

ECOSYSTEM ENGINEERING EFFECTS OF NATIVE AND NON-NATIVE
CONSUMERS IN A SUBTROPICAL SPRING-FED RIVER ECOSYSTEM

THESIS

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by

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ABSTRACT

ECOSYSTEM ENGINEERING EFFECTS OF NATIVE AND NON-NATIVE CONSUMERS IN A SUBTROPICAL SPRING-FED RIVER-ECOSYSTEM

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Ecosystem engineers can directly and indirectly modify the availability of resources, alter or create habitats, affect nutrient cycling, and disrupt energy flows, and modify trophic linkages. The San Marcos River is home to a wide range of both non-native and native consumers that affect ecosystem function and processes. Invasive armored catfish (Loricariidae: *Hypostomus*) are of concern due to their high grazing behavior and potential to redistribute large amounts of benthic sediment. Native big claw river shrimp (*Macrobrachium carcinus*) in the San Marcos River are large omnivorous and predatory consumers who have the potential to influence nutrient recycling and movement of sediments. The first part of my study I conducted a replicated 2 x 2 factorial design stream channel experiment to determine the individual and interactive effect of these two species. The presence of catfish decreased primary producer periphyton,

sediment, leaf litter decomposition and catfish also affected nutrient ratios of particulate matter. In contrast, shrimp had little effect on ecosystem processes. The presence of shrimp affected sediment and they exhibited higher mass-specific N excretion rate than catfish. The presence of shrimp seemed to mediate the direct affect of catfish on ecosystem processes. Fish have the ability to affect nutrient availability and primary production through excretion. The second part of my study was to examine excretion rates and ratios of invasive catfish and other abundant fish species from the San Marcos River. Fishes exhibited substantial variation in body nutrient composition (N and P), ranging from 2-8% P and 8-18% N. Fishes also exhibited a large range in mass-specific P and N excretion rates and ratios of N:P excreted. Body P%, Body C:P and N:P significantly differed among the 6 fish families studied. *Hypostomus* sp. exhibited the highest %P. Body % N and %C, and body N:P and C:P was significant when fish were grouped by species. Again, *Hypostomus* sp. exhibited among the lowest N:P and C:P. Similarly loricariids exhibited the lowest mass-specific P excretion rates and high N:P excreted nutrients. This is most likely because they sequester P through their bony armored-like plates. Variation in nutrient recycling mediated by phylogenetic constraints on stoichiometry, suggest that species of fish can influence ecosystem-wide recycling.

CHAPTER I

1. Introduction

Ecosystem engineers are defined as organisms that directly and/or indirectly modify the availability of resources and maintain, alter, or create habitat (Jones et al. 1994, 1997). Ecosystem engineers also have the ability to affect nutrient recycling, energy flows, and trophic linkages (Boogert et al. 2006). In stream ecosystems, ecologists have examined the effects of taxa which appear to function as ecosystem engineers, including beavers (Naiman et al. 1986), large-bodied shrimp (Pringle et al. 1993; Crowl et al. 2001), and crayfish (Huryn and Wallace 1987; Creed 1994). In addition, many fish can act as ecosystem engineers i.e., common carp (*Cyprinus carpio*) (Power 1990; Flecker 1992, 1996, 1997). Many of these fishes are benthivorous and can influence water quality and nutrient dynamics, alter phytoplankton biomass and composition and decrease submerged macrophytes (King and Hunt 1967). The effects of these benthivorous fishes can affect nutrient dynamics and littoral community structure directly through consumption and bioturbations and indirectly through excretion (Matsuzaki et al. 2007).

Subtropical spring-fed river systems are known to contain abundant and diverse assemblages of consumers (Winemiller 1990). Consumers such as fish and macroinvertebrates play an important role in benthic algal standing crops, species

composition, nutrient cycling and primary production (Flecker 1992, 1996; Power 1984, 1990). Nutrients, often being limiting resources in river ecosystems can be affected both directly and indirectly by consumers. The importance of fish as consumers has been demonstrated in many studies. Schindler (1992) demonstrated that 95% of the variations in chlorophyll concentrations were explained by phosphorus excretion by planktivorous fish (Sockeye salmon: *Oncorhynchus nerka*), while Schaus and Vanni (2000) demonstrated that low N:P ratio of gizzard shad (*Dorosoma cepedianum*) excreta shifted the phytoplankton structure to cyanobacteria. Macroinvertebrates as consumers in river systems have also been widely studied. Crayfish for example may be key processors of materials in stream ecosystems and contribute significantly to material cycling and energy flow.

In freshwater river ecosystems, human disturbances affect the impact of non-native and invasive species being dispersed and established (Havel et al. 2005). The introduction of invasive non-indigenous species (INIS) is one of the most serious issues for freshwater ecosystems because these introductions frequently lead to the loss of biodiversity and the change in ecosystem function (Naiman et al. 1995; Mooney and Hobbs 2000). INIS and their effect on freshwater ecosystems are of great concern to fresh water conservation and management.

The Suckermouth catfish from the family Loricariidae is comprised of ~600 species distributed in the neotropics (Delariva and Agostinho 2001). Suckermouth catfish in the genus *Hypostomus* (hereafter referred to as catfish) are non-native fish and

are considered ecosystem engineers. They are efficient algivores (Power et al. 1989) because of their ventral mouths and bony plates effectively scraping sediments, detritus, periphyton and invertebrates off the surface of the substratum (Gradwell 1971; Delariva and Agostinho 2001; Power 2003). Loricarid catfishes were introduced to North American water bodies via escapes and illegal intentional releases and have established themselves in subtropical and spring-fed freshwater ecosystems (Nico and Martin 2001). Catfish in freshwater ecosystems are of great concern because of their high grazing efficiency (Power 1984) and potential to out-compete to affect ecosystem functioning by redistributing large amounts of benthic sediment and destroying habitat by their burrowing behavior (Burgess 1989; Power 2003). In addition to their grazing activities, catfish can indirectly affect periphyton by increased turbidity and reducing light (Cline et al. 1982; Van Nieuwenhuysse and LaPierriere 1986; Graham 1990). These effects may further cascade to other members of the river food web, such as affecting filter feeding macroinvertebrates (Alderage et al. 1987). Presumably catfish were primarily introduced into the San Marcos River via aquarium releases (Perkin and Bonner *in review*, Perkin 2009).

The San Marcos River (San Marcos, Texas) is also home to the native big claw river shrimp (*Macrobrachium carcinus*; hereafter referred to as shrimp). Freshwater shrimp are widely distributed throughout the globe, including the Caribbean, Mexico, Colombia, West Indies, Brazil (Bowles et al. 2000), and along the Gulf coast of the USA including Florida, Mississippi, and Texas (Bowles et al. 2000). *Macrobrachium carcinus* is the largest species of river shrimp occurring in the United States; adult males can grow up to 300 mm in total body length and weigh up to 1 kg (Bowles et al. 2000).

Historically shrimp occurred in 11 of Texas' river basins with outlets into the Gulf of Mexico, including the Brazos, the Guadalupe, and the Rio Grande (TPWD 2005). In the headwaters region of the San Marcos River, *M. carcinus* are estimated to be ~2 years old because post larval shrimp are thought to traverse the estuary-to-headwaters distance (~325 river km) at a rate of 0.5 km/day (Horne and Beisser 1977). Similar to the catfish, shrimp can be considered ecosystem engineers due to large body size and omnivorous behavior (Covich and McDowell 1996). Shrimp can also play important roles in ecosystem function (Cummings et al. 2005), including nutrient spiraling and sediment transport (Dangles and Guerold 2001). For example, macroinvertebrate shredders convert larger leaf and wood particles (course particulate organic matter, CPOM; >1mm) to smaller particles (fine particulate organic matter, FPOM; 0.45 μm - 1 mm), providing an energy source for other riverine consumers such as collectors (Roeding and Smock 1989). Freshwater shrimp can affect a diversity of processes in stream ecosystems, such as decrease organic and inorganic matter transport (March et al. 2001, 2002). Predation by riverine freshwater shrimps also alters invertebrate assemblages (Pringle et al. 1993; March et al. 2001, 2002).

While the impacts of non-native species on ecosystems have been widely studied, little is known about the individual and combined impacts of native and non native animals on stream ecosystem processes and how their effects vary in time and space. The purpose of my chapter 1 of my thesis was to explore the ecosystem engineering effects of

a non-native Suckermouth catfish and a native fresh water river shrimp in the San Marcos River ecosystem. Although ecologists have examined the impacts of larger crustaceans like crayfish and other species of freshwater shrimps, little is known of the impacts of *M. carcinus* with the possible interaction of catfish on ecosystem processes. My objective was to determine the separate and interactive effects of these two species on ecosystem function (i.e, organic matter, inorganic matter accumulation, water chemistry, primary productivity and nutrient recycling, community respiration, and downstream transport of organic and inorganic matter).

2. Materials and Methods

To estimate algal standing stock and organic/inorganic matter accumulation, four ceramic tiles (16.24 cm x 16.24 cm) were placed at the downstream section of each stream channel. Two tiles were enclosed within a 2-cm aperture wire cage and two were open to the direct activities of the shrimp and catfish. All tiles were allowed to grow periphyton for three weeks prior to the experiment. One caged and one uncaged tile was removed from each stream channel on each sampling date. Upon being pulled from the stream channel, the upper surfaces of tiles were cleaned with a nylon-bristled brush and rinsed into a clean acid-washed beaker with Milli-Q water. Chlorophyll *a*, organic matter, inorganic matter, and C, N and P content of materials on tiles were determined from the water in these beakers. Chlorophyll *a* was filtered onto Pall A/E filters and extracted with 99% HPLC grade acetone for 4 hours in the dark and analyzed on a Turner Trilogy™ Lab Fluorometer (Turner Designs Inc. Sunnyvale California). Organic and

inorganic matter on tiles were determined by filtering onto pre-weighed Pall A/E filters and determining dry mass before and after ignition at 450°C for 4 h. Carbon and N in tile material was filtered onto pre-ashed Whatman GF/F filters (nominal pore size = 0.7 μm), dried at 60°C for 48 h, and analyzed on a CE Elantech Carbon-Nitrogen analyzer.

Phosphorus on tiles were filtered onto Whatman GF/F filters, digested with concentrated HCl at 100°C, and measured as PO_4^{3-} using the molybdenum blue method.

To examine primary production in each stream channel, three glass slides (315 mm^2) were placed in a floating periphyton growth setup (Wildlife Supply Company, Buffalo, NY). Slides were removed from each set up every two weeks and were placed into screw-cap centrifuge tubes in the dark. Chlorophyll *a* was extracted using 99% HPLC grade acetone for 4 hours and then analyzed on a fluorometer. Upon removal of periphyton containing slides, clean slides were immediately placed into floating set ups.

Community metabolism was estimated by measuring dissolved oxygen (DO) concentrations immediately before sunrise (presumably time of minimum DO concentration) and immediately before sundown (presumably time of maximum DO concentration) with a YSI Model 85 sonde (YSI Inc. Yellow Springs, OH).

Decomposition rates were determined using leaf packs of Texas Oak (*Quercus texana*), a common Central Texas riparian species. Four leaf packs, each containing ten leaves and weighing 5 g dry mass, were placed in each stream channel. Two of the leaf packs in each stream channel was enclosed within 3-cm aperture mesh bag, and two were left open with the petioles tied together with monofilament line. All leaf packs were weighted down with metal washers to ensure submersion. On each sampling date, one unbagged and one bagged leaf pack was pulled from each stream channel. Leaf packs

were dried at 60° C for 48 h and weighed to assess percent mass loss over the time interval leaves were in stream channels. Leaf litter decomposition rate was determined as percent change in mass over the period each pack was in the stream channel. For the purposes of this analysis, I only analyzed the percent mass lost on the second sampling date. After weighing, dry leaf material was homogenized and C, N, and P content was determined using a CE Elantech CN analyzer and HCl digestion and analysis as PO_4^{3-} using the molybdenum blue method (Wetzel and Likens 2000).

To assess effects of shrimp and catfish on water column nutrient dynamics, water samples were taken from the downstream section of each stream channel on each sampling date by collecting grab samples with brown HDPE bottles. Total phosphorus (TP), total nitrogen (TN), soluble reactive phosphorus (SRP; PO_4^{3-}), ammonium (NH_4^+), nitrate (NO_3^-), and particulate nutrients (C, N, and P) were determined. TP and TN were determined from unfiltered water samples. TP was measured as PO_4^{3-} , after digestion with potassium persulfate using the molybdenum blue method (Wetzel and Likens 2000) on a Varian Cary 50 Ultraviolet-Visible light (UV-Vis) spectrophotometer. TN samples were digested with alkaline potassium persulfate and analyzed as NO_3^- on a Varian Cary 50 UV-Vis spectrophotometer using second derivative UV spectroscopy (Crumpton et al. 1992). Dissolved nutrients were determined from water filtered through pre-ashed Pall A/E filters (nominal pore size = 1 μm) and measured with a Varian Cary 50 UV-Vis spectrophotometer. SRP was determined with the molybdenum blue method (Wetzel and Likens 2000). NH_4^+ was determined with the phenate method (Solorzano 1969). NO_3^- was determined with second derivative UV spectroscopy (Crumpton et al. 1992). Non-volatile suspended solids (NVSS) and suspended particulate organic matter (SPOM) were

determined by filtering water onto pre-weighed A/E filters and measuring dry mass before and after ignition at 450°C for 4 h (Knoll et al. 2003).

At the end of the experiment, I examined nutrient recycling by catfish and shrimp by estimating nutrient excretion by these consumers. On the last day of the experiment, I removed each shrimp or catfish from each stream channel with a net and quantified nutrient excretion rates (N-NH₄⁺ and P-PO₄³⁻). Nutrient excretion estimates were conducted using methods similar to those of Mather et al. (1995), Schaus et al. (1997), and Higgins et al. (2006) in which live organisms were placed in filtered (Pall A/E) stream water in clean acid-washed plastic tubs and allowed to excrete for ~1 h. Estimation of N and P excretion by organisms were measured as NH₃ and PO₄³⁻ accumulation over the time interval. Ammonia and PO₄³⁻ samples were analyzed with the phenate method (Solorzano 1969) and the molybdenum blue method (Wetzel and Likens 2000), respectively.

Statistical Analysis

Ecosystem response variables such as periphyton standing stock, organic matter decomposition and sediment and organic matter transport and accumulation, periphyton production, stream channel community metabolism and water chemistry, means of each variable were taken across both sampling dates and analyzed via two-way analysis of variance (ANOVA) with cross classified factors. Data not meeting assumptions of normality and homoscedasticity were log transformed for analysis. For all analysis, I set α at 0.05, and all data were analyzed with SPSS 15.0 for Windows (SPSS® Inc.).

3. Results

The presence of catfish caused a significant decline in periphyton biomass (Chl *a*) on the open uncaged tiles, whereas the presence of shrimp exhibited no effect on periphyton biomass in uncaged tiles (Fig. 1A, Table 1). However, I did not detect significant treatment effect of the presence of catfish or shrimp on periphyton biomass of closed tiles (Fig. 1B). I detected a significant effect of the presence of catfish and the presence of shrimp on organic matter and inorganic matter on uncaged tiles, but there was no significant effect of catfish or shrimp on organic and inorganic matter on caged tiles (Fig 1C-F, Table 1.1). I also detected a significant interaction treatment effect between the two species.

I detected a significant effect of the presence of catfish on the nutrient ratios of material on open tiles. The presence of catfish significantly reduced C:N, C:P, and N:P for particulate matter on uncaged tiles (Fig. 2A, C, E; Table 2). However, I did not find significant treatments effects on C:N, C:P, and N:P for matter on caged tiles (Fig. 2B, D, F; Table 2). I detected a significant catfish x shrimp interaction effect on uncaged tile matter C:P and N:P indicating that the effects of catfish and shrimp on nutrient ratios of uncaged tile matter were not independent.

I found no significant treatment effect on periphyton production on glass slides in the water column or on pre-dawn and the pre-sunset DO concentrations across treatments (Fig. 3A-C; Table 3). I found a marginally significant effect of the presence of catfish on mass loss of unbagged leaf packs at the end of the experiment, but there was no significant treatment effect of catfish or shrimp on leaf mass loss in closed leaf packs in mesh bags (Fig. 4A-B; Table 4). The presence of catfish and shrimp did not significantly

affect nutrient ratios of leaf litter during the experiment; I did not detect a significant treatment effect on C:N, C:P and N:P of leaf matter in both bagged and unbagged leaf packs (Fig. 4C-H; Table 4). I additionally did not detect a significant treatment effect on total and dissolved nutrients or suspended materials in the water column (TP, TN, NH₄, NO₃, SRP, NVSS, and SPOM) (Fig. 5A-G; Table 5).

Stream Channel Nutrient Excretion

I first examined whether P and N excretion by both catfish and shrimp differed among treatments. I found no significant difference (one-way ANOVA) in mass-specific N and P excretion rates and the N:P of excreted nutrients of catfish when by themselves or in the presence of shrimp (N: $F_{1,7} = 0.675, p = 0.443$; P: $F_{1,7} = 0.477, p = 0.516$; N:P: $F_{1,7} = 0.060, p = 0.815$), nor did I detect a significant difference in N and P excretion of shrimp when catfish were present and absent (N: $F_{1,4} = 0.499, p = 0.513$; P: $F_{1,4} = 0.196, p = 0.688$; N:P: $F_{1,4} = 1.07, \hat{p} = 0.377$). Thus, I compared N and P excretion of catfish and shrimp by pooling data from catfish from across treatments and pooling data from shrimp across all treatments. Shrimp exhibited significantly higher mass-specific N excretion rates (Fig. 6A, Table 6), but due to the relatively high variability in P excretion rates by shrimp I did not detect a significant difference between catfish and shrimp in mass-specific P excretion rates or the N:P of nutrients excreted (Fig. 6B-C, Table 6).

4. Discussion

In the experiment presented here, the presence of catfish was found to have

substantial direct effects on ecosystem function. As predicted, the presence of catfish decreased periphyton biomass (chl *a*), and organic and inorganic matter on uncaged tiles. Presumably, through their foraging and movement, catfish consumed periphyton and removed sediments from substrates. However, the presence of herbivorous fishes can also indirectly increase periphyton. These effects are generally consistent with other species of herbivorous native fishes; herbivorous central stoneroller (*Campostoma animalum*) can affect both structural and functional parameters in stream ecosystems by decreasing periphyton height and type, primary productivity, carbon dynamics, bacterial biomass and the size distribution of benthic organic matter (Gardner 1993). However, the effects of herbivorous fishes on primary producers are not consistent among species or ecosystems. Foraging of the loricariid *Ancistrus spinosus* in its natural habitats can increase periphyton primary production due to removal of sediments from substrate (Power 1990). In my experiment, the presence of catfish only affected the leaf litter decomposition rates of unbagged leaf packs, which may be due to catfish grazing on biofilms on leaf litter. Webster and Benfield (1986) similarly noted that catfish foraging on biofilms on the leaf litter facilitated detritus break down. The presence of catfish also affected C:P, C:N, and N:P of material on uncaged tiles. The presence of catfish lowered C:P and C:N of material on tiles because of a decrease in C. This C decrease may be due to removal of carbonates and/or sediments from tiles through their foraging actions and movement. Effects of the presence of catfishes on N:P of tile material could also be due to catfish grazing causing a shift in algal communities through their grazing (Hillebrand et al. 2002; Hillebrand et al. 2008) or through a highly localized effect of nutrient enrichment by catfish via excretion (e.g., McIntyre et al. 2008). Such a shift in algal

composition and nutrient content has been observed where grazing pressure by fishes is intense (Flecker et al. 2002); however I did not assess algal compositional shifts in stream channels.

In contrast to the effects of catfish, the presence of shrimp had little effect on ecosystem function and processes. Although the presence of shrimp did not affect periphyton biomass, shrimp decreased organic and inorganic matter on uncaged tiles. Similarly, foraging and movements of *Macrobracium* sp. was found to significantly decrease organic and inorganic matter in a Puerto Rico stream (March et al. 2002). Contrary to predictions, the presence of shrimp in my experiment did not affect leaf litter decomposition. These large-bodied shrimp are generally thought to be omnivorous and can consume leaf litter (Covich and McDowell 1996). However, big claw river shrimp in the San Marcos River may exhibit a greater tendency to be predacious; stable isotope analysis indicates that shrimp's trophic position is >3 in the San Marcos River (Cohen et al. *in review*). In addition, the use of dead fish to supplement shrimp diets in the experiment may have dampened their consumptive effects on leaf litter because a fish source subsidy may have been sufficient to prevent a shrimp utilization of detritus. It is very possible that when give a choice, fish are a preferred food source by shrimp because of its greater nutritive value.

Consumer species can have indirect effects on nutrient cycling and ecosystem function (Hall et al. 2003; Knoll et al. *in review*). However, I found little evidence indicating that the presence of catfish or shrimp indirectly affected the ecosystem dynamics through nutrient recycling. The presence of catfish and shrimp did not affect periphyton biomass, organic matter, inorganic matter, or nutrient ratios of material on

caged tiles. In addition, the presence of shrimp and catfish did not affect periphyton production or decomposition and nutrient content of bagged leaf litter. Had there been an increase nutrient supply via recycling through excretion, I might have observed increased primary production and decomposition rates, and a change in nutrient ratios of caged tiles and bagged leaf packs. At the end of the experiment, the two consumer species in question exhibited different nutrient recycling characteristics. Shrimp exhibited significantly higher mass-specific N excretion rates than catfish. However, these species-specific differences in nutrient excretion did not cascade and affect the nutrient ratios of caged periphyton on bagged leaf litter biofilms.

Other researchers have found that herbivores can have indirect (nutrient-mediated) effects on primary producer biomass and nutrient stoichiometry (Knoll et al. *in press*). Knoll et al. (*in press*) found that nutrient mediated indirect effects enhanced periphyton biomass when loricariids (*Ancistrus triradiatus*) were experimentally separated from direct contact with periphyton. Similarly, Flecker et al. (2002) found that the presence of grazing fishes negatively affected periphyton biomass and composition and the severity of N-limitation of algal communities. In this study presented, a lack of observed indirect effects may be due to the short duration of the experiment (28 days). Indirect nutrient-mediated effects may require longer to propagate through food webs and ecosystems. For example, the magnitude of nutrient-mediated effects of invasive New Zealand mudsnails (*Potamopyrgus antipodarum*) was time dependent (Arango et al. 2009). In addition, a lack of indirect nutrient recycling effects may be because water residency times in experimental stream channels were relatively brief (10 min, C. Pray, unpubl. data). Other studies which have observed significant, indirect nutrient-mediated

effects were conducted in systems with much longer water residence times, such as pool mesocosms (Knoll et al. *in press*) or experimental stream channels that continuously recirculate (Hargrave 2006). Another potential reason why I observed no strong indirect nutrient recycling effects maybe due to a lack of catfish growth during the experiment (C. Pray, unpubl. data; Knoll et al. *in review*). Since loricariids have high P body content (Vanni et al. 2002), it is predicted that consumption growth and nutrient recycling would lead to sequestration of P in their bodies and thus reduce P supply (relative to N) for periphyton (Hood et al. 2005). Because catfish did not grow in the stream channel experiment, they did not serve as nutrient sinks in the experiment (e.g., Kraft 1992), causing a shift in nutrient dynamics.

As predicted, I detected an interaction effect between the presence of catfish and the presence of shrimp on periphyton biomass, organic matter and inorganic matter on uncaged tiles. The presence of shrimp also appeared to mediate the effects of catfish on C:P and N:P of matter on uncaged tiles. I hypothesize that this interaction toward catfish is most likely due to antagonistic or aggressive behavior by shrimp. Similarly, others have observed mediating impacts of aggressive shrimp toward other decapod detritivores (Covich and McDowell 1996). Indeed, the presence of *M. carcinus* in tropical streams leads to slower leaf litter decomposition through lowering detritivory by other decapods (March et al. 2001). Such antagonistic behaviors by shrimp toward invasive catfishes may be present in the San Marcos River as both consumers compete for habitat sites; however, whether this interaction occurs and if so, to what extent remains unknown.

Although big claw river shrimp are large-bodied consumers, they can reach relatively high densities and can play substantial roles in structuring stream communities

(Covich et al. 1991, 1996; Crowl and Covich 1994). Historically, shrimp densities in the San Marcos River were much higher than current levels, to the extent that populations were commercially harvested during the 1800s (Bowles et al. 2000). Today their numbers are substantially lower: roughly 20-30 individuals exist in the headwater reach of the San Marcos River (C.L. Pray, unpubl data). Some factors that have been identified for their decline are river impoundment, destruction of riverine habitats, water quality degradation, diminished stream flows, competition and predation from exotic species, and overharvest (Bowles et al. 2000). Currently the big claw river shrimp are listed by Texas Parks and Wildlife as a high priority species (TPWD 2008) but given their historical declines in the San Marcos River, it is critical to continue population monitoring and preservation of habitats. Although the results of this experiment indicate that shrimp have little direct effect on lower trophic levels and ecosystem function, their effects might be most intense at the top of the food web because they are large-bodied predators (e.g., Polis and Strong 1996). Thus, their extirpation from the San Marcos River might have substantial effects which were not observed at the scale of this study. Invasive loricariid catfishes in the upper San Marcos River are highly abundant and represent 25-50 % of ichthyomass (W.H. Nowlin, unpubl. data). Catfish can directly negatively affect periphyton, organic and inorganic matter, and increase leaf litter decomposition. Given the relative biomass of these fishes in the river, *Hypostomus* sp. may have profound affects on the dynamics of the San Marcos River. To date, effective strategies to reduce catfish biomass in the San Marcos River are lacking. Methods to prevent future releases and to control already established populations of catfish are clearly required.

5. Tables and Figures

Table 1.1: Results of two-way ANOVA for cross-classified factors examining the effects of the presence of catfish and shrimp on periphyton biomass (Chl a), organic matter (OM), and inorganic matter (IM) on open and closed tiles in the stream channel experiment. F , and p are given for each response variable. Significant p -values are denoted with an *. Degrees of freedom for all response variables is 1,10.

Response variable	Catfish		Shrimp		Catfish x Shrimp	
	F	p	F	p	F	p
Chl a - open tiles	27.89	<0.001*	1.37	0.268	4.85	0.052*
Chl a - closed tiles	1.86	0.202	3.14	0.107	0.62	0.449
OM - open tiles	21.78	0.001*	10.93	0.008*	21.96	0.001*
OM - closed tiles	0.024	0.881	2.48	0.147	1.31	0.279
IM - open tiles	21.78	<0.001*	11.71	0.007*	23.08	<0.001*
IM - closed tiles	0.16	0.699	2.78	0.126	1.64	0.23

Table 1.2: Results of two-way ANOVA for cross-classified factors examining the effects of the presence of catfish and shrimp on nutrient ratios of periphyton matter on open and closed tiles in the stream channel experiment. F , and p are given for each response variable. Significant p -values are denoted with an *. Degrees of freedom for all response variables is 1,10.

Response variable	Catfish		Shrimp		Catfish x Shrimp	
	F	p	F	p	F	p
C:N - open tiles	13.72	0.004*	1.2	0.300	0.31	0.593
C:N - closed tiles	0.07	0.803	0.22	0.651	0.04	0.85
C:P - open tiles	8.94	0.014*	2.26	0.164	7.48	0.021*
C:P - closed tiles	0.06	0.816	0.01	0.998	4.72	0.055
N:P - open tiles	7.44	0.021*	2.43	0.15	9.22	0.013*
N:P - closed tiles	0.11	0.75	0.01	0.917	4.66	0.056

Table 1.3: Results of two-way ANOVA for cross-classified factors examining the effects of the presence of catfish and shrimp on primary production and community metabolism in the stream channel experiment. F , and p are given for each response variable. Significant p -values are denoted with an *. Degrees of freedom for all response variables is 1,10.

Response variable	Catfish		Shrimp		Catfish x Shrimp	
	F	p	F	p	F	p
Primary production	0.144	0.713	0.223	0.647	0.743	0.409
Pre-dawn DO	0.122	0.734	0.410	0.541	0.088	0.772
Pre-sunset DO	0.233	0.64	1.555	0.241	1.012	0.338

Table 1.4: Results of two-way ANOVA for cross-classified factors examining the effects of the presence of catfish and shrimp on leaf litter mass loss and nutrient ratios in open and closed leaf packs. *df*, *F*, and *p* are given for each response variable. Significant *p*-values are denoted with an *.

Response variable	Catfish			Shrimp			Catfish x Shrimp		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
% remaining - open packs	1,10	4.59	0.058*	1,10	0.457	0.514	1,10	0.824	0.385
% remaining - closed pack	1,10	0.27	0.618	1,10	0.444	0.52	1,10	0.001	0.978
C:N - open packs	1,9	0.43	0.53	1,9	0.545	0.479	1,9	0.041	0.844
C:N - closed packs	1,9	0.84	0.382	1,9	0.413	0.536	1,9	0.67	0.434
N:P - open packs	1,9	0.02	0.897	1,9	0.795	0.396	1,9	0.306	0.594
N:P - closed packs	1,9	0.03	0.876	1,9	0.241	0.635	1,9	1.856	0.206
C:P - open packs	1,9	4.43	0.650	1,9	0.69	0.428	1,9	1.400	0.268
C:P - closed packs	1,9	0.15	0.712	1,9	0.282	0.608	1,9	0.396	0.545

Table 1.5: Results of two-way ANOVA for cross-classified factors examining the effects of the presence of catfish and shrimp on water column nutrients, non-volatile suspended sediments (NVSS) and suspended organic matter (SPOM). F , and p are given for each response variable. Significant p -values are denoted with an *. Degrees of freedom for all response variables is 1,10.

Response variable	Catfish		Shrimp		Catfish x Shrimp	
	F	p	F	P	F	p
TP	1.09	0.321	1.112	0.317	0.276	0.611
TN	1.15	0.308	0.011	0.92	1.568	0.239
NH4+	1.96	0.192	2.678	0.133	2.494	0.145
NO32-	1.48	0.252	1.402	0.264	1.494	0.25
PO43-	0.01	0.927	2.864	0.121	0.238	0.636
NVSS	0.1	0.924	1.088	0.321	0.136	0.72
SPOM	0.34	0.572	0.452	0.517	3.194	0.104

Table 1.6: Results of one-way ANOVA examining differences in mass-specific N and P excretion rates of catfish and shrimp at the end of the stream channel experiment. F , and p are given for each response variable. Significant p -values are denoted with an *. Degrees of freedom for all response variables is 1,10.

Response variable	F	p
N excretion	17.5	<0.001*
P excretion	0.22	0.646
Excretion N:P	2.3	0.146

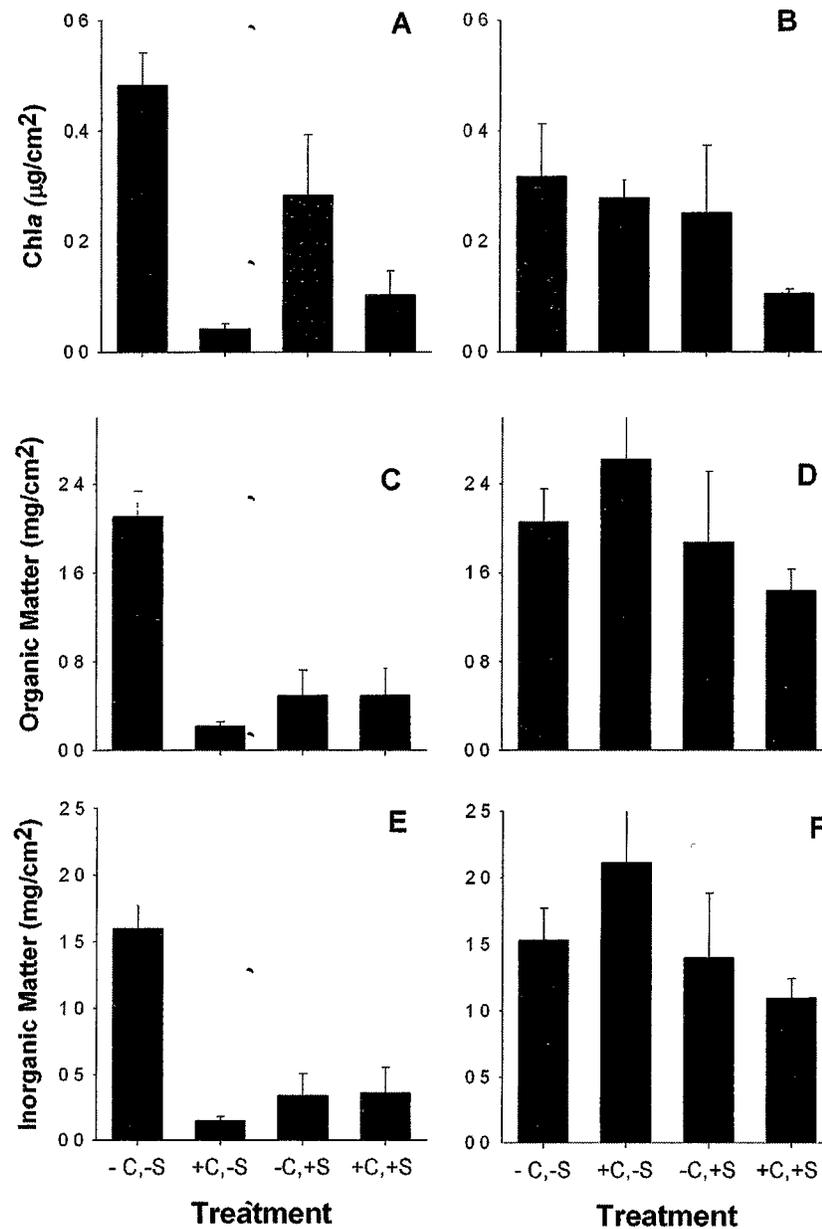


Figure 1.1: Response of periphyton biomass (Chl *a*) on (A) open and (B) closed tiles, organic matter on (C) open (D) closed tiles, and inorganic matter on (E) open and (F) closed tiles. Bars represent the mean (± 1 SE) of each treatment combination. – and + C = catfish absent and catfish present, respectively. – and + S = shrimp present and absent, respectively.

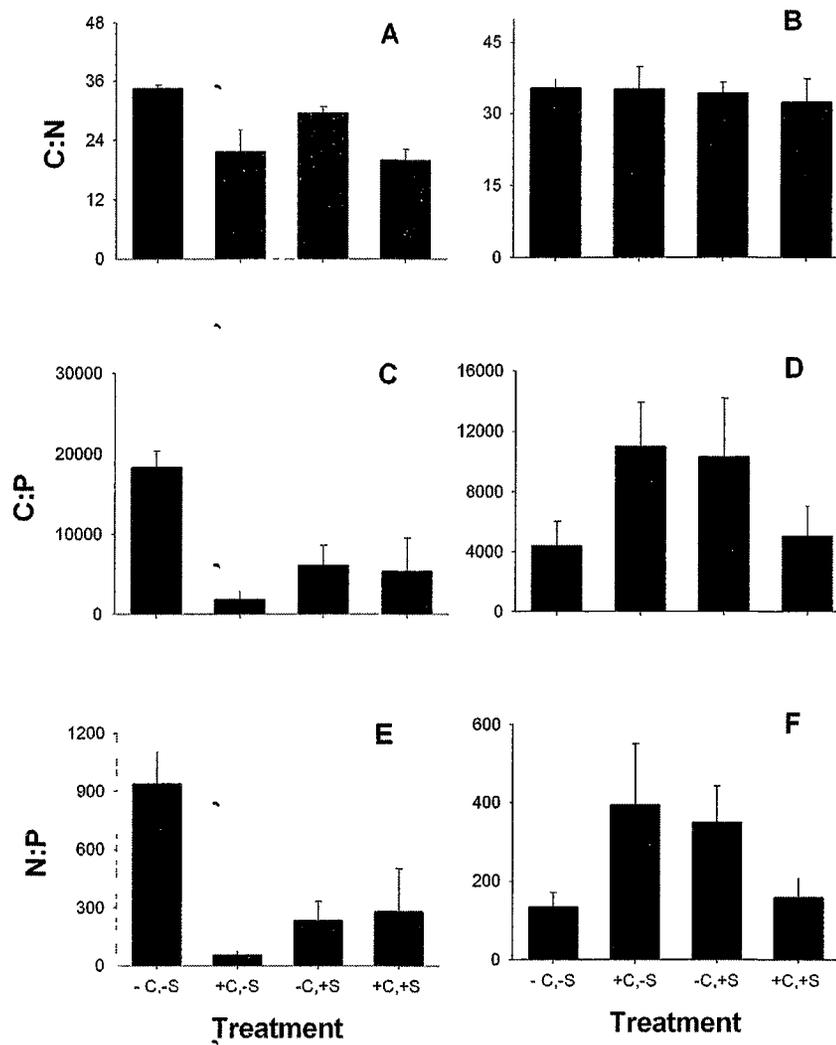


Figure 1.2: Response of C:N of particulate matter on (A) open and (B) closed tiles, C:P on (C) open (D) closed tiles, and N:P on (E) open and (F) closed tiles. Bars represent the mean (± 1 SE) of each treatment combination. - and + C = catfish absent and catfish present, respectively. - and + S = shrimp present and absent, respectively.

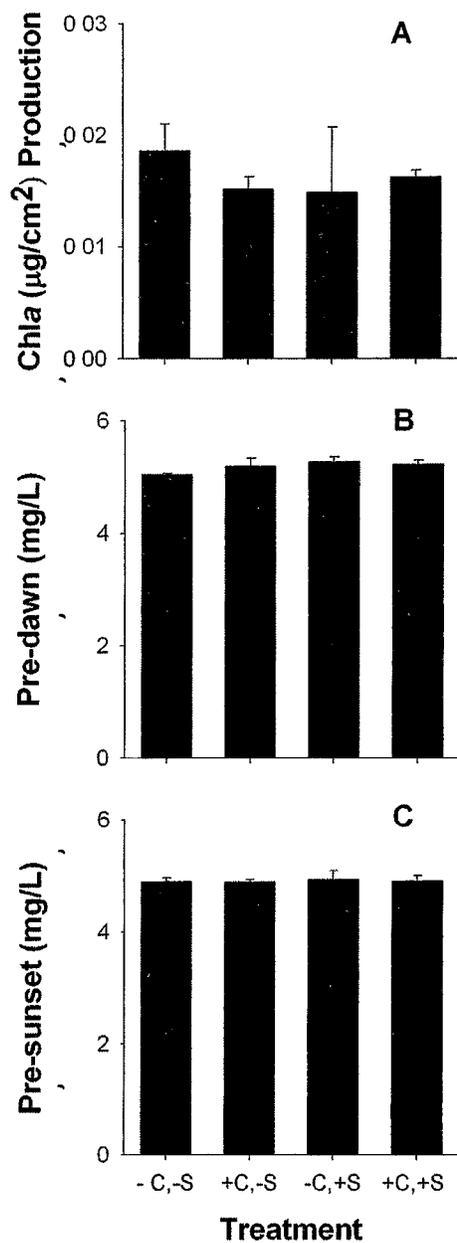


Figure 1.3: Response of (A) primary production (Chla accumulation rate), (B) pre-dawn dissolved oxygen concentration, and (C) pre-sunset dissolved oxygen concentration in the stream channel experiment. Bars represent the mean (± 1 SE) of each treatment combination. - and + C = catfish absent and catfish present, respectively. - and + S = shrimp present and absent, respectively.

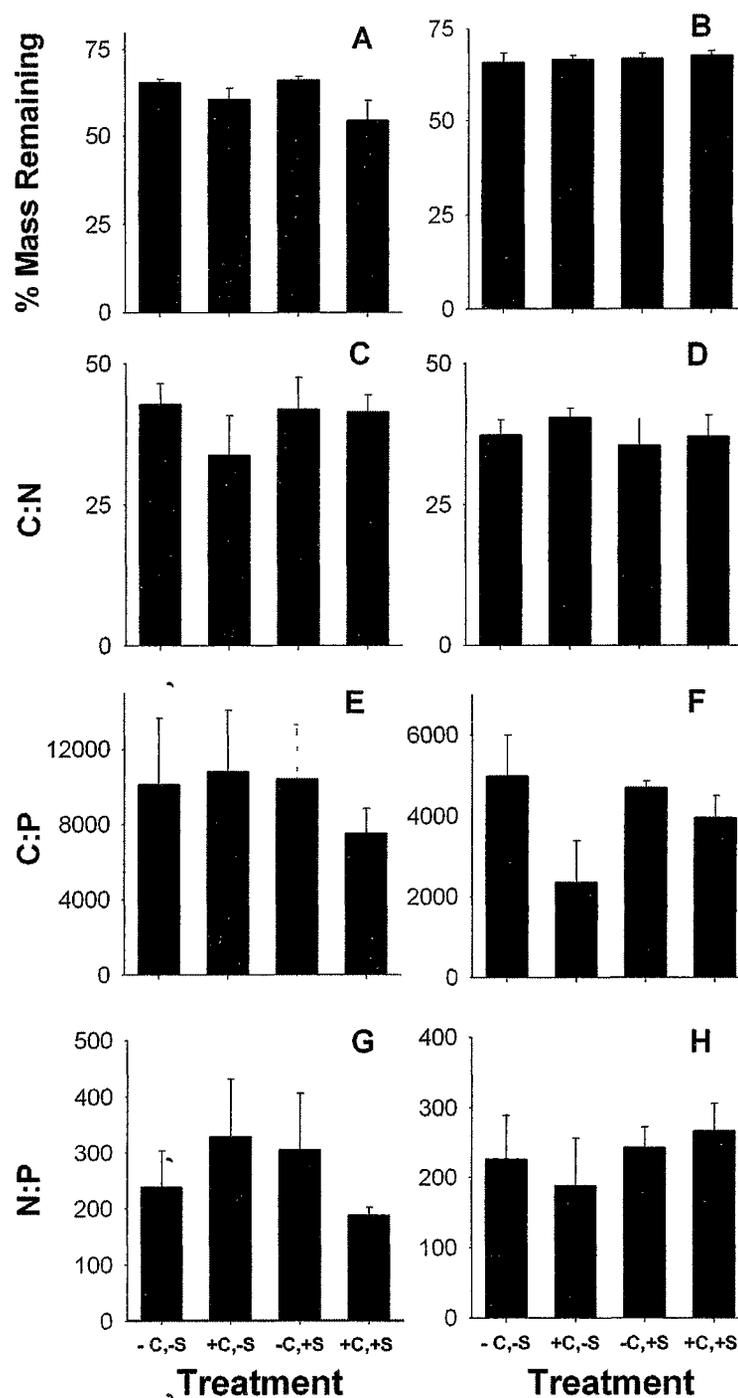


Figure 1.4: Response of leaf litter mass loss rate in (A) unbagged and (B) bagged leaf packs, C:N of (C) unbagged (D) bagged leaf packs, C:P of (E) unbagged and (F) bagged tiles, and N:P of (G) unbagged and (H) bagged tiles. Bars represent the mean (± 1 SE) of each treatment combination. - and + C = catfish absent and catfish present, respectively. - and + S = shrimp present and absent, respectively.

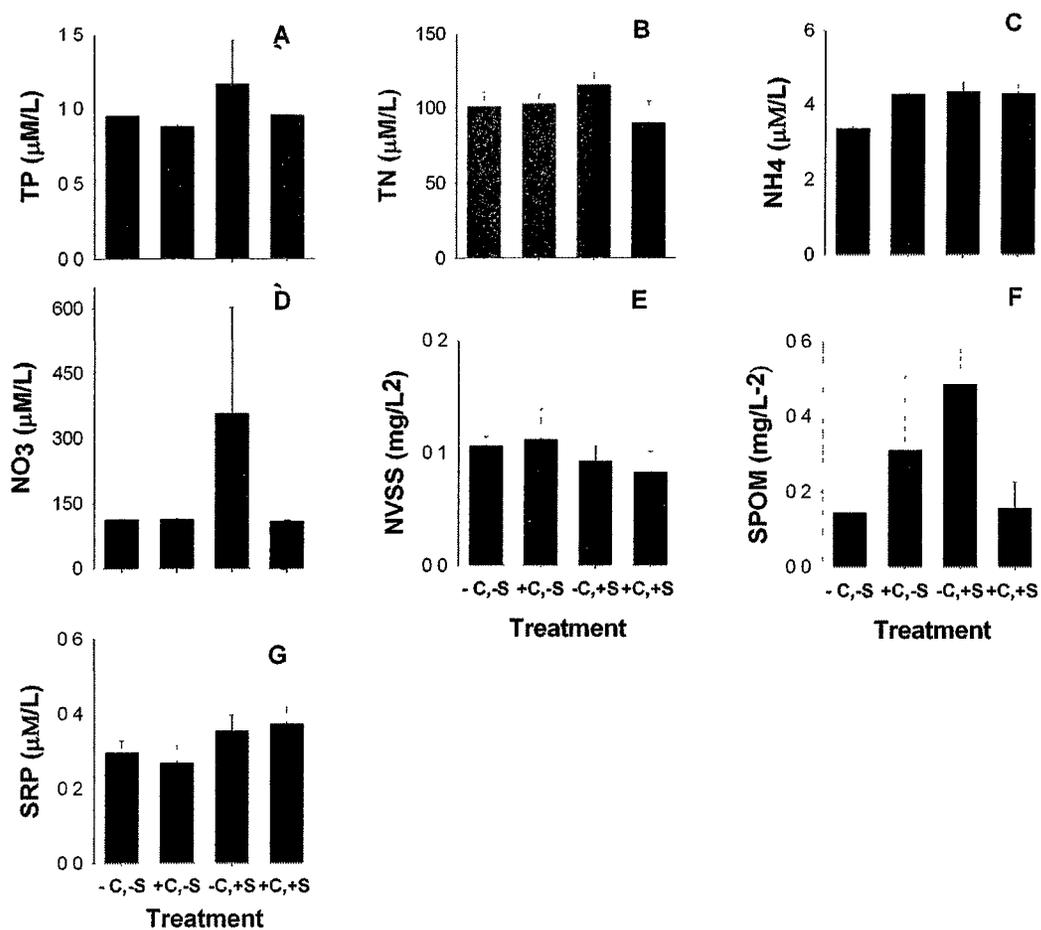


Figure 1.5: Response of water column (A) TP, (B) TN, (C) NH_4^+ , (D) NVSS, (E) SPOM, and (F) NO_3^- concentrations in the stream channel experiment. Bars represent the mean (± 1 SE) of each treatment combination. – and + C = catfish absent and catfish present, respectively. – and + S = shrimp present and absent, respectively.

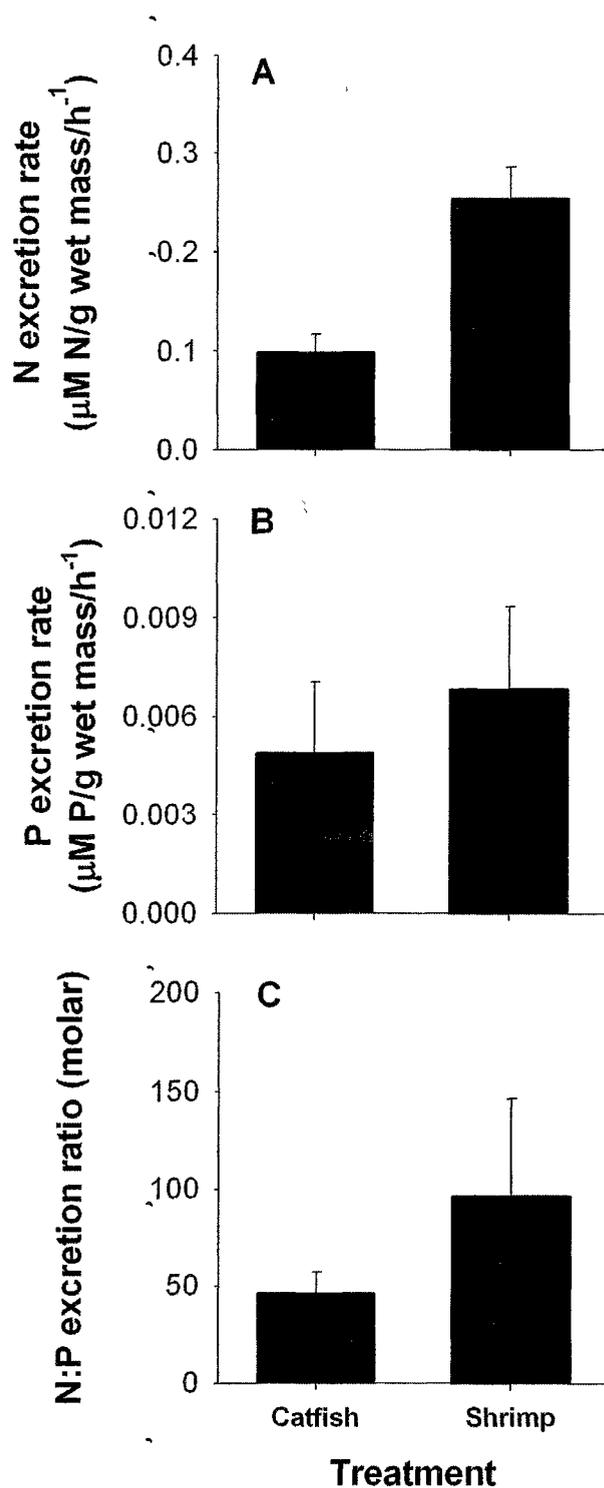


Figure 1.6: Mass-specific (A) nitrogen and (B) phosphorus excretion rates, and the (C) N:P of excreted nutrients of armored catfish and big claw river shrimp at the end of the experiment. Bars represent the mean (± 1 SE) of each species.

CHAPTER II

6. Introduction

Ecosystem engineers are defined as organisms that directly and/or indirectly modify the availability of resources and maintain, alter, or create habitat (Jones et al. 1994, 1997). Ecosystem engineers also have the ability to affect nutrient recycling, energy flows, and trophic linkages (Boogert et al. 2006). In stream ecosystems, ecologists have examined the effects of taxa which appear to function as ecosystem engineers, including beavers (Naiman et al. 1986), large-bodied shrimp (Pringle et al. 1993; Crowl et al. 2001), and crayfish (Huryn and Wallace 1987; Creed 1994). In addition, many fish can act as ecosystem engineers i.e., common carp (*Cyprinus carpio*) (Power 1990; Flecker 1992, 1996, 1997). Many of these fishes are benthivorous and can influence water quality and nutrient dynamics, alter phytoplankton biomass and composition and decrease submerged macrophytes (King and Hunt 1967). The effects of these benthivorous fishes can affect nutrient dynamics and littoral community structure directly through consumption and bioturbations and indirectly through excretion (Matsuzaki et al. 2007).

Subtropical spring-fed river systems are known to contain abundant and diverse assemblages of consumers (Winemiller 1990). Consumers such as fish and macroinvertebrates play an important role in benthic algal standing crops, species

aquatic animals, excrete nutrients in dissolved forms that are readily available to osmotrophs, and can store large proportions of ecosystem nutrients in their tissues (Vanni 2002). Different species of fish vary in excretion rates of N and P due to phylogenetic constraints on body stoichiometry (Schindler and Eby 1997; Sterner and Elser 2002; Vanni et al. 2002; McIntyre 2006) thus; fish community composition could affect aggregate rates of nutrient recycling as well the ratio of available N and P (McIntyre et al. 2007).

Invasion of exotic species is one of the greatest threats facing aquatic ecosystems (Sala 2000). Introduction of non-native consumers into aquatic ecosystems cause changes in community dynamics, resulting in substantial alteration of ecosystem function (Simon and Townsend 2003; Aragano et al. 2009). The effect of non-native herbivorous species on nutrient dynamics of freshwater ecosystems has been the focus of numerous studies (Hall et al. 2003; Carlsson et al. 2004; Aragano et al. 2009). Introduction of non-native herbivores into aquatic systems can result in not only the regulation of primary production and primary producer biomass (Strayer et al. 1999), but also the modification of energy fluxes and nutrient cycling in food webs (Hall et al. 2003; Carlsson et al. 2004; Aragano et al. 2009). Most of these studies focus invertebrate consumers (i.e., gastropod, bivalves, and crustaceans), but information on the nutrient cycling impacts of invasive herbivorous fishes is comparatively lacking (Hall et al. 2003). Herbivory in fishes is relatively rare, but ecologists have hypothesized that herbivorous or other lower trophic level fishes may be successful invaders in many freshwater systems because they utilize a food resource that is rarely limiting (Moyle and Light 1996; Gido and Franssen 2007). For example, loricariid catfishes (also known as armored catfishes) have invaded

numerous North American subtropical and spring-fed freshwater ecosystems and are of great concern because of their high grazing efficiency (Power 1984) and potential to competitively displace native algivorous fishes (Hubbs et al. 1978). These fishes also have the ability to affect ecosystem function through the suspension of sediments during nesting and foraging (Burgess 1989; Power 2003). Despite the potential serious consequences for these invasive armored catfishes for ecosystem and community dynamics, little is known of their effects on nutrient cycling in invaded ecosystems and how their nutrient recycling characteristics differ from native herbivorous fishes.

Armored catfishes (hereafter referred to as 'catfishes') have potential to substantially affect nutrient cycling in ecosystems. Armored catfishes have relatively high body P concentrations (percent P per unit body mass) due to their bony armor plates containing Ca-PO₄ (Hood et al. 2005). Thus, catfish growth is P-limited when food sources are relatively low in P (Hood et al. 2005). When catfish consume algal resources with C:P ratios higher than their body C:P (e.g., a stoichiometrically imbalanced diet), this will likely have a profound effect on the excretion and recycling of nutrients (Sterner and Elser 2002). Indeed, Hood et al. (2005) found that two species of loricariid catfishes in their native tropical streams excrete dissolved nutrients at substantially higher N:P than other fishes in these habitats. However, when in non-native habitats armored catfishes may play a novel role in the nutrient cycling of the invaded ecosystem. For example, catfishes, like other invasive species, can become a dominant portion of the community biomass and their excretion of dissolved nutrients at high N:P may act to increase periphyton C:P, causing P-limitation of both periphyton and eventually catfish growth (Hood et al. 2005). Although there are considerable implications of invasive catfishes to

the nutrient dynamics in novel environments, information on these effects is not available.

The purpose of this study is to examine nutrient excretion rates and ratios of invasive catfish and other abundant fish species within the spring-fed subtropical San Marcos River, Texas. During the summer of 2008, I examined the body and nutrient excretion stoichiometry of fishes in the river. To measure nutrient recycling, I quantified (N), and (P) recycling (via excretion) and body nutrient composition of 20 species of fish from the San Marcos River. In particular, I was interested in determining the contribution of invasive armored catfishes (in the genus *Hypostomus*) to nutrient dynamics of the San Marcos River.

7. Materials and Methods

Study Site

The San Marcos River is spring-fed and characterized by clear water and high macrophyte biomass. The river exhibits little seasonal variation in physiochemical conditions and maintains temperature roughly 22°C (Groeger et al. 1997). In addition, the San Marcos River has many endemic or range-specific organisms including the San Marcos salamander (*Eurycea nana*), Texas wild rice (*Zizania texana*), the fountain darter (*Etheostoma fonticola*), and the Comal Springs riffle beetle (*Heterelmis comolensis*). All of these organisms were at least historically present in the upper reaches of the river and are listed by the U.S. Fish and Wildlife Service as endangered or threatened (U.S Fish and Wildlife Service, 1996).

Loricariid catfishes were likely introduced to the San Marcos River sometime in

the 1980s via intentional aquarium releases. It is now thought that catfish represent 25 - 50% of the upper San Marcos River ichthyomass (WH Nowlin, pers. obs.), though it has been qualitatively noted that their numbers in the upper San Marcos River have greatly increased since major floods that occurred in 1998 and 2000. Previous study has revealed the catfishes in the San Marcos River are algivorous and that their populations represent a trophic pathway not present in the river prior to their introduction (Cohen et al., in review).

Nutrient Excretion Estimates and Fish Body Stoichiometry

To explore the influence of nutrient excretion by catfish in the nutrient dynamics of the San Marcos River, I conducted nutrient excretion measurements on fishes captured from the river from November 2007 to May 2009. In all, I quantified excretion rates and body nutrient composition of 95 individual fishes from 14 species, representing 6 families (Table 2.1). Obviously, my capture technique (seining) selected for smaller bodied fishes; however, smaller-bodied fish taxa are numerically and presumably biomass dominant in the upper San Marcos River (Perkin et al., *in review*). In addition, the number of fish species we sampled (14 species) is lower than the typical species richness found in most of the fish species surveys of the river (~30 species) (Perkin et al., *in review*). It is critical to note that I did not attempt to make an exhaustive assessment of excretion rates from all fish species in the river, but rather, I wanted to evaluate the nutrient recycling and stoichiometry of invasive catfishes in relation to a representative portion of the San Marcos River fish community.

Fish for nutrient excretion estimates were collected at a site at the headwaters

immediately below the discharge from Spring Lake and at Thomson Island, roughly 2 km above the confluence with the Blanco River. These sites were chosen because of previous information on their fish populations was available and accessibility to capture fish. Fish were captured with seines and immediately moved to shore to conduct nutrient excretion experiments. Nutrient excretion estimates were conducted using methods similar to those of Mather et al. (1995), Schaus et al. (1997), and Higgins et al. (2006). Estimation of N and P excretion by fishes were measured as NH_4^+ and PO_4^{3-} accumulation. Excretion rates of catfish were compared to other abundant fish species in the San Marcos River.

Filtrate samples from excretion experiments were analyzed for NH_4^+ using the phenate method (Solorzano 1969). Phosphate was determined with the molybdenum blue method (Wetzel and Likens 2000). I quantified body nutrient content by grinding fish to a fine powder with a clean mortar and pestle. Carbon and nitrogen (N) samples from fish tissues dried at 60°C for 48 h, frozen, and analyzed on a CE Elantech Carbon-Nitrogen analyzer. Phosphorus in fish tissues were digested with concentrated HCl at 100°C , and measured as PO_4^{3-} using the molybdenum blue method.

Statistical Analysis

In order to examine the relationships between nutrient recycling via excretion, fish body nutrient content and body size (wet mass), I utilized ordinary least squares (OLS) linear regression. I regressed nutrient excretion rates (N and P), and the nutrient excretion ratio (N:P) as a function of body nutrient content (% P, N, and C) and body mass. All data were \log_{10} -transformed prior to analyses. Each fish for which I measured

excretion, body mass, and body nutrient content measurements was used as an individual observation in regression analyses; thus, the number of observations used in regressions varied among species (Table 2.2). Given the differences in n among observations among fish taxa, I examined the relationships between nutrient excretion, body nutrient content and body size across all species, and not within and among individual species.

Significance for OLS analyses was inferred at $\alpha=0.05$.

I compared body nutrient content (% C, N and P), body nutrient ratios (N:P, C:P, C:N), mass-specific excretion rates (N and P), and the nutrient excretion ratio (N:P) fish taxa and using one-way ANOVA. I made these comparisons at the family level and the species level. All analyses were performed on arcsin- (for % C, N and P) and \log_{10} -transformed data (excretion rates and excretion ratios). I initially set $\alpha = 0.05$ and then used a sequential Bonferroni procedure to adjust α for multiple comparisons (Rice 1989; Moran 2003). I ranked response variable p -values from least to greatest and compared the lowest p -value to α/j , where j is the number of comparisons. I inferred significance if the p -value of a response variable was lower than the adjusted α . I compared greater p -values progressively to $j - 1, j - 2$, etc., until the p -value of a response variable exceeded the adjusted α . If a significant difference was detected among families or species for a response variable, I used Tukey HSD tests to determine homogeneous subsets. All statistical analyses were performed on SPSS Version 15.

8. Results

Fishes in the San Marcos River exhibited variation in body nutrient composition (N and P); percent body nutrients of fishes in the river ranged from 2 – 8% P and 8 – 18%

N (Fig. 2.1). Fishes also demonstrated a wide range in mass-specific P and N excretion rates and the ratio of N:P excreted (Fig. 2.1). Phosphorus excretion rates of fishes was a negative function of body % P (Fig. 2.1 A), but showed a much stronger relationship with body size (wet mass) of fishes (Fig 1B; Table 2.2). Nitrogen excretion rates did not significantly vary with body % N (Fig. 2.1 C), but like P excretion, had a strong relationship with fish body size (Fig. 2.1 D; Table 2.2). The ratio of excreted N and P (N:P) did not significantly vary with body N:P, but was a significant function of fish body size (Fig. 2.1; Table 2.2). In contrast, body size had a very limited role in the nutrient composition across fish species. Percent P of fishes was a marginally significant positive function of body mass ($r^2= 0.04$, $F_{1,95}= 3.655$, $P= 0.059$), but neither % N or % C were related to body size (N: $r^2=0.01$, $F_{1,95}= 0.890$, $P= 0.348$; C: $r^2= 0.01$, $F_{1,95}= 0.0010$, $P= 0.975$). Increasing % P with body size caused body N:P and C:P to weakly, but significantly decrease N:P (N:P: $r^2= 0.07$, $F_{1,95}= 7.44$, $P= 0.008$) and increase in C:P (C:P: $r^2= 0.07$, $F_{1,95}= 7.270$, $P= 0.07$) with body size.

The observed relationships between nutrient excretion, body nutrient content and body size were largely driven by taxonomic and presumably phylogeny of the fishes examined in this study. Fish body % P fishes significantly differed among fish families with the invasive loricariids exhibiting the highest %P and Cyprinidae and Percidae having the lowest % P (Fig. 2.2 A; Table 2.3). However, % N and % C did not significantly differ among families (Fig. 2.2 C+E; Table 2.3). Body C:P and N:P significantly differed among families, with the loricariids having the lowest body N:P and C:P (Fig. 2.2 B+D; Table 2.3). Cyprinidae, Percidae, and Characidae exhibited the highest body N:P and C:P. Body C:N did not significantly differ among families (Fig.

2.2 F; Table 2.3).

Significant differences in body % nutrients and ratios were also present when fishes were grouped by species (Fig. 2.3; Table 2.3). In general, the differences and patterns observed among families were present when fishes were analyzed by species. *Hypostomus* sp. (family Loricariidae) exhibited the highest body % P, but many of the species within Centrarchidae (*L. gulosus*, *L. macrochirus*, and *M. salmoides*) also exhibited relatively high % P. Although body % N did not differ among families, differences in body % N and % C were obvious when fish were grouped by species (Fig. 2.3 C and E, Table 2.3). *L. auritus* had the lowest % N and % C of all species and *L. macrochirus*, *M. salmoides*, and *G. geiseri* exhibited the highest % N or/or % C (Fig. 2.3 C and E). These differences in body % nutrients translated into significant differences among species in body N:P and C:P, but not C:N. Again, *Hypostomus* sp. exhibited among the lowest N:P and C:P; however, other species maintained body C:P and N:P ratios similar to those of *Hypostomus* sp. (*L. gulosus*, *L. auritus*, *G. geiseri*) (Fig. 2.3 B and D; Table 2.3).

There was significant variation among families in the mass-specific excretion of nutrients and ratio of excreted nutrients (Fig. 2.4; Table 2.4). Loricariids exhibited the lowest mass-specific P excretion rates, whereas the poeciliids had the highest P excretion rates (Fig. 2.4 A). Cyprinids exhibited the highest mass-specific N excretion rates (Fig. 2.4 B). Consequently, the N:P of excreted nutrients from loricariids was relatively high (~6:1) and was lowest for the poeciliids (0.3:1) (Fig 2.4 C). Differences among families were still generally apparent when fishes were grouped by species (Fig. 2.5; Table 2.4). *Hypostomus* sp. was among the species with the lowest mass-specific P excretion rate and

all three species in Poeciliidae (*G. affinis*, *G. geiseri*, and *P. latipinna*) had the highest P excretion rates (Fig. 2.5 A). Most species in Cyprinidae exhibited the highest N excretion rates (Fig. 2.5 B). Although *Hypostomus* sp. had among the highest excretion N:P of species in the San Marcos River, several other species in the river also exhibited similarly high excretion N:P, including *L. macrochirus*, *M. salmoides*, and *C. anomalum* (Fig. 2.5 C).

9. Discussion

Fishes of the San Marcos River exhibited variation in body nutrient composition and nutrient excretion. In the present study, variation in fish body stoichiometry (%P, %N, N:P, C:P, and C:N) was related to taxonomic affiliation, but had little relationship with body size. In addition, the recycling of nutrients (excretion rates and ratios) by fishes was a function of body size and taxonomic identity of fishes. The results of this study indicate that taxonomic identity of consumers in riverine food webs is important in determining the rates and ratios by which nutrients are recycled, potentially affecting ecosystem function (e.g., Vanni et al. 2002; McIntyre et al. 2008). The role of species identity in determining ecosystem function has been examined (Grimm 1995; Vanni et al. 2002), but ecologists are still in need of information on how the effects of different consumers may have implications for ecosystem function (Vitousek and Hooper 1993). The relationship between species identity and the relative strength of ecosystem-level effects is particularly important for systems that contain non-native and invasive species, because these taxa can have strong impacts on ecosystem dynamics (Carlsson et al. 2004).

Ecologists have identified several factors thought to control consumer-driven nutrient recycling in food webs. The body stoichiometry of the consumer in question relative to the nutrient content of its food (e.g., ecological stoichiometry) has been hypothesized to be an important factor controlling rates and ratios of recycled nutrients (Sterner 1990; Elser and Urabe 1992). In addition, consumer body size is also an important factor influencing nutrient recycling (Peters 1983; Vanni et al. 2002); allometric theory predicts that mass-specific rates of nutrient recycling will decline with body size (Peters 1983; West et al. 1997). In the present study, body size was an important factor controlling mass-specific nutrient recycling across all species of fishes, with mass-specific nutrient excretion rates declining with body mass and N:P of excreted nutrients increasing with body size. In contrast, nutrient content and body stoichiometry of fishes (% P, % N, body N:P) exhibited much weaker (%P) or non-significant relationships (% N, body N:P) with nutrient recycling across fish species. Thus, my findings indicate that across species, allometry was a stronger predictor of recycling rates and ratios than body stoichiometry. Other studies examining nutrient recycling by fishes have similarly noted that body size has a strong influence on nutrient excretion rates and ratios (Schaus et al. 1997; Vanni et al. 2002).

Although nutrient recycling across fish species sampled from the San Marcos River was more closely related to allometry, when fishes were grouped by family or species, I found that taxonomy was important in determining body stoichiometry and nutrient recycling rates and ratios. These taxonomic specific differences are presumably related to phylogeny of the species I examined (Vanni et al. 2002). When fishes were grouped by family, invasive loricariids exhibited the highest body % P (~5%) and the

lowest body N:P (27:1) and C:P (116:1). Loricariid catfishes also exhibited the lowest mass-specific P excretion rates and the highest N:P of excreted nutrients. However, the magnitude of the differences between loricariid catfishes and other species within the San Marcos River were not as great when body and excretion stoichiometry were examined at the species level. When examined at the species level, several species exhibited similar body (*Gambusia* spp., *Lepomis* spp., *M. salmoides*) and nutrient excretion stoichiometry (*Gambusia* spp., *Lepomis* spp., *M. salmoides*, *C. anomalum*, and *P. apistris*). Vanni et al. (2002) also found that differences in the body and excretion stoichiometry among fishes in a Venezuelan stream community were more evident when fishes were grouped by family rather than by species. Although half of the families I examined in the San Marcos River contain one species (Loricariidae and Characidae) or I was only able to collect one species for excretion and stoichiometry estimates (Percidae), the remaining half of the families examined by this study contained multiple species (Centrarchidae, Cyprinidae, and Poeciliidae). Within these families, Cyprinidae exhibited relatively restricted variation among species in body and excretion stoichiometry, whereas the species within Centrarchidae exhibited a fairly wide variation in nutrient dynamics. These findings indicate two important features of nutrient recycling by the San Marcos River fish community. First, these patterns indicate that some families of fishes within the San Marcos River are likely to show greater 'biogeochemical redundancy' (Grimm 1995; Vanni et al. 2002) than other families (i.e., Cyprinidae *versus* Centrarchidae). This redundancy may be critically important when considering conservation strategies in the river and whether local extinction of individual species from the fish community is related to loss or modification of ecosystem function (e.g., nutrient recycling). Second,

these results indicate that several of the fish species such as *L. auritus* and *L. gulosus* in the San Marcos River are 'biogeochemically' similar to the invasive *Hypostomus* sp., displaying similar body and nutrient excretion stoichiometry. However, as the relative abundance of *Hypostomus* in the San Marcos River has increased over the last 10-15 years, their importance in the nutrient dynamics of the river may have increased. Indeed, high body % P, low P excretion rates and high N:P excretion ratios of loricariids in the San Marcos River may be important in determining ecosystem-level nutrient cycling.

In my study, feeding guild affiliation did not have as big of an effect on patterns of body and excretion stoichiometry as did taxonomy and phylogeny. Eleven of the 14 fish species examined in this study are considered carnivorous and consume invertebrates and/or other fishes (Simon 1998); however, despite trophic similarity these species have different body nutrient compositions and recycle nutrients at very different rates and ratios. For example, *Lepomis* sp. and *Percina apistris* have substantially different body nutrient stoichiometry and belong to Centrachidae and Percidae respectively, but both families are considered to be largely carnivores. Likewise, *Hypostomus* and two native herbivorous cyprinids (*D. nigrotaeniata* and *C. anomalum*) (Cohen et al., *in review*) co-occur in the San Marcos River, but these three species exhibit differences in body and recycling stoichiometry. *D. nigrotaeniata* and *C. anomalum* display lower body % P and higher body N:P and C:P than *Hypostomus* sp. A likely reason for this contrast is due to taxonomic differences in body structure between loricariids and cyprinids; soft-bodied cyprinids have less skeletal development than most other fish (Sterner and George 2000) and loricariids have substantial bony armor-like plates containing Ca-PO_4^{3-} . Consequently, loricariids are predicted to sequester relatively more dietary P and have

lower mass-specific excretion of P than other groups of fishes (Hood et al. 2005). In this study, *Hypostomus* exhibited lower mass-specific P excretion rates and higher N:P of excreted nutrients (~6:1) than *D. nigrotaeniata* (~2:1); however, *C. anomalum* exhibited very similar excreted N:P (6:1) to *Hypostomus*. The reasons for the differences between these two cyprinid species is unknown at this time, and further studies on the species-specific stoichiometries in relation to potential variation in diet is required.

The introduction and establishment of *Hypostomus* into the San Marcos River is likely to have effects on influencing nutrient dynamics associated with herbivory in the river. Historically, *D. nigrotaeniata* was the dominant herbivore in the upper San Marcos River (Perkin et al., *in review*), but currently *Hypostomus* constitutes as much as 50% of the total ichthyomass (W.H. Nowlin, unpubl. data). This shift in dominant herbivores in the upper San Marcos River may have profound impact on the N:P of recycled nutrients, and thus algal nutrient limitation (Elser et al. 1988), composition (Vanni and Layne 1997), and rates of primary production (Elser and Urabe 1999; Sterner et al. 1992; Vanni et al. 1997). Such a shift in nutrient dynamic with an increase in loricariid biomass may lead to higher dissolved N:P ratios for periphyton growth and subsequently affecting periphyton N:P and C:P ratios.

Populations of loricariid catfishes in the San Marcos River may serve as a relatively long-term P sink. Due to their high body P content, *Hypostomus* have the ability to sequester P throughout their lifespan, thus populations of *Hypostomus* in the San Marcos River may function as nutrient sinks as long as population biomass is expanding and sequestering P (e.g., Kraft 1992). Soluble reactive P (PO_4^{3-}) concentrations in the upper San Marcos River are relatively low and dissolved inorganic

N: PO₄³⁻ molar ratio of the river water is high (360:1) leading to intense P-limitation of the periphyton community (Groeger et al. 1997). *Hypostomus* also are likely to increase periphyton C:P, leading to further P-limitation of catfish growth (Hood et al. 2005).

In summary, ecological stoichiometry can provide a predictive framework to examine the impacts of invasive species effects on ecosystem function. To date, numerous studies have examined at the community ecosystem level, impacts of exotics (Parker et al. 1999), but there have been relatively few studies on the ecological stoichiometry of invasive species. Hall et al. (2003) utilized a stoichiometric approach to examine the effects of the exotic freshwater snail, *Potamopyrgus antipodarum* and found that *P. antipodarum* dominated C and N fluxes in stream ecosystems. Here, I found that overall fish body stoichiometry is related to taxonomic identity, especially at the family level. Invasive loricariids in the San Marcos River appear to be stoichiometrically unique and may have profound effects on ecosystem function. Further studies examining the relative importance of *Hypostomus* on nutrient fluxes in the San Marcos are required.

10. Tables and Figures

Table 2.1: List of fish species from the upper San Marcos River collected for body nutrient content analyses and excretion measurements. Family and common name are provided for each species. *n* is the number of individuals from each species analyzed for body nutrients and excretion rates.

Family	Species	Common name	<i>n</i>
Cyprinidae	<i>Cyprinella venusta</i>	blacktail shiner	7
	<i>Campostoma anomalum</i>	central stoneroller	9
	<i>Dionda nigrotaeniata</i>	Guadalupe roundnose minnow	6
	<i>Notropis amabilis</i>	Texas shiner	11
Characidae	<i>Astyanax mexicanus</i>	Mexican tetra	6
Loricariidae	<i>Hypostomus sp.</i>	suckermouth catfish	21
Poeciliidae	<i>Gambusia affinis</i>	western mosquitofish	2
	<i>Gambusia geiseri</i>	bigspring mosquitofish	2
	<i>Poecilia latipinna</i>	sailfin molly	4
Centrarchidae	<i>Lepomis auritus</i>	redbreast sunfish	10
	<i>Lepomis gulosus</i>	warmouth	2
	<i>Lepomis machrochirus</i>	bluegill	2
	<i>Micropterus salmoides</i>	largemouth bass	7
Percidae	<i>Percina apistris</i>	Guadalupe darter	6

Table 2.2: Results of OLS regression analysis examining the relationships between body nutrients (% dry mass), wet mass, body nutrient ratios, mass-specific nutrient excretion rates (P and N), and the N:P of excreted nutrients. The regression equation (if the relationship was significant), the *df*, *F*, and *p* are given for each relationship. Significant *p*-values are denoted with an *.

<i>x</i>	<i>y</i>	Equation	r^2	$F_{1,95}$	<i>p</i>
Log ₁₀ body % P	Log ₁₀ P excretion rate ($\mu\text{M P}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$)	$y = -0.92x - 0.16$	0.041	3.97	0.049*
Log ₁₀ wet mass (g)	Log ₁₀ P excretion rate ($\mu\text{M P}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$)	$y = -0.68x + 0.08$	1.0701	220.66	<0.001*
Log ₁₀ body % N	Log ₁₀ N excretion rate ($\mu\text{M N}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$)	-	-	-	0.071
Log ₁₀ wet mass (g)	Log ₁₀ N excretion rate ($\mu\text{M N}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$)	$y = -0.34x - 0.12$	0.325	45.21	<0.001*
Log ₁₀ body N:P	Log ₁₀ excretion N:P	-	-	-	0.384
Log ₁₀ wet mass (g)	Log ₁₀ excretion N:P	$y = 0.35x - 0.04$	0.337	47.83	<0.001*

Table 2.3: Results of one-way ANOVA examining differences among families and species in % body nutrients and body nutrient ratios. *F*, *df*, and *p* are given for each response variable. Significant *p*-values are denoted with an *.

Taxonomic Level	Variable	F	df	p
Family	% P	5.09	5, 95	<0.001*
	C:P	9.41	5, 95	<0.001*
	%N	1.11	5, 95	0.359
	N:P	9.14	5, 95	<0.001*
	% C	0.28	5, 95	0.924
	C:N	0.78	5, 95	0.568
Species	% P	2.06	13, 95	0.025*
	C:P	4.53	13, 95	<0.001*
	%N	5.79	13, 95	<0.001*
	N:P	4.71	13, 95	<0.001*
	% C	3.03	13, 95	0.001*
	C:N	1.22	13, 95	0.280

Table 2.4: Results of one-way ANOVA examining differences among families and species in mass-specific nutrient excretion rates and the N:P of excreted nutrients. F , df , and p are given for each response variable. Significant p -value are denoted with an *.

Taxonomic Level	Variable	F	df	p
Family	P excretion	17.52	5, 95	<0.001*
	N excretion	6.96	5, 95	<0.001*
	Excretion N:P	14.25	5, 95	<0.001*
Species	P excretion	13.06	13, 95	<0.001*
	N excretion	12.93	13, 95	<0.001*
	Excretion N:P	10.54	13, 95	<0.001*

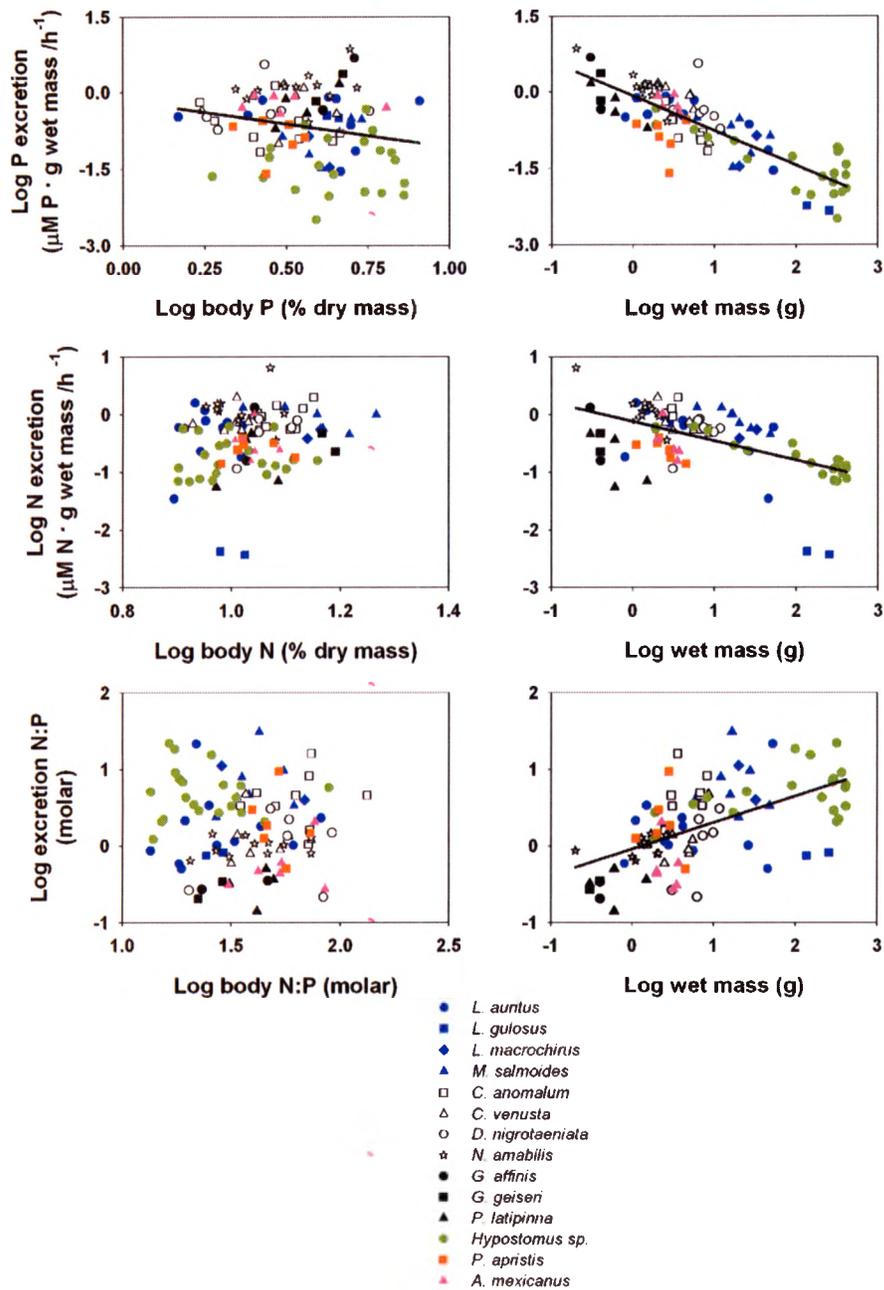


Figure 2.1: Relationships between nutrient content (N and P), nutrient excretion, and body size in the San Marcos River fish community. Each species of fish is represented by a different symbol (see legend). Fishes within the same family are the same color.

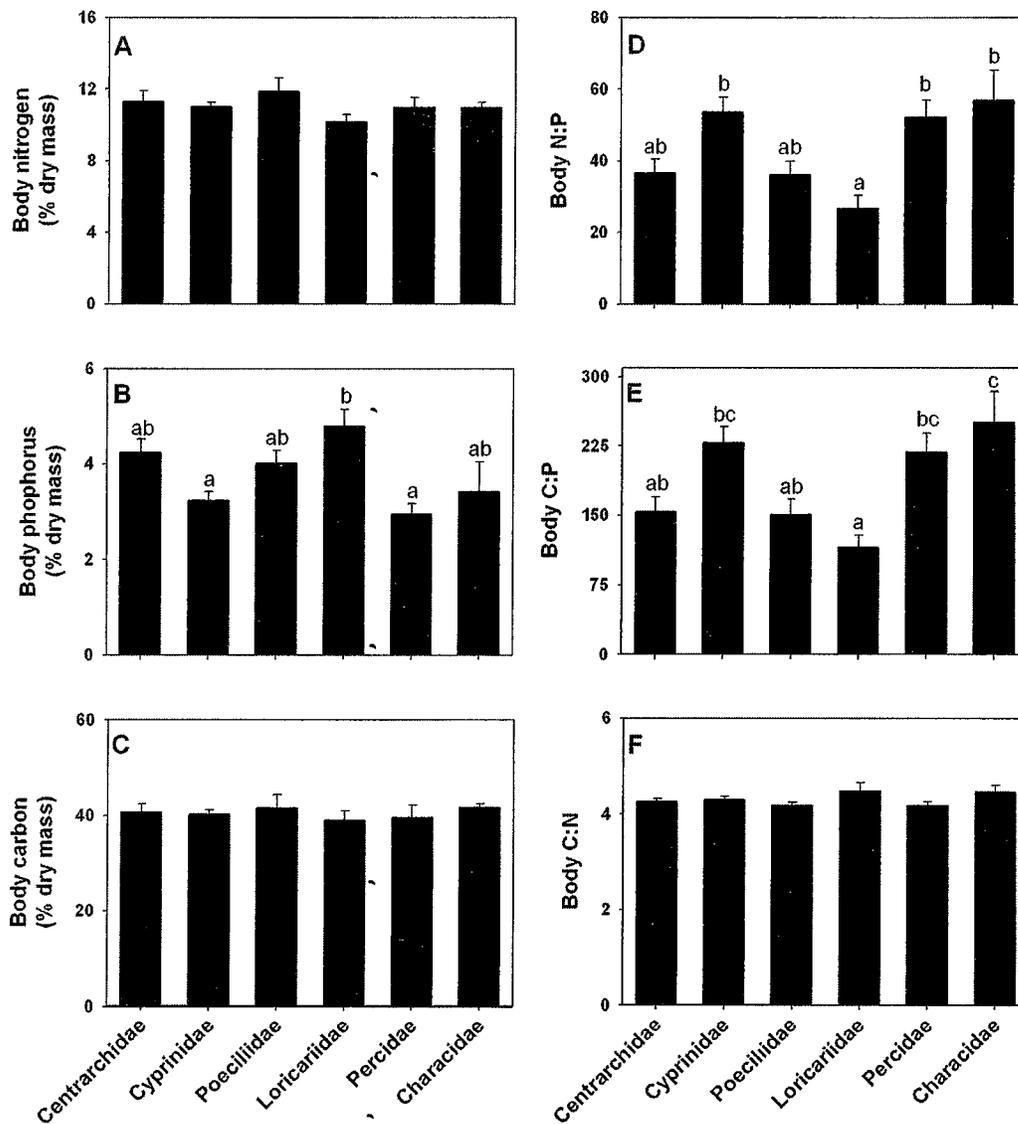


Figure 2.2: Mean (\pm 1SE) percent nutrient composition (per unit dry mass) of the different fish families sampled in this study.

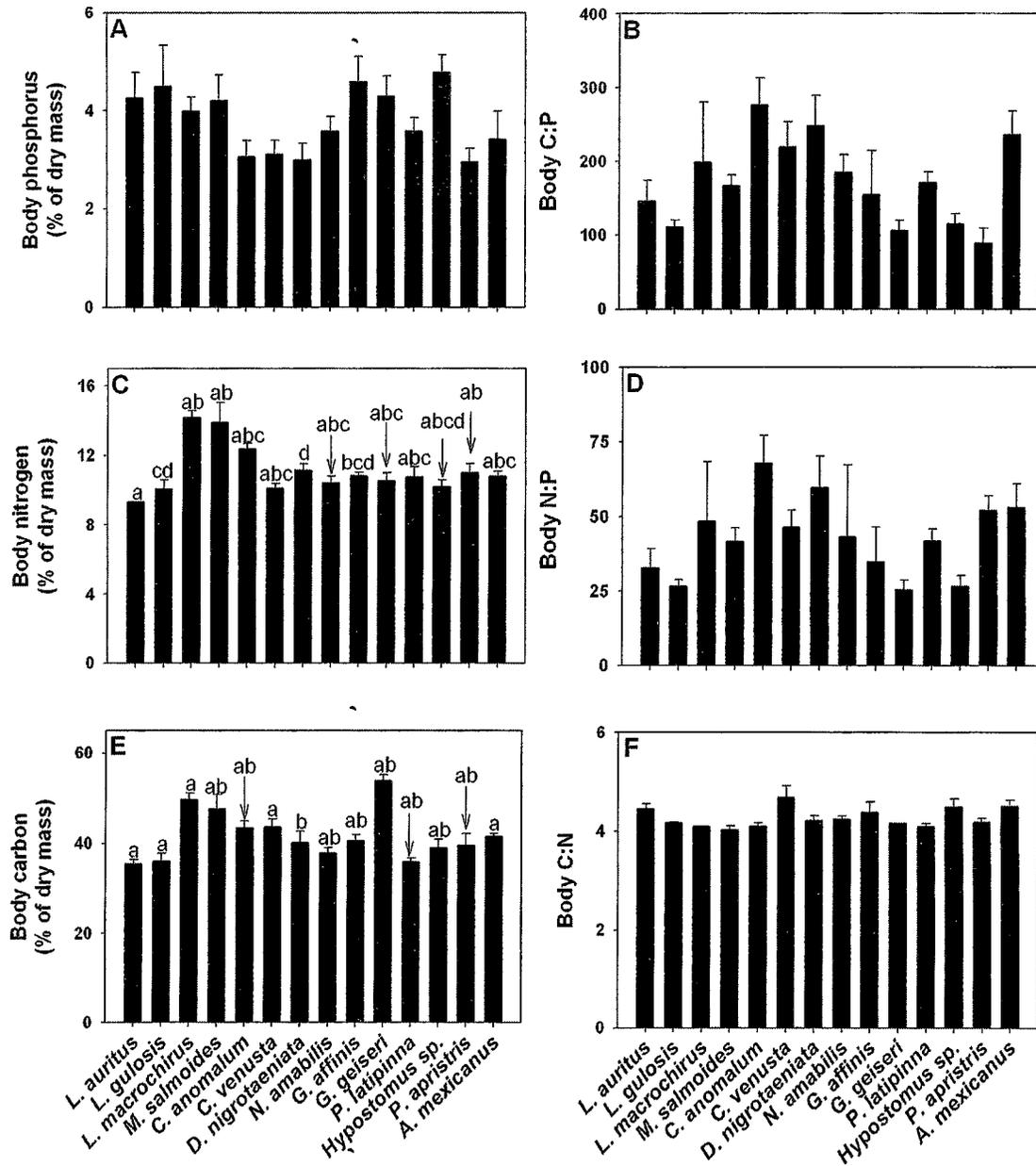


Figure 2.3: Mean (\pm 1SE) percent nutrient composition (per unit dry mass) of the different fish species sampled in this study.

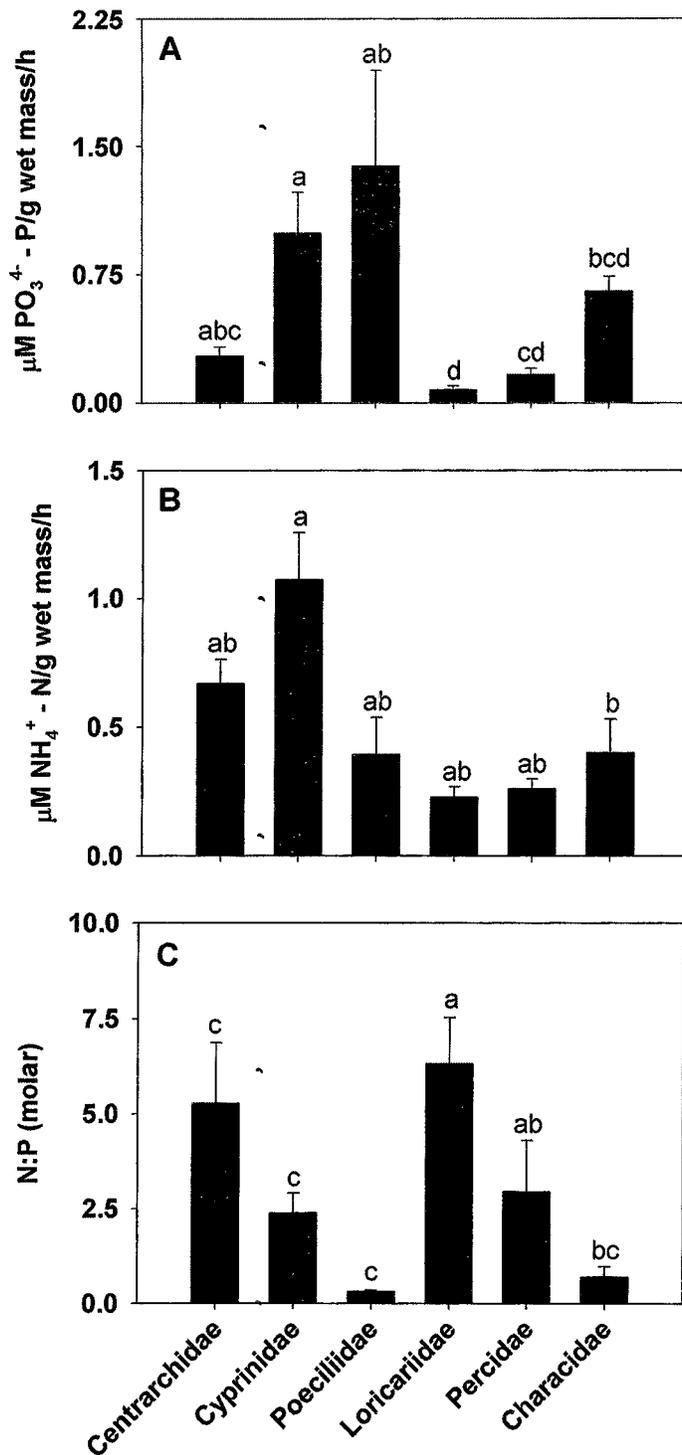


Figure 2.4: Mean (± 1 SE) mass specific nutrient excretion rates and N:P of excretion of the different fish families sampled in this study.

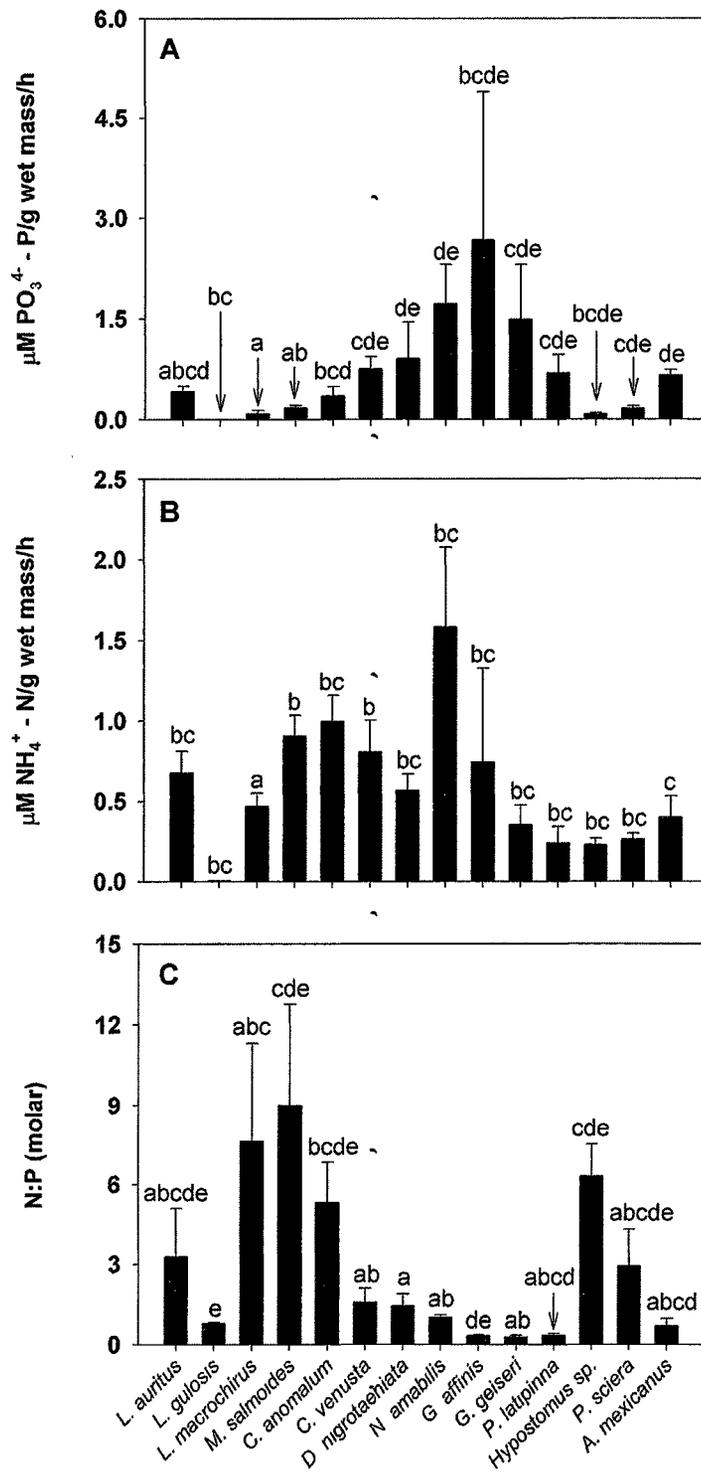


Figure 2.5: Mean (\pm 1SE) mass specific nutrient excretion rates and N:P of excretion of the different fish families sampled in this study.

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