table 2). Excretion for both P and N showed the greatest rate of increase from $15^{\circ} \mathrm{C}$ to $20^{\circ} \mathrm{C}$ and increased with increasing temperature until $30^{\circ} \mathrm{C}$ (P) and $25^{\circ} \mathrm{C}(\mathrm{N})$, where average rate of excretion decreased (Figure 1). The rate of P excretion was greatly reduced from $30^{\circ} \mathrm{C}$ to $35^{\circ} \mathrm{C}$, whereas N excretion rate decreased the most from $25^{\circ} \mathrm{C}$ to $30^{\circ} \mathrm{C}$, with little change from $30^{\circ} \mathrm{C}$ to $35^{\circ} \mathrm{C}$ (Figure 1).

## Predicted excretion

For P excretion, a broken stick model (MacArthur 1957) was applied because the $\mathrm{R}_{\mathrm{T}}$ for P was a third degree polynomial and as such, the second curve of this function fell below zero under $15^{\circ} \mathrm{C}$ and does not explain the relationship between temperature and P excretion (Fig. 1). So, if daily average ambient temperature was less than $15^{\circ} \mathrm{C}$, then $\mathrm{r}_{\mathrm{T}}$ ( 0.0357 T ) was used, and if temperature was equal to or greater than $15^{\circ} \mathrm{C}$ then $\mathrm{r}_{\mathrm{T}}$ $\left(0.002 \mathrm{~T}^{3}+0.1301 \mathrm{~T}^{2}-2.4658 \mathrm{~T}+15\right)$ was used. This type of model was not necessary for N excretion, as a quadratic function best explained the relationship between N excretion and temperature at all temperatures; the $\mathrm{r}_{\mathrm{T}}$ used for N was $\left(-0.0002 \mathrm{~T}^{2}+0.0016 \mathrm{~T}-0.0001\right)$ (Fig. 1). Average daily temperatures for Harmon Creek ranged from $1-27.9^{\circ} \mathrm{C}(17.4 \pm$ $0.11^{\circ} \mathrm{C}$; mean $\pm$ SD) from 1 July 2006 - 1 July 2016. Within seasons, average daily temperatures ranged from $1-26.5^{\circ} \mathrm{C}$ (mean $14.8 \pm 0.16^{\circ} \mathrm{C}$ ) for Spring, $16.8-26.1^{\circ} \mathrm{C}$ (mean $22.9 \pm 0.13^{\circ} \mathrm{C}$ ) for Summer, and $5-27.9^{\circ} \mathrm{C}$ (mean $18.8 \pm 0.15^{\circ} \mathrm{C}$ ) for Autumn. I increased each average daily temperature by $+2^{\circ} \mathrm{C},+4^{\circ} \mathrm{C}$, and $+6^{\circ} \mathrm{C}$ to simulate potential effects of elevated temperature of surface water. Predicted average $P$ and $N$ excretion by the fish community were greatest during Summer and least during Spring in both ambient and elevated temperature scenarios (Fig. 3). Predicted excretion for both N and P was relatively low November - March, then notably increased April - July and declined in August (Fig. 3). Within each season, predicted excretion rates increased in all elevated temperature scenarios relative to excretion rates predicted for actual stream temperatures; however, the magnitude of this increase changed across seasons (Fig. 3;4). Percent change in excretion per temperature degree increase was lowest in Summer while the greatest change occurred during Spring and Autumn. Average monthly predicted
excretion was greatest in July, but the percent change from ambient to elevated temperatures showed that the magnitude of this change in excretion from ambient to elevated temperatures was minimal compared to the magnitude of change in Spring and Autumn months (Fig. 4). Average predicted seasonal $\mathrm{N}: \mathrm{P}$ was highest in Spring, followed by Autumn and lowest in Summer over the 10-year period (Fig. 5). In the elevated temperature models, the average predicted seasonal $\mathrm{N}: \mathrm{P}$ decreased across all seasons as ambient temperature was increased (Fig. 5).

## CHAPTER IV

## Discussion

In this study, I used population and biomass estimates, excretion rates of four common fish species, and average daily ambient temperature to model the effects of increased temperature on fish-mediated nutrient cycling in a small, East Texas stream. My prediction that elevated temperature would enhance fish-mediated nutrient cycling was supported in my models. However, this nutrient enhancement was not only dependent on temperature. Rather, my data suggest that population size and individual body size also play an important role in fish-mediated nutrient cycing and are coupled with effects of temperature. For example, my data support that total excretion of N and P is highest in Summer, but the greatest effect of increased temperature, relative to ambient temperature, occurs in Spring and Autumn, when stream temperatures are cool, individual excretion rates are high, and fish populations are large and composed of large individuals. Furthermore, because of the important role fishes play as comsumers in aquatic systems, other ecosystem functions can be impacted via bottom-up regulation by increased temperature, population size and total biomass. For example, in elevated temperature scenarios, primary production and decomposition could be indirectly enhanced by increased consumer interactions, through the breakdown and return of nutrients via excretion for autotrophic and microbial production. Below, I discuss the specifics of my findings and demonstrate that increased temperature effects on fishmediated nutrient cycling are likely tied to individual metabolism and population dynamics.

Fish populations are dynamic over time. Not only will total fish populations fluccuate, but species abundance and composition within the fish community will also change seasonally (Nikolskii 1969). The population estimates in Harmon Creek over the 10 -year period support this literature. The abundances of the 18 fish species collected in Harmon creek from 2006-2016 varied both seasonally and annually. Dent and Lutterschmidt (2001) also sampled fish from sites along the same stretch of Harmon Creek described in this study in Spring 2000. In my study, seven species were collected in addition to the 11 species collected by Dent and Lutterschmidt (Table 1). The seven undocumented species, in order of abundance, are: Ribbon Shiner, Blackspotted Topminnow, Largemouth Bass, Redear Sunfish, Green Sunfish, Warmouth, and Goldstripe Darter. Additionally, Blacktail Shiner, Western Mosquitofish, and Blackstripe Topminnow were found to be the three most abundant species in both studies (Dent and Lutterschmidt 2001). My data show that for nearly all 18 fish species, population size was lowest in Summer seasons and highest in Spring and Autumn seasons, and that average individual biomass was high in Autumn seasons and fluccuated in Spring and Summer seasons over the 10-year period (Fig. 7). These data suggest overall, that fish populations in Spring were large and composed of both large and small individuals, fish populations in Summer were small, composed of both large and small individuals, and Autumn fish populations were large, composed of large individuals.

Metabolism of organisms drives all biological processes and is most influenced by its relationship with body size and temperature (Kleiber 1932; MTE, Brown et al. 2004). My results showed that fish excretion rates increased as a function of wet fish mass in all temperature treatments. These findings were significant and support these
generalized theories (Table 1). For example, P and N temperature-dependent excretion rates for the four abundant fish species increased from $15^{\circ} \mathrm{C}$ to $30^{\circ} \mathrm{C}(\mathrm{P})$ and $15^{\circ}$ to $35^{\circ} \mathrm{C}$ (N). The rate of P excretion was reduced from $30^{\circ} \mathrm{C}$ to $35^{\circ} \mathrm{C}$, and there was minimal change in rate from $30^{\circ} \mathrm{C}$ to $35^{\circ} \mathrm{C}$ for N excretion (Fig. 1). These temperature-dependent relationships for P and N were non-linear and found to be significant (Table 2). This temperature effect on fish excretion likely resulted from the dependence of metabolic activity in organisms on temperature (Elser et al. 1996; Gillooly et al. 2001; Glazier 2010; Killen et al. 2010; Ohlberger et al. 2012; Messmer et al. 2016). Thus, similar to temperature effects on metabolic processes in ectotherms, a quadratic function best explained the temperature-dependent effects on N excretion rate in my experiment. For P excretion rate, a broken stick model was applied and excretion rate was broken into two units according to temperature. A third degree polynomial function best explained temperature effects at temperatures equal to and above $15^{\circ} \mathrm{C}$ and a linear function best explained temperature effects at temperatures below $15^{\circ} \mathrm{C}$. This variation in rate of P and N excretion in response to elevated temperature could present important consequences for fish-mediated nutrient cycling in aquatic ecosystems in warmer climate scenarios. For example, in cases of elevated temperature, individual body size could be reduced as larger individuals are more susceptible to higher temperature than smaller individuals (Daufresne et al. 2009; Gardner et al. 2011; Ohlberger 2013; Vindenes et al. 2014; Messmer et al. 2017). This potential change in individual biomass could affect N and P excretion by fishes, thereby affecting nutrient cycling and potentially altering important ecosystem functions (e.g., primary production and decomposition) (Arendt 2007).

Excretion of nutrients is a function of metabolism and therefore directly affected by temperature in ecotherms (Vanni, 2002). Overall, in my model simulations of ambient and elevated temperature scenarios, predicted P and N excretion by fish increased with each temperature increase. These results support those found in literature. Specifically, the results of my model show fish-mediated nutrient cycling was greatest in Summer, likely because ambient stream temperatures were high, and lowest Autumn through Spring (Fig. 3). However, temperature-dependent excretion rates were non-linear (Fig. 1); this indicates that the effects of increasing temperature on fish-mediated nutrient cycling did not remain constant across seasons or years. Because the magnitude of the effect of temperature on fish-mediated nutrient cycling varied across seasons, the actual change in nutrient response from ambient to elevated temperatures was lowest in Summer (Fig. 4). Thus, my data suggest that the greatest impact of increased temperature on fishmediated nutrient cycling will occur during cooler seasons, specifically Autumn and Spring (Fig. 4). This is likely because stream temperatures during these seasons fell within the temperature range of greatest rate increase within the temperature-dependent excretion rate functions previously described (Fig. 1).

Population dynamics have proved to be an important factor in nutrient-cycling (Kitchell et al. 1979; Holmlund and Hammer 1999). In comparing the results of my excretion models for N and P at both ambient and elevated temperatures with the seasonal changes in population size and biomass, I found that these seasonal changes corresponded with one another (Fig. 2, 6). This indicates that temperature is not the only factor to influence changes in fish-mediated nutrient cycling. Rather, population size and biomass of individuals, in addition to temperature, also play an important role in
determining fish-mediated nutrient effects in aquatic ecosystems (e.g., Hall et al. 2007). Specifically, the greatest impact to fish-mediated nutrient cycling occurs when temperatures are cool, individual excretion rates are high, populations are large and composed of large individuals. My results suggest this would most likely occur in Autumn and Spring seasons. Thus, fish-mediated nutrient effects under future climate change scenarios are dependent on seasonal temperature and population dynamics within the fish community. These conclusions of my model are limited to streams with similar annual temperature profiles to the stream used for the experimental and modeling portion of this study. I suggest that these temperature conditions are indicative of other small, second order, forested streams in southeast Texas. Therefore, it is likely that streams with different annual temperature conditions (warmer, cooler) than the stream used in the study will exhibit different fish-mediated nutrient dynamics. For example, summer temperatures in northern streams may reflect autumn to spring temperatures in southern streams. This could suggest that effects of temperature on fish excretion in some northern streams would be greatest in summer rather than autumn, as compared to the stream we used. Conversely, in tropical streams where annual temperatures are close to optimum for fish metabolic activity, increases in temperature could have little effect increasing nutrient cycling; rather, elevated temperature could result in a negative response in fishmediated nutrient cycling. This type of latitudinal analysis was beyond the scope of this manuscript; however, I argue that these types of studies are necessary to understanding the all-encompassing effects of increased temperature as a result of global warming on aquatic ecosystems.

While N and P excretion by fishes is important in nutrient cycling, the ratio of these nutrients also play an important role ((Elser et al. 1988; Sterner and Elser 2002; Vanni 2002). In my results, predicted average seasonal $\mathrm{N}: \mathrm{P}$ at ambient temperatures was highest in Spring, followed by Autumn and lowest in Summer over the 10-year period. This suggests that N may be more available in the environment in Spring seasons and less so in other seasons. In the elevated temperature models, the predicted average seasonal $\mathrm{N}: \mathrm{P}$ decreased across all seasons as ambient temperature was increased (Fig. 5). This indicates that as temperatures rise, fishes may sequester more nitrogen as phosphorus is excreted and nitrogen could become limiting in this stream ecosystem. Ecosystem functions (e.g., primary production and decomposition) could be impacted via bottom-up regulation by increased temperature if N becomes limiting. In turn, these effects could further alter fish-mediated nutrient cycling through availability and acquisition of nutrients, thereby causing dynamic change to the ecosystem in response to increased temperatures.

I did not directly study the effects of temperature on the population dynamics of these fishes. My seasonal data suggest that these fish populations are highest in Autumn and Spring and lowest in Summer, however we could not account for changes in population in the elevated temperature scenario models. This limits the applicability of my data with respect to using population and biomass data that does not change in response to elevated temperature. While this assumption in my model is flawed, I argue that my predictions, which were based on population dynamics over a ten-year span of climatic conditions, are conservative when considering the positive feedback response to increasing temperatures, which could positively affect these fish populations.

Additionally, diet contents of fishes were not included within this study. Ecological stoichiometry (EST, Sterner and Elser 2002) has demonstrated to be very important with respect to fish nutrient cycling. To fully understand the effects of elevated temperature on fish-mediated nutrient dynamics, experiments should include the analysis of gut contents, stable isotopes, or some equivalent measure of diet for consumers, in addition to excretion experiments (Vanni, 2002), as well as population size and biomass estimates.

Surface temperatures are projected to increase by as many as $3-5^{\circ} \mathrm{C}$ over the next 100 years (IPCC 2014). It is therefore important to understand the effects that this rise in temperature will have on consumer roles in aquatic ecosystems. Fishes play an important role as consumers by recycling nutrients from basal resources and creating nutrient flux through subsidies from terrestrial ecosystems (Hargrave 2006; 2010). My study suggests that increased temperature as a consequence of global warming will increase nutrient cycling and flux by fishes, which should result in an increase in both basal and subsidized resources within the system (Yvon-Durocher et al. 2010; Boyero et al. 2011). This increase in resources should promote a positive feedback within the food web, enhancing consumer populations and foraging activity, which will in turn strengthen fish-mediated nutrient cycling in aquatic ecosystems. However, these effects of increased temperature may be further complicated by the change in the indirect and direct food web interactions of consumers resulting from changes to basal metabolic demands. Additional experiments are needed to further investigate how increased temperature affects food web dynamics via changes in individual metabolism.

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Figure 1. Temperature-dependent excretion rate by fishes for phosphorus (top) and nitrogen (bottom).


Figure 2. Predicted average phosphorus (top) and nitrogen (bottom) excretion by fishes in Harmon Creek at ambient temperature (blue) and ambient temperature $+2^{\circ} \mathrm{C}$ (green), $+4^{\circ} \mathrm{C}$ (orange), and $+6^{\circ} \mathrm{C}$ (red) across the 10 -year sampling period.


Figure 3. Predicted average monthly phosphorus (top) and nitrogen (bottom) excretion by fishes in Harmon Creek at ambient temperature (blue) and ambient temperature $+2^{\circ} \mathrm{C}$ (green), $+4^{\circ} \mathrm{C}$ (orange), and $+6^{\circ} \mathrm{C}$ (red) across the 10 -year sampling period.


Figure 4. Percent change per degree increase for predicted average monthly phosphorus (top) and nitrogen (bottom) excretion by fishes in Harmon Creek at ambient temperature $+2^{\circ} \mathrm{C}$ (green), $+4^{\circ} \mathrm{C}$ (orange), and $+6^{\circ} \mathrm{C}$ (red) across the 10 -year sampling period. Percent change/degree increase was calculated by subtracting average excretion at ambient temperature from average excretion at the elevated temperature, dividing by average excretion at ambient temperature, then multiplying by 100 .


Figure 5. Predicted average seasonal $\mathrm{N}: \mathrm{P}$ at ambient (blue) and elevated temperatures (green $+2^{\circ} \mathrm{C}$, orange $+4^{\circ} \mathrm{C}$, red $+6^{\circ} \mathrm{C}$ ) based on predicted excretion of nitrogen and phosphorus at ambient and elevated temperatures over a 10-year period.


Figure 6. Estimated population size (blue) and total biomass (orange) of fishes in Harmon Creek over a 10 -year period.


Figure 7. Average population size (blue) and average individual biomass (orange) of fishes in Harmon Creek over a 10-year period.


Figure 8. Average seasonal population size for Spring (blue), Summer (red), and Autumn (green) of fishes in Harmon Creek over a 10-year period.

Table 1. Average seasonal and annual abundance and average $\%$ seasonal and annual abundance of fishes collected in Harmon Creek over a 10 -year period. Species with 0 averages were rarely collected over the 10 -year period but still included in this table.

| SPECIES | Spring | Summer | Autumn | Annual | $\%$ <br> Spring | $\%$ <br> Summer | $\%$ <br> Autumn | $\%$ <br> Annual |
| :--- | :---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Ameiurus natalis |  | 4 | 1 | 1 |  |  |  |  |
| Cyprinella lutrensis | 118 | 16 | 26 | 69 | 9 | 1 | 1 | 4 |
| Cyprinella venusta | 548 | 639 | 705 | 614 | 41 | 58 | 35 | 37 |
| Etheostoma parvipinne |  |  |  |  |  |  |  | 17 |
| Fundulus notatus | 94 | 196 | 340 | 211 | 7 | 18 | 17 | 13 |
| Fundulus olivaceus | 4 | 13 | 23 | 12 |  | 1 | 1 | 1 |
| Gambusia affinis | 189 | 50 | 513 | 382 | 14 | 5 | 26 | 23 |
| Lepomis cyanellus |  |  |  |  |  |  |  |  |
| Lepomis gulosus |  |  |  |  |  |  |  |  |
| Lepomis macrochirus | 23 | 10 | 34 | 27 | 2 | 1 | 2 | 2 |
| Lepomis megalotis | 18 | 6 | 30 | 23 | 1 | 1 | 1 | 1 |
| Lepomis microlophus |  | 1 |  |  |  |  |  | 1 |
| Lythrurus fumeus | 9 | 1 | 17 | 18 | 1 |  | 1 | 1 |
| Micropterus punctulatus | 1 | 11 | 5 | 4 |  | 1 |  |  |
| Micropterus salmoides | 3 | 22 | 5 | 5 |  | 2 |  |  |
| Notropis texanus | 89 | 88 | 82 | 78 | 7 | 8 | 4 | 5 |
| Percina sciera |  | 11 | 1 | 2 |  | 1 |  |  |
| Pimephales vigilax | 232 | 31 | 212 | 231 | 17 | 3 | 11 | 14 |

Table 2. Linear relationships between body mass and mass-specific excretion rate of fishes at temperature treatments for both phosphorus and nitrogen.

|  | Temperature <br> Treatment | $\mathrm{X}, \mathrm{Y}$ <br> Relationship | $\mathrm{R}^{2}$ | P |
| :--- | :---: | :---: | :---: | ---: |
| Phosphorus |  |  |  |  |
|  | $15^{\circ} \mathrm{C}$ | $\mathrm{y}=2.2091 \mathrm{x}$ | 0.3615 | 0.0004 |
|  | $20^{\circ} \mathrm{C}$ | $\mathrm{y}=2.5504 \mathrm{x}$ | 0.3603 | 0.0015 |
|  | $25^{\circ} \mathrm{C}$ | $\mathrm{y}=5.3014 \mathrm{x}$ | 0.6777 | $<0.0001$ |
| Nitrogen | $30^{\circ} \mathrm{C}$ | $\mathrm{y}=6.4504 \mathrm{x}$ | 0.6396 | $<0.0001$ |
|  | $35^{\circ} \mathrm{C}$ | $\mathrm{y}=5.4751 \mathrm{x}$ | 0.3029 | 0.0044 |
|  |  |  |  |  |
|  | $15^{\circ} \mathrm{C}$ | $\mathrm{y}=0.0196 \mathrm{x}$ | 0.6393 | $<0.0001$ |
|  | $20^{\circ} \mathrm{C}$ | $\mathrm{y}=0.0217 \mathrm{x}$ | 0.7163 | $<0.0001$ |
|  | $25^{\circ} \mathrm{C}$ | $\mathrm{y}=0.03 \mathrm{x}$ | 0.4950 | $<0.0001$ |
|  | $30^{\circ} \mathrm{C}$ | $\mathrm{y}=0.0277 \mathrm{x}$ | 0.7473 | $<0.0001$ |
|  | $35^{\circ} \mathrm{C}$ | $\mathrm{y}=0.0317 \mathrm{x}$ | 0.7170 | $<0.0001$ |

Table 3. Temperature-dependent excretion rate relationships for both phosphorus and nitrogen.

|  | T | $\mathrm{r}_{\mathrm{T}}$ | $\mathrm{R}^{2}$ | P |
| :---: | :---: | :---: | :---: | :---: |
| Phosphorus |  |  |  |  |
|  | $<15^{\circ} \mathrm{C}$ | $\mathrm{y}=0.1473 \mathrm{~T}$ | 1 |  |
| Nitrogen | $\geq 15^{\circ} \mathrm{C}$ | $\mathrm{y}=-0.0018 \mathrm{~T}^{3}+0.1178 \mathrm{~T}^{2}-2.2484 \mathrm{~T}+15$ | 0.9869 | 0.0025 |
|  |  | All T | $\mathrm{y}=-2 \mathrm{E}-05 \mathrm{~T}^{2}+0.0016 \mathrm{~T}-0.0001$ | 0.8535 |

VITA

Jessica Lynn McWilliams

## EDUCATION

M.S. Biology Sam Houston State University, Huntsville, TX. December 2017.

Biology, Minor in Secondary Education Sam Houston State University, Huntsville, TX. May 2013.

Pre-Nursing Lonestar College System, Tomball, TX. May 2009.

## EMPLOYMENT

Graduate Research Assistant. Department of Biology, Sam Houston State University, Huntsville, TX. 2016-2017.
Graduate Teaching Assistant. Department of Biology, Sam Houston State University, Huntsville, TX. 2013-2015.
Undergraduate Research/Lab Assistant. Department of Biology, Sam Houston State University, Huntsville, TX. 2011-2013.
Undergraduate Teaching Assistant. Department of Biology, Sam Houston State University, Huntsville, TX. 2011-2012.

## CERTIFICATION

CPR/First Aid certification; 2012-2016.
USA Archery Instructor certification; 2013-2016.
CNA certification; 2006.

## TEACHING EXPERIENCE

## Sam Houston State University

Lecturer- General Ecology Lab (BIOL 3409); Spring 2017.

- 2 sections ( 40 students); temporary lecturer for 1 class day

Lecturer- General Ecology Lecture (BIOL 3409); Fall 2016.
-1 section (40 students); temporary lecturer for 4 class days (MWF)
Lecturer- Contemporary Biology Lecture (BIOL 1408); Fall 2015.

- 2 sections ( 75 students, 150 students); temporary lecturer for 3 weeks (MWF)
Teaching Assistant- General Ecology Lab (BIOL 3409); Fall/Spring 2011-Fall 2015.
- 4 sections/semester, $\sim 18$ students/section

Teaching Assistant- Introduction to Cellular Biology Lab (BIOL 2440); Summer 2014, 2015.

- 2 sections/semester, $\sim 25$ students/section

Student Teaching- Tomball ISD $8^{\text {th }}$ grade Earth Science, $9^{\text {th }}$ grade Biology, $12^{\text {th }}$ grade regular/PAP Anatomy \& Physiology; Spring 2013.

- 280 classroom hours; designed lesson plans and evaluated using PDAS

Training New Teaching Assistant- General Ecology Lab (BIO 3409); Fall/Spring 2013-2014.

- Co-authored lab manual for TA use for course.

Methods Block- Huntsville ISD 9 th grade Biology; Fall 2012.

- 85 classroom hours; designed lesson plans and evaluated using PDAS


## RESEARCH EXPERIENCE

Effects of experimental warming on fish-mediated nutrient cycling; Harmon Creek; SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; 2016-2017.
Population and Biomass Estimate Study of Fishes of Harmon Creek; Harmon Creek; SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; 2016-2017.
Reproductive Productivity Study- Sheepshead Minnow; SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; 2016-2017.
Pilot Study- Bluehead Shiner; SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; 2017.
Population Estimate Study- Bluehead Shiner; Caddo Lake/Big Cypress Bayou River, TX; June 2016-2017.
Species Identification- freshwater fish species, Caddo Lake/Big Cypress Bayou River, TX; June 2016-2017.
Salt Tolerance Study- Bullhead Minnow; Harmon Creek, SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; June 2015.
Parasite Load Study- Presence in Harmon Creek Fishes and Seasonal Variation; Harmon Creek, SHSU Center for Biological Field Studies, TRIES Laboratories, Huntsville, TX; June 2014- December 2014.
Sample Processing/Data Analyses- invertebrate/algae sorting, fish species identification and preservation; 2011-2014.
Conservation Research- Endangered fish species; Balmorhea State Park, Balmorhea, TX; 2011- 2013.
Species Identification/density- aquatic environment, Big Thicket National Preserve, TX; Fall 2011.
Species Identification/density- aquatic environment, Southern and Eastern OK; Fall 2011. Thermal Preference Study- Endangered fish species; Balmorhea State Park, Balmorhea, TX;Fall 2011.
Density Study- native and invasive fish species; Harmon Creek, SHSU Center for Biological Field Studies, Huntsville, TX; Spring 2011.

## RESEARCH INTERESTS

Conservation of endangered species fresh water fish ecology
Fresh water fish life history
Aquatic community structure and function
Effects of climate change on nutrient dynamics in aquatic ecosystems
Effects of abiotic factors on aquatic ecosystems

## ORAL PRESENTATIONS

5. Potential Effects of Salinity Change on Fish Assemblage Structure in the Red River Drainage (Texas-Oklahoma).
At: Sam Houston State University Graduate Research Exchange, 2015.
6. General Ecology and Research Opportunities.

At: Sam Houston State University High School Outreach Event, 2014.
3. Potential Effects of Salinity Change on Fish Assemblage Structure in the Red

River Drainage (Texas-Oklahoma).
At: Sam Houston State University Graduate Research Exchange, 2014.
2. Past and Current Research Experience + Biology Degree Opportunities.

At: Teen Career Conference- SHSU Dept. of Biological Sciences exhibitor; Houston Zoo, 2014.

1. Potential Effects of Salinity Change on Fish Assemblage Structure in the Red

River Drainage (Texas-Oklahoma).
At: Sam Houston State University Graduate Research Symposium, 2013.

## POSTER PRESENTATIONS

1. Effects of Experimental Warming on Fish-Mediated Nutrient Cycling.

At: Texas Chapter of American Fisheries Conference; 2017.

## AWARDS

Sam Houston State University
Graduate Studies Scholarship \$1000; 2013
Outstanding Undergraduate Teaching Award in Biology; 2013
President's List; Fall 2012
Dean's List; Fall 2012
Dean's List; Fall 2011

## PROFESSIONAL SOCIETIES

Texas Chapter of the American Fisheries Society, 2014-Present.
Ecological Society of America, 2013-2014.
Texas Academy of Science, 2013-2014.
Biological Sciences Graduate Student Organization of SHSU, 2013-2017

## COMMUNITY INVOLVEMENT

Public Outreach- SHSU Dept. of Biological Sciences promotional commercial; Spring 2015. Science Fair Judge- Magnolia High School; Spring 2013-2016. Educational Outreach- SHSU Center for Biological Field Studies \& Huntsville ISD $12^{\text {th }}$ grade Aquatic Science; Fall 2012; Broaddus ISD $9^{\text {th }}$ grade Biology; In Development/2012-2015.
Girl Scouts- Girl Planning Board Advisor, Archery Instructor, First Aid, and Volunteer; Spring Creek Service Unit; 2012- 2015.
Field Day- Volunteer; Decker Prairie Elementary, Tomball, TX; 2013.
Fall Festival- Volunteer; Decker Prairie Elementary, Tomball, TX; 2001-2005, 2012-
2013. Down's Syndrome Picnic- Volunteer; Houston, TX; 2001-2005.

Spring Fling Carnival- Volunteer; Tomball Elementary, Tomball, TX; 2001-2005.

