THE EFFECTS OF INVASIVE SPECIES AND EUTROPHICATION ON RIVERINE NUTRIENT DYNAMICS

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Crystal Marie LeBoeuf, B.S.

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ABSTRACT

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SUPERVISING PROFESSOR: DR. WESTON H. NOWLIN

Invasion of exotic species has been identified as one of the greatest threats to aquatic ecosystems. The invasion of aquatic ecosystems by herbivorous and detritivorous fishes is especially concerning because they can alter trophic pathways and nutrient cycling. Increased nutrient loading and productivity may allow for more successful invasion of ecosystems and may also modify the effects of these fishes on ecosystem properties. Herbivorous suckermouth catfish have invaded spring-fed ecosystems in North America and can have profound impacts on ecosystem function. I present the results of a two-part study in which I investigated (1) whether the spatial variation in the abundance of suckermouth catfish in the San Marcos River (Texas, USA) was related to variation in productivity, and (2) if the effects of catfish on ecosystem processes were influenced by nutrient enrichment. To examine the first question, I conducted a

field survey examining the habitat associations of catfish in the river and found that catfish densities were highest at the most upstream site, which was characterized by deeper depths, lower flows, smaller substrates, and lower canopy cover and turbidity. However, spatial variation in catfish densities was not related to productivity (measured as periphyton biomass). To examine the second question I conducted a stream channel experiment in which I cross-classified the presence and absence of catfish and nutrient additions. Catfish reduced periphyton biomass, reduced periphyton N:P, altered the severity of periphyton P limitation, and altered detrital processing. The presence of nutrient enrichment altered leaf litter decomposition rates and the nutrient stoichiometry of decomposing leaf litter. I did not find an interaction between the effects of catfish and nutrient enrichment. The results of this study indicate that the spatial variation in population density of catfish in the San Marcos River are not strongly associated with variation in productivity and that the effects of this invasive herbivore on ecosystem dynamics are not dependent upon nutrient loading.

1. INTRODUCTION

The invasion of exotic species presents one of the largest threats to aquatic ecosystems (Sala et al. 2000). The successful establishment of exotic species in ecosystems is dependent on characteristics of both the habitat (Lonsdale 1999, Stachowicz et al. 2002) and the invading species (Rejmanek & Richardson 1996, Kolar & Lodge 2001). Obviously, some exotic species are more successful invaders than others (Rejmanek & Richardson 1996, Kolar & Lodge 2001), and those that succeed typically have competitive superiority over native species (Seabloom et al. 2003) through post-invasion adaptations (Ellstrand & Schierenbeck 2000, Siemann & Rogers 2001). Exotic species released into novel environments may experience a decrease or release from regulation by native competitors and predators (Keane and Crawley 2002), leading to the competitive exclusion of trophically-similar species (Douglas et al. 1994, Gido and Franssen 2007). In addition, introduction of non-native species into aquatic ecosystems can lead to alteration of community dynamics and ecosystem processes (Flecker and Townsend 1994, Hall et al. 2003, Scott et al. in review).

Invasion of ecosystems by herbivorous and detritivorous fishes is a substantial concern for the conservation of native fish assemblages and the preservation of ecosystem function. Moyle and Light (1996a) hypothesized that by utilizing rarely limiting food resources, benthic-feeding fishes are likely to establish populations in novel habitats, potentially becoming invasive. These predictions are supported by field

observations that benthivorous fishes are commonly-found non-native taxa in fish assemblages (Gido and Franssen 2007). The invasion by these fishes is particularly concerning because invading algivores and detritivores can outcompete native fishes in the same trophic guild, alter nutrient cycling, and modify trophic pathways (Baxter et al. 2004, Simon et al. 2004, Gido and Franssen 2007, Cohen et al. in review, Scott et al. in review.).

Spring-influenced ecosystems often exhibit high diversity and levels of endemism, but also face a diversity of anthropogenically-generated stressors (Bowles and Arsuffi 1993, Crowe and Sharp 1997, Earl and Wood 2002). As systems of low variability, spring systems are sensitive to the successful invasion of exotic species (Moyle and Light 1996b). Many spring ecosystems face considerable disturbance through anthropogenic eutrophication and subsequent loss of water quality (Carpenter et al. 1998). Anthropogenic eutrophication of aquatic ecosystems has an array of consequences including the alteration of productivity, nutrient cycling, and changes in species diversity and the loss of ecosystem services (Carpenter et al. 1998). In addition, increased resource availability has been identified as a pivotal factor influencing the success of invasion (Vitousek et al. 1997, Davis et al. 2000, Thompson et al. 2001). It is here hypothesized that the success of invasion is higher in high-nutrient ecosystems (Davis et al. 2000), and this prediction has been supported experimentally (Romanuk and Kolasa 2005). If eutrophication indeed leads to higher invasibility, there is a need to understand if nutrient enrichment may make spring ecosystems more invasible and how invasive species and nutrient enrichment interact to affect ecosystem function and nutrient dynamics in spring ecosystems

Armored suckermouth catfishes (family Loricariidae, hereafter referred to as catfish) are herbivorous fishes that are prolific invaders. Catfishes are native to neotropical South America (Power 1990), but have invaded subtropical and spring-fed systems in North America, including Hawaii, Florida, Puerto Rico, Texas, and Mexico (Courtenay et al. 1974, Ludlow and Walsh 1991, Page 1994, Edwards 2001, Hoover et al. 2004, Gibbs et al. 2008). Their presence as an exotic species in novel habitats is concerning because they have strong effects on nutrient and trophic dynamics in both their native and invaded habitats (Vanni et al. 2002, Cohen et al. in review, Scott et al. in review). Catfish directly affect periphyton biomass through consumption (Scott et al. in review, Cohen et al., in review). In addition, grazing activities by catfish increases benthic sediment redistribution and transport (Scott et al. in review). Further, catfish indirectly affect algae by altering nutrient dynamics (Hood et al. 2005, Knoll et al. 2009). Catfish are armored with bony scutes and will selectively retain P from their food in order to maintain these structures (Hood et al. 2005). Consequently, armored catfish excrete dissolved nutrients at relatively high N:P (Vanni et al. 2002) and decrease periphyton C:P ratios through their nutrient recycling (Knoll et al. 2009, Scott et al. in review). Although armored catfish are prevalent invaders of spring-fed ecosystems, little is known of how their populations respond to resource availability or how their ecosystem-level effects interact with nutrient loading.

The purpose of the present study is to examine the interaction between invasive Loricariid catfish (*Hypostomus* sp.) and nutrients in the San Marcos River, Texas, USA, a spring-influenced river ecosystem. Catfish are abundant in the river and now make up 20-50% of the ichthyomass (W. Nowlin, unpubl. data), causing substantial

effects on trophic dynamics, algal biomass, periphyton nutrient dynamics, and sediment transport (Cohen et al. in review, Scott et al. in review). In addition, a portion of the San Marcos River receives substantial nutrient inputs from waste water effluent (the San Marcos Sewage Treatment Plant). Therefore, there is clearly a need to understand the interactions and implications of both catfish and nutrient loading in the San Marcos River.

In the present study, I address two main questions: First, is spatial variation of catfish populations in the San Marcos River related to spatial differences in nutrient enrichment in the river? That is, do increasing nutrient levels lead to higher invasibility of catfish in portions of the San Marcos River? To examine this question, I conducted a field study examining longitudinal variation of catfish populations in the San Marcos River and relate catfish densities to differences in environmental conditions including periphyton standing stock. I hypothesized that spatial variation in catfish densities would be related to variation in periphyton biomass. Second, I examined how the effects of catfish and nutrient loading individually and interactively affect ecosystem dynamics in this spring-fed river ecosystem. To do this, I conducted a replicated stream channel experiment and predicted that the presence of catfish will lead to a decrease in periphyton biomass and increased sediment disturbance and transport. In addition, I utilized a stoichiometric approach to this experiment and hypothesized that catfish would alter periphyton C:nutrient and N:P ratios through their grazing and excretion activities. I also predicted that the addition of nutrients would stimulate periphyton biomass and production, but the presence of catfish will largely negate these stimulatory effects because catfish are highly efficient grazers. This study represents one of the first attempts to examine whether

resource availability affects populations of an invasive herbivore and whether the effects of this species are dependent upon nutrient levels.

2. MATERIALS AND METHODS

2.1 *General Study-Site Description*

The San Marcos River emerges as the San Marcos Springs from the San Antonio portion of the Edwards aquifer at the base of the Balcones escarpment in the city of San Marcos in Central Texas (Guyton & Associates 1979, Elser et al. 1996). Some 200 springs discharge into Spring Lake, the headwaters of the river; spring water constitutes the majority of flow in the San Marcos River system (Hynes 1970). Water flows over two waterfalls at the end of Spring Lake and forms the San Marcos River which continues to its confluence with the Blanco River, 7.2 km downstream (Figure 1). The upper San Marcos River (the reach from below Spring Lake to its confluence with the Blanco River) is characterized by clear water, and nearly constant temperatures (~22 °C) and physiochemical conditions (Groeger et al. 1997). The river also contains multiple endemic and state and federally listed species, including the San Marcos salamander (*Eurycea nana*), the fountain darter (*Etheostoma fonticola*), and Texas wild rice (*Zizania texana*).

2.2 *Habitat Association Study*

The first part of this study involved a longitudinal field study of the San Marcos River in order to assess catfish population distribution and habitat associations. Three sites were selected in the spring-influenced section of the river: Sewell Park, Rio Vista Park,

and the Sewage Treatment Plant (Figure 1). Sewell Park is the furthest upstream site and is located approximately 0.6 km downstream of Spring Lake; Rio Vista Park is located 2 km downstream of Spring Lake, and the furthest downstream site is located just below the San Marcos Sewage Treatment Plant, approximately 4 km downstream of Spring Lake. Catfish in the San Marcos River are generally more active at night (C. LeBoeuf, pers. obs.), so nocturnal snorkel surveys to estimate catfish densities were performed at each site, monthly (period from June 2008 – May 2009). Catfish were counted along five, cross-channel transects along a 50 m reach; preliminary observations indicated that five transects along a 50 m reach were sufficient to determine catfish density at each site reach. Divers assembled on the bank with the diver furthest downstream entering the water first, successionally followed by subsequent divers going upstream (Dolloff et al. 1996). Divers surveyed to 0.5 m to either side of their viewing area. All divers were trained on protocols before diving. The length of each transect was recorded and the number of catfish per unit area was calculated for each transect. The total number of fish observed per m^2 was averaged for each site on each sampling date.

Seasonal habitat assessments were performed at the same three sites, along the same reaches where snorkel surveys were performed, by measuring the following parameters: water depth, flow rate, dominant benthic substrate, % canopy cover, and standing crop of periphyton. Habitat characterizations were performed November 2008, February 2009, June 2009, and August 2009 at all sites. Depth (cm) and flow (m/s) were measured at 5 points along each of 5 transects at each site using a Marsh-McBirney Flowmate 2000 electromagnetic flowmeter. Dominant substrate was assessed at the same points and classified as sand, gravel, pebble, cobble, boulder, or bedrock (Wentworth 1922).

Canopy cover (% overstory density) was assessed at the midpoint of each transect using a Wildco forest densiometer. In order to measure algal standing crop, ten rocks were randomly collected from each 50 m reach and their upper surfaces scrubbed for periphyton with a nylon bristle brush and rinsed with Milli-Q H_2O into 50 mL screwtop centrifuge tubes. This periphyton slurry was filtered onto Pall A/E filters, and filters were placed in black plastic vials and frozen until analysis.. Chlorophyll *a* was extracted for 4 hours with HPLC-grade acetone and measured on a Turner Designs Trilogy fluorometer. The upper surface area of each rock used for periphyton measurements was estimated by covering the scrubbed area with foil and weighing the foil, and surface area was estimated by a standard foil surface area-weight relationship (Sponseller et al. 2001). Water temperature (°C), dissolved oxygen (mg/L), specific conductance (µs/cm), and salinity (ppt) were measured using a YSI Model 85 (Yellow Springs Instruments Incorporated, Yellow Springs, OH) at each site. In order to measure turbidity (NTU), water samples were collected in 2-L opaque Nalgene bottles at each site and kept in coolers until analysis on a HF Scientific DRT-15CI Portable Turbidimeter.

2.3 *Stream Channel Experiment*

In order to examine the separate and combined impacts of invasive catfish and nutrient enrichment, I conducted an experiment involving stream channel mesocosms located beneath the Freeman Aquatic Biology Building at the Texas State University (San Marcos, TX). The experiment consisted of a 2 x 2 fully saturated manipulation of the two factors: catfish presence and nutrient enrichment. Each treatment combination (catfish absent, enrichment absent; catfish presence, enrichment absence; enrichment

presence, catfish absence; catfish presence and enrichment presence) was replicated 5 times. Catfish presence treatments consisted of 3 catfish per channel; catfish between 19-29 cm were caught using seines and kicknets in the San Marcos River. Each catfish in each stream channel was individually marked using fin clips, weighed (g), and total length (cm) were determined before addition. Three catfish died early in the experiment, and were immediately removed and replaced with catfish of similar size upon discovery. The presence of nutrient enrichment consisted of adding dissolved N (940 mg KNO_3^{2-} and 3958 mg NH_4Cl) and P (213 mg $NaH_2PO_4 \cdot H_2O$) every 3 days using slow-drip Nalgene bottles in a ratio of 54:1 N:P, in order to approximate nutrient concentrations found downstream of the San Marcos Sewage Treatment Plant. The beginning of the experiment was marked by the introduction of catfish and nutrient enrichment and ran for eleven weeks.

Stream channels consisted of ten cement channels, each supplied with water from an artesian well fed from the Edwards aquifer. Thus, the stream channels had the same water as the springs feeding the San Marcos River. Stream channels consisted of ten cement channels, each fed with individual well heads. Each of the ten cement channels was divided in half using a PVC pipe frame lined with heavy gauge (6-mil) plastic, yielding a total of 20 channels. I created a reservoir at the head of each channel, capturing the inflow and equally dispersing it between the two portions of the divided channel. Forty watt full-spectrum fluorescent lights (light intensity ~ 200 $\mu mol \cdot cm^{-2}$) were hung 48 cm above all channels, and lighting was provided 16:8 light/dark cycle via timers. Substrates consisting of sand, pebble, gravel, and cobble in proportions similar to that of the San Marcos River (50% cobble, 50% sand, pebble, and gravel) were added to

each channel bottom. Rocks were collected from the San Marcos River each week for three weeks prior to the start of the experiment and scrubbed for periphyton. The scrubbed rocks were then equally distributed among channels. Equal aliquots of the periphyton slurry were added to channels to facilitate periphyton colonization of substrates. Aquatic macroinvertebrates were collected each week for three weeks prior to the experiment using a kick net from the San Marcos River and placed in a bucket of river water. Bucket contents were then divided into equal aliquots and distributed among channels. Because macroinvertebrates were allowed to 'drift' downstream and out of channels, this procedure was repeated weekly throughout the experiment.

Unglazed ceramic tiles (15.2 x 15.2 cm) were added to all channels to measure periphyton biomass, benthic organic matter (OM), and benthic inorganic matter (IM). In order to assess indirect effects of each factor (catfish and nutrients), half of the tiles were placed in 2 cm aperture wire mesh cages. Each channel received 4 uncaged and 4 caged tiles. One caged and one uncaged tile was removed from each stream channel at 3, 6, 9, and 11 weeks. Upon removal, tiles were scrubbed for periphyton with a nylon bristle brush and rinsed with Milli-Q H_2O into acid-washed 37 mL plastic, lidded containers. A portion of this slurry was filtered onto Pall A/E filters for determination of biomass through determination of chlorophyll *a* concentration. Filters were frozen in black plastic vials and chlorophyll *a* was extracted for 4 hrs using HPLC-grade acetone and measured on a Turner Designs Trilogy fluorometer. In addition to chlorophyll *a*, subsamples of this slurry were used to determine OM and IM on tiles by filtering onto pre-ashed and pre-weighed Pall A/E filters. Filters were dried at 60 °C for 48 hrs, weighed, ashed at 450 °C for 5 hrs, and weighed to calculate concentration of OM and IM on tiles

($mg \cdot cm^2$). Finally, subsamples of the slurry were filtered on to pre-ashed Whatman GF/F filters to determine C and N (Flash EA 1112 Series NC Soil Analyzer) and P concentration (HCl digestion) on tiles.

Leaf litter comprises a substantial portion of stream organic matter (Maltby 1992a) and its breakdown is a fundamental stream ecosystem function (Paul et al. 2006). Thus, in order to assess leaf litter breakdown rate, twelve leaf packs were added to each channel three weeks prior to beginning the experiment. Leaf packs consisted of tying 4.4 ± 0.88 g of sycamore (*Plantanus* sp) leaves together at the petiole with monofilament fishing line. All leaf packs were pre-weighed and numbered with a plastic tag. Again, in order to assess indirect effects of each factor (catfish and nutrients), half of the leaf packs were enclosed in 3 mm aperture plastic mesh so they would be inaccessible to catfishes. Leaf packs were weighted in order to fully submerge the leaves. Two packs (one open and one enclosed) were removed from each channel at weeks 3, 5, 7, 9, and 11. Packs were removed using a 25 μm sieve and the material rinsed with Milli-Q H_2O into a plastic bag and placed on ice until analysis. Leaf packs were pulled apart and rinsed with Milli-Q H_2O over a 1 mm sieves for coarse particulate organic matter. Leaf materials were dried at 60 °C for one week and weighed and percent mass lost from each leaf pack was calculated. Material from each pack was homogenized and analyzed for C and N on a Flash EA 1112 Series NC Soil Analyzer and P using HCl digestion (APHA 1992).

Floating periphyton samplers (Wildco, Inc.), each containing 3 glass slides were set during the first week after the start of the experiment in each channel to measure periphyton production via chlorophyll *a* accumulation. Slides were removed and replaced at 3, 5, 7, 9, and 11 weeks. Slides were frozen in plastic screw-cap centrifuge

tubes in the dark until analysis for chlorophyll *a* using the above methods. Primary production for each stream channel was calculated as the mean chlorophyll *a* accumulation (μg/chl *a*/cm^2/d) of the three slides which were removed from the sampler on each sampling date.

Dissolved oxygen (DO) was measured at weeks 5, 7, and 10 in order to assess community metabolism. Water samples from each channel were collected in 60 mL glass BOD bottles immediately before dawn to capture the potential DO minimum and immediately before dusk to capture the potential DO maximum and analyzed using the Winkler titrimetric method (Roland et al. 1999) on a Varian Cary 50 UV-Vis spectrophotometer.

On weeks 3, 5, 7, 9, and 11 water was collected from the end of each channel using brown high density polyethylene (HDPE) bottles to analyze concentration of nitrate (NO_3^-), phosphate (PO_4^{3-}), ammonium (NH_4^-), total nitrogen (TN), and total phosphorus (TP). Water for NO_3^-, PO_4^{3-}, and NH_4^+ analyses was filtered through ashed Pall A/E filters and acid-preserved. Phosphate was measured as soluble reactive phosphorus (SRP) using molybdenum blue method (Wetzel and Likens 2000) on a Varian Cary 50 UV-Vis spectrometer. Nitrate was determined with second derivative UV spectroscopy (Crumpton et al. 1992). Ammonium was determined with the phenate method (Wetzel and Likens 2000). Total nitrogen and TP was measured as NO_3^- and PO_4^{3-}, respectively, on a Varian Cary 50 UV-Vis spectrometer following persulfate digestion.

Nutrient diffusing substrata (NDS) (Francoeur 1999, Flecker et al. 2002) were added to stream channels at Week 4 and Week 9 and incubated for 14-18 days to examine the effects of nutrient additions and catfishes on nutrient limitation of periphyton

communities. NDS were constructed using 20 mL plastic vials filled with nutrient-amended agar and topped with Pall A/E filters. Filters were held in place by vial caps with holes drilled through the tops. Each channel received two replicates of each nutrient amended NDS treatment (+N or +P) and 2 replicates of a non-amended (control) NDS treatment. Agar (23 g/L H_2O) was infused with KNO_3 for N and Na_2HPO_4 for P enrichment. Nutrient additions were as follows: 50.6 g/L KNO_3 for N enrichment and 71.0 g/L Na_2HPO_4 for P enrichment (N loading = 530.9 mg/m^2·day; P loading = 21.8 mg/m^2·day). After incubating in stream channels for two weeks, NDS were removed and filters were removed and frozen until analysis for chlorophyll *a* using the previously mentioned methods. For each stream channel, the chlorophyll *a* responses of each nutrient amendment treatment (no nutrients, N only, P only) were averaged, and the responses to nutrient amendment were determined by calculating the response ratio as *ln* (chl a_E/chl a_C), where chl a_E is the chlorophyll *a* concentration of the nutrient enriched NDS and chl a_C is the chlorophyll *a* concentration of the unenriched NDS (Gough et al. 2000).

At the end of the experiment, catfish were caught using dip nets, and wet weights (g) were recorded. I quantified nutrient recycling rates and body nutrient composition of catfish using method of Schaus et al. (1997). Animals were placed in separate acid-washed plastic containers containing filtered stream water. After 1 hour, contents of containers were filtered through Pall A/E filters, collected in Nalgene bottles, and acid-preserved. Filtrate samples were analyzed for ammonium and SRP using the methods described above. Excretion rates were calculated as the change in ammonia-N or SRP per unit wet mass of catfish per unit time (μmol· g w wt^{-1} · hr^{-1}). To quantify body

nutrient contents of fish, fish were immediately pithed after excretion trials, and entire animals were dried at 60 °C and ground to a fine powder. Samples were analyzed for C and N on a Flash EA 1112 Series NC Soil Analyzer and particulate P using HCl digestion.

I also assessed condition of catfish at the end of the experiment by determining lipid content (Arrington et al. 2006). Lipid content of catfish was estimated following Folch et al. (1957) and Post and Parkinson (2001). A 0.5 ± 0.0001g sample of dried, homogenized catfish tissue was weighed and placed in a 30 ml screw-top test tube, and 8 mL of chloroform and 8 mL of methanol were added. This mixture was heated to boiling in a 61 °C water bath. Test tubes were then removed, cooled to room temperature, and liquid was decanted, and brought to 25 mL using chloroform. This volume was filtered through No. 1 Whatman filter paper into a 125 mL separatory funnel. This was followed with 10 mL of 0.9% saline solution, the entire mixture shaken, and allowed to separate. The bottom liquid layer in the funnel was drained into a pre-weighed aluminum weigh boat. Dish contents were evaporated at 70 °C, allowed to cool to room temperature, and weighed to the nearest 0.0001g on a Mettler Toledo MS104S analytical balance. This remaining lipid represents the mass of lipid per 0.5 g of dry catfish tissue.

2.4 *Data Analyses*

Habitat Association Study

Site estimates of physical and chemical data in habitat assessments were calculated by averaging by site for each season. Principal components analysis (PCA) was performed using site means for each season of physical habitat data. Dominant

substrates were taken as the mode of each site and were represented with dummy variables. All variables were z-score transformed (Krebs 1999). The resulting variable loadings and plots were used to describe habitat characteristics for each site. To examine if catfish densities varied among sties or through time, I utilized a single-factor repeated measures ANOVA. I did not detect a significant effect of time (*F=1.147; DF=6; p=0.394*), thus I utilized a single factor ANOVA to detect differences between sites. In an attempt to meet assumptions of homoskedasticity and normality, catfish densities were $\log_{10}(x+1)$ transformed prior to analyses.

Stream Channel Experiment

Chlorophyll *a* concentration for open and closed tiles, leaf litter decomposition for open and closed leaf packs, primary production, measures of community metabolism (pre-dawn and pre-dusk DO concentration), and stream channel water nutrient concentrations were analyzed with a two-way repeated measures ANOVA. This analysis allowed me to assess the main effects of catfish, nutrient enrichment, and time, as well as the interdependence of the effects of these factors. Because periphyton nutrient deficiency was only assessed on two dates, a separate two-way ANOVA was performed for each date comparing the responses to each nutrient amendment for all treatment combinations. Catfish growth, condition, excretion, and elemental composition responses at the end of the experiment were averaged by channel because the 'channel' was considered the unit of replication. Initial weight and final weight, Δ mass over the experiment, nutrient recycling rates, body nutrient ratios (C:N, C:P, and N:P), and percent lipid of catfish were analyzed using paired t-tests to compare those fish in

channels with vs. without nutrient enrichment. All statistical analyses were performed with R software. Significance for all analyses were inferred at $p \leq 0.05$.

3. RESULTS

3.1 *Habitat Association Study*

Principal component analysis axes I and II cumulatively explained 76.88% of the variation among seasonal sample sites in the upper section of the San Marcos River (Figure 2a). Principal component I represents a gradient among the sites along the river associated with the following loadings: flow (-0.498), canopy cover (-0.435), turbidity (-0.416), substrate (-0.398), chlorophyll *a* (-0.019) and depth (0.481). The most upstream site, Sewell Park, has deeper water, lower flow rates, smaller-sized benthic substrates, lower canopy cover, and lower turbidity. Principal component II represents largely within site variation across sampling dates, in particular the seasonal variation in % canopy cover at the downstream Sewage Treatment Plant site. Principal component II has the following loadings: canopy cover (-0.202), flow (-0.087), turbidity (0.071), depth (0.075), substrate (0.301), and chlorophyll *a* (0.922).

Results from the snorkel surveys indicated that catfish densities exhibited significant spatial variation in the river ($DF = 2$, $F = 21.715$, $p = 1.59 \times 10^{-5}$), with the upstream Sewell Park site having the highest catfish densities ($\bar{X} \pm 1$ SE: 0.52 ± 0.06), followed by Rio Vista Park (0.21 ± 0.04), and the San Marcos Sewage Treatment Plant site (0.02 ± 0.05) (Figure 2b

3.2 *Stream Channel Experiment*

The presence of catfish led to a significant reduction in periphyton biomass on open tiles (Table 1, Figure 3a). Nutrient addition did not significantly affect periphyton biomass on open tiles, but there was a significant nutrient × time interaction indicating that the effects of nutrients varied through time (Table 1). Neither catfish nor nutrients had a significant effect on periphyton biomass of closed tiles, although the presence of nutrients tended to increase periphyton biomass (Figure 3b). The effect was likely nonsignificant due to the high variability in chlorophyll *a* concentration on closed tiles across treatments. The presence of catfish led to a significant decrease in IM on open tiles (Table 1, Figure 3c). In addition, there was a time effect on open tile IM indicating that IM across all treatments in general declined over the first 3 sampling dates, but increased on one last sample date (Table 1, Figure 3c). The presence of catfish led to a significant increase in IM on closed tiles (Table 1, Figure 3d). The main effects of catfish and time were significant for OM on both open and closed tiles, with presence of catfish decreasing the concentration of OM (Table 1, Figure 3e and f).

Neither catfish nor nutrients had a significant effect on periphyton C:N, C:P, or N:P of open tiles, although open tile periphyton C:N and N:P significantly varied through time; periphyton C:N declined and N:P generally increased in all treatments across the experimental period (Table 1, Figures 4 a,c, and e). Due to loss of several filters and problems with laboratory analytical equipment, I excluded the first date of data for C:N, C:P, and N:P of periphyton on closed tiles from analyses. I analyzed the remaining three

sampling dates in the repeated measures ANOVA and found that closed tile periphyton C:N significantly varied through time (Table 1, Figure 4b). Again, neither catfish nor nutrients exhibited a significant effect on closed tile C:P; however the presence of catfish significantly reduced N:P on closed tiles (Table 1, Figure 4d and f).

The presence of catfish and nutrients significantly increased the rate of leaf litter decomposition in open leaf packs (Figure 5a). I also detected a significant effect of time, indicating that open leaf packs across treatments lost mass over the course of the experiment. In addition, a significant catfish × time interaction was detected because the presence of catfish caused a more precipitous decline in leaf litter mass loss. Neither the presence of catfish nor nutrients had an effect on leaf litter mass loss in closed leaf packs (Figure 5b), but there was a significant effect of time because all closed packs lost mass over the course of the experiment. The presence of catfish affected the C:N of open leaf litter, but this effect varied through the experimental period (as indicated by the significant catfish × time interaction); the presence of catfish lead to a significant increase in C:N starting about halfway through the experimental period (Figure 6a). Neither catfish nor nutrients affected closed leaf pack C:N (Figure 6b). In contrast to the effects of catfish, the presence of nutrient additions lead to significantly lower leaf litter C:P and N:P in both open and closed leaf packs, indicating the enrichment of leaf litter in P (Figure 6c-f).

Neither catfish nor nutrients had a significant effect on the rate of periphyton production; however periphyton production rates progressively increased in all treatments over the course of the experiment (Figure 7a). Neither catfish nor nutrients significantly affected pre-dawn or pre-dusk DO concentrations (Figure 7b and c). The pre-dawn DO

concentration significantly increased over the course of the experiment, as indicated by a significant time effect. However, the magnitude of this temporal increase was dependent upon the presence of catfish (i.e. a significant catfish × time interaction); by the end of the experiment, the presence of catfish lead to significantly lower pre-dawn DO concentration.

Neither catfish nor nutrients had a significant effect on water nutrient concentrations, including total nitrogen, nitrate, ammonium, total phosphorus, and SRP. However, time was a significant factor in all of the response variables (Table 1). On the third sampling date (day 46), TN precipitously decreased, but SRP and TP dramatically increased across all treatments (Figure 8). Total nitrogen, SRP, and TP returned to previous levels by the next sampling date. Ammonia concentration in all stream channels also increased on day 46, but remained elevated for approximately 2 weeks and then declined by the last sample date. The cause behind this dramatic temporal variation in nutrients across all treatments is unknown. There could have been a pulse of these nutrients from the aquifer, but a review of local precipitation data does not indicate a storm event that might be associated with such a pulse. Although the inclusion of data from this sampling date (day 46) indicates the potential for substantial spatial variation in nutrients from the supplying aquifer source, the exclusion of this date from analyses does not affect whether there are significant catfish or nutrient effects.

Periphyton Nutrient Deficiency

Periphyton growth responses on NDS on the first date (Week 4) indicated that amendments of both N and P led to a negative growth response of periphyton relative to control substrates (e.g. a negative *ln r*; Table 2, Figure 9a and b). However, there was a significant effect of the presence of nutrients on periphyton responses to N amendments and a significant effect of the presence of catfish on periphyton responses to P amendments. The presence of nutrients exacerbated the inhibition of N on periphyton growth on NDS (i.e. a greater inhibition of periphyton growth responses to N in stream channels receiving nutrient additions). In contrast, the presence of catfish lessened the inhibition of P amended periphyton growth on NDS (i.e. the presence of catfish in stream channels led to less inhibition of periphyton growth on P amended NDS). The second date (Week 9) showed negative periphyton growth response on N enriched substrates for all stream channel treatments, however there were no significant treatment effects (Figure 9a). In addition, on the second date the presence of catfish led to significant P limitation of periphyton communities (i.e. a positive growth response of periphyton on P amended NDS) (Figure 9b).

3.3 *Catfish Nutrient Excretion and Growth Responses*

At the end of the experiment, I detected no differences in the mass-specific NH_4^+ excretion rate of catfish in stream channels with and without nutrient additions (Figure 10a). However, catfish from channels with nutrient additions exhibited significantly lower mass-specific P excretion rates (Table 3, Figure 10b).

At the end of the experiment, all catfish in stream channels receiving nutrient additions and those which did not, lost mass (Table 3); however, catfish in stream channels which received nutrient additions generally lost less weight than catfish in stream channels which received no nutrients, but these differences were not significant (Figure 11a). Lipid analysis revealed greater percent lipid content in catfish in channels with nutrient additions (Figure 10b), but these differences were again nonsignificant. Nutrient ratios of catfish bodies (C:N, C:P, and N:P) did not significantly differ between stream channels receiving nutrient additions and stream channels that did not (Figure 10c-e).

4. DISCUSSION

4.1 *Habitat Associations of Catfish in the San Marcos River*

In the present study, I observed strong spatial variation in catfish densities longitudinally along the San Marcos River. The most upstream site (Sewell Park) had the greatest densities of catfish and densities progressively declined downstream. Declining catfish densities coincided with variation in several environmental characteristics; the upstream site exhibited relatively greater water depths, lower flows, smaller benthic substrates, lower percent canopy cover, and lower turbidity than downstream sites. The finding that catfish densities varied with these environmental variables is consistent with studies examining their spatial distributions in their native habitats. Power (1984) and Power et al. (1989) found densities of multiple catfish species in the Rio Frijoles (Panama) were negatively correlated with canopy cover (due to an inverse relationship between canopy cover and periphyton biomass) and water depth (due to avoidance of shallow areas and piscivorous wading birds). In addition, Power (1984) observed a preference of catfish for areas which had extensive 'ledging'; ledging is a process in which erosion undercuts the stream bank. Although I did not directly measure ledging in the present study, the bank sides of the upstream Sewell Park site are cement walls which have been extensively undercut and eroded, and catfish are frequently associated with these undercuts (C. LeBoeuf, pers. obs.). These results also indicate that the longitudinal gradient in catfish densities I observed is likely due to local variation in habitat structure

and not longitudinal variation in physiochemical characteristics of the river. Although nutrient concentrations increase from upstream to downstream due to the presence of the San Marcos Sewage Treatment Plant, other physiochemical characteristics, such as water temperature, do not spatially vary in this region of river or exhibit increased temporal variability from the most upstream to downstream sites (Groeger et al. 1997).

Contrary to predictions, catfish densities were not highest at sites with the greatest periphyton biomass. Periphyton biomass was highest at Rio Vista Park, followed by the Sewage Treatment Plant, and Sewell Park. This result contrasts with those of Power (1984) who found a positive correlation between catfish densities and periphyton productivity in the Rio Frijoles, Panama. It is important to note that I measured periphyton standing stock and not production and these two measures are not necessarily related (Wetzel 2001). In addition, I did not determine if periphyton species composition or quality varied among sites. The composition and quality of primary producers have strong effects on the abundance, biomass, and growth of grazers (Stelzer and Lamberti 2002, Sterner and Elser 2002). Mobile consumers can preferentially select higher quality diets (Cruz-Rivera and Hay 2000), and grazers seeking high-quality food resources may increase in density at sites due to movement rather than reproduction (i.e. functional rather than numerical response; Hillebrand 2002). However, catfish densities at all sites did not significantly vary over the time course of the study, therefore it is unlikely that catfish were moving among sites to select for higher quality food, at least at the scale of observation I performed (i.e. reach-level observations). In addition, Power (1984) found that individual catfish exhibit relatively high site fidelity to specific 'home pools', but re-distribute among pools in response to changes in food quality or overall pool availability.

Thus, catfish densities in the San Marcos River may respond within reach to variation in periphyton quantity or quality, but the scale of observation in the current study was too coarse to detect these responses. Finally, catfish in the San Marcos River consume mostly detritus of periphytic origin (up to 88% of catfish diets; Cohen et al. in review). Utilization of abundant detrital material may indicate that catfish are not food limited in the San Marcos River and are not functionally nor numerically responding to among site differences in algal periphyton.

4.2 *Experimental Stream Channels*

The presence of catfish generally had greater effects on ecosystem properties than nutrient additions in the stream channel experiment. Catfish significantly reduced periphyton biomass, redistributed IM and OM on benthic surfaces, and altered the rate of leaf litter decomposition. The presence of catfish had relatively small effects on periphyton and leaf pack nutrient stoichiometry, but affected the nutrient deficiency status of periphyton communities. The presence of nutrient enrichment affected leaf litter decomposition rates, but in contrast to the effects of catfish, had abundant effects on the nutrient stoichiometry of decomposing leaf litter. Although both the presence of catfish and nutrients had effects on multiple ecosystem properties and processes, I found little evidence of an interaction between these two factors.

The presence of catfish had both direct and indirect effects on multiple ecosystem characteristics which influence resource availability and habitat structure. Catfish significantly decreased periphyton on tiles they could access, and these effects are consistent with studies which have examined the effects of Loricariids (Knoll et al. 2009,

Scott et al. in review). In addition, catfish decreased IM and OM on tiles they could access, while they increased the amount of IM and decreased OM on closed tiles. Catfish consume periphyton (Cohen et al. in review) and their foraging and movements can cause benthic sediment redistribution (Power 1984, Scott et al. in review). In the present study, catfish movement and grazing cleared organic and inorganic matter from open tiles and likely redeposited IM on closed tiles.

Although the presence of catfish led to indirect effects on benthic sediment distribution and accumulation, I found no evidence that catfish indirectly affected periphyton biomass on closed tiles or periphyton production. Scott et al. (in review) observed a similar lack of indirect effects of catfish on periphyton biomass on ungrazed surfaces. Knoll et al. (2009) found that periphyton biomass on substrates inaccessible to grazing increased in the presence of the Loricariid *Ancistrus* due to its nutrient recycling via excretion; however their experiment was conducted in pool mesocosms with more still-water (lentic) conditions. The present study utilized stream channels with flow-through conditions which may have obscured more subtle, indirect effects of nutrient recycling by catfish on periphyton production. Power (1990) found that the effects of Loricariids on benthic substrates were biomass-dependent; at relatively high biomasses, catfish would deplete algal biomass, but at lower densities, catfish would enhance periphyton growth through the removal of sediments from benthic surfaces. Power (1990) only observed indirect effects at 'low' catfish densities; however catfish densities in my experiment (2 fish/m^2) were similar to catfish densities in the San Marcos River (0.25 fish/m^2).

The presence of catfish exhibited direct effects on leaf litter decomposition; inputs of terrestrial detritus are an important part of material cycling and energy flow in stream ecosystems (Wallace et al. 1997, Hall et al. 2000, Zhang et al. 2004). The presence of catfish led to significantly greater leaf litter breakdown rates in open leaf packs. These results concur with Scott et al. (in review) who suggests catfish increase fragmentation of leaf litter by directly grazing on leaf litter associated biofilms and/or through their movement on the benthos. Indeed, other species of algivorous fish, such as central stoneroller (*Campostoma anomalum*), have been shown to fragment and consume a limited amount of terrestrial detritus (Evans-White et al. 2003). The diet of Loricariid catfish in the San Marcos River also consists largely of detritus, but the detritus is of algal origin (Cohen et al. in review). In the present study, I have no reason to believe that catfish were directly consuming terrestrial OM, thus it is likely that their movements were the leading cause of leaf litter fragmentation and not direct consumption.

Contrary to predictions, the presence of catfish did not significantly affect the periphyton nutrient stoichiometry of open tiles; however the presence of catfish led to a decrease in periphyton N:P in closed tiles, indicative of an enrichment in the P content of periphyton. The lack of effects on open (grazer accessible) substrates differs from a number of other studies examining the effects of grazers on algal nutrient composition (Hillebrand et al. 2008, Scott et al. in review). Scott et al. (in review) found that the presence of armored catfish reduced periphyton C:P, C:N, and N:P on substrates which catfish had direct access to (i.e., uncaged tiles). Stoichiometric theory predicts that catfish, with their relatively high body P content, excrete dissolved nutrients at relatively high N:P, leading to depletion in periphyton P content and increased periphyton N:P

(Sterner 1990, Vanni et al. 2002, Knoll et al. 2009). Although the findings of the current study do not concur with predictions of stoichiometric theory, Hillebrand et al. (2008) similarly noted these effects. Hillebrand et al. (2008) performed a meta-analysis on the results of 119 experiments which examined the stoichiometric effects of benthic grazers on periphyton communities and found that the presence of grazers with high body P content in general decreased C:P and increased N:P of periphyton (indicating enrichment of periphyton in P). Hillebrand et al. (2008) concedes that this general trend across experiments contradicts stoichiometric predictions, but hypothesizes this trend may be the result of a complex but poorly understood interaction between grazer growth rates, flexibility in grazer body P content, and P requirements for grazer growth.

In contrast to the effects of catfish, the presence of nutrient enrichment had no effect on periphyton biomass or productivity ('green world'), but largely affected the detrital component ('brown world') of the stream food web. The presence of nutrient addition led to increased leaf litter decomposition and led to changes in leaf litter stoichiometry. These results indicate that rates of terrestrial detrital decomposition in the San Marcos River are likely nutrient limited (Cross et al. 2007) and that rates of periphyton production in the river are not as constrained by nutrient availability. In the present study, I also observed that the presence of nutrient enrichment led to significant decreases in C:P and N:P of open and closed leaf packs, but C:N of leaf litter did not respond to nutrient additions. Cross et al. (2003) similarly found decreases in leaf litter N:P and C:P in experimentally enriched streams, but leaf litter C:N did not respond to enrichment. Increased nutrient (in this case P) content of leaf litter in streams receiving nutrient additions may be attributable to increased litter-associated bacterial and fungal

biomass and production (Cross et al. 2003). In detrital systems, nutrient enrichment can reduce stoichiometric constraints on utilization of organic matter, leading to greater incorporation of these energy sources into food webs (Cross et al. 2007). The San Marcos River food web is largely algal-based C, but the results of the present study indicate that nutrient enrichment will likely lead to an increased incorporation of terrestrial detritus in the food web. In addition, these results suggest that the microbial decomposition of leaf material is likely P-limited; however, this finding is not overly surprising because the San Marcos River water tends to be relatively N-rich (~2300 DIN μg/L on average) and periphyton production tends to be P-limited (Groeger et al. 1997).

In the present study, I found that the presence of catfish had little effect on periphyton stoichiometry, but the presence of catfish affected the severity of P-limitation of periphyton communities and this effect intensified as the experiment progressed. Although there was an inhibition of periphyton growth on P-enriched NDS across all treatments on the first sampling date, periphyton growth responses on P-enriched NDS was less negative in the presence of catfish. By the second sampling date, however, the presence of catfish led to a positive growth response of periphyton communities on P-enriched NDS, indicating P-limitation of periphyton communities. These findings are in general agreement with predictions, but are not consistent with stoichiometric responses I observed in the presence of catfish (i.e. largely little to no effect on periphyton P content). Although I saw no response in periphyton C:P, periphyton C:P was >200:1 across treatments, suggesting P-limitation of periphyton communities (periphyton C:P >190:1 is generally indicative of P-limitation; Hillebrand and Sommer 1999). In the present study, it is possible that even though catfish lost weight, they sequestered enough P over the

course of the experiment to lead to an exacerbation of P limitation. However, sequestration of P into catfish may have been relatively small, so that an obvious stoichiometric response (e.g., increase in periphyton C:P in the presence of catfish) was not observable. Indeed, variation in periphyton stoichiometry within replicates of the same treatment was relatively high, which may have additionally obscured any relationship between periphyton C:P and P-limitation status. Alternately, differences between tile periphyton C:P and growth responses of periphyton on NDS may be due to differences in the algal taxa which may have differentially colonized these two different substrate types, ceramic tiles vs. glass fiber filters (Von Schiller et al. 2007). However, the likelihood of this scenario remains unknown because I did not assess differences in algal species composition between substrate types.

Periphyton growth responses were consistently negative on N-enriched NDS across all treatments, thus periphyton growth was clearly not limited by N at any point in the experiment. On the first sampling date, there was a significant effect of nutrient enrichment on inhibition of periphyton growth on N-enriched NDS, but the effect dissipated by the second sampling date. Negative periphyton growth responses on N-enriched NDS are not surprising because it is not likely that periphyton communities in the San Marcos River are limited by N and the additional N supplied in N-enriched NDS inhibited periphyton growth. Dissolved inorganic N (DIN = $NH_4^+ + NO_3^-$) in the water in stream channels (DIN = 1250 μg/L) and the San Marcos River (DIN ~2300 μg/L); Groeger et al 1997) is relatively high , indicating that DIN is likely supplied in excess of demand. Interestingly, periphyton C:N ratios across all treatments (open mean C:N = 24.1; closed mean C:N = 43:1) were at levels high enough to exhibit N-limitation (C:N

> 10 indicating N-limitation; Hillebrand and Sommer 1999). However elevated periphyton C:N in the current experiment may be due to a relatively large detrital fraction in periphyton (Frost et al. 2005) or the presence of large amounts of inorganic C (i.e., carbonates), rather than being reflective of low N content in periphyton cells.

The present study found no evidence of an interaction between the effects of catfish and nutrient additions on ecosystem properties. Other studies have found that the effects of herbivorous and benthivorous fish effects are dependent on nutrient levels (Drenner et al. 1989, Drenner et al. 1998, Flecker et al. 2002, Stelzer and Lamberti 2002, Evans-White and Lamberti 2006). However, recent meta-analyses of experiments examining the separate and interactive effects of nutrients and grazers on primary producers have found little support for a consistent interaction between these two factors (Hillebrand 2002, Gruner et al. 2008). Although primary producers can be controlled both by nutrient supply and the presence of grazers (Hillebrand 2002, Hillebrand et al. 2002, Gruner et al. 2008), the effects of each of these factors on primary producers can differ both spatially and temporally limiting the potential for interactive effects (Hillebrand 2002). In the present study, treatments receiving catfish were always exposed to catfish, but nutrient additions were made with slow-drip bottles on a three day interval. Thus, the addition of nutrients may be more pulsed than the presence of catfish, leading to the impacts of increased nutrient levels to be more temporally variable than the effects of catfish. In addition, periphyton assemblages may experience spatial differences in grazing pressure, leading to a lack of interaction between periphyton and grazers (Steinman 1996, Hillebrand 2002); in the present study, it is possible that catfish did not

consistently occupy and graze from all areas equally within channels, leading to spatial variability in their effects within each channel.

Catfish growth responses at the end of the stream channel experiment indicated that catfish did not have adequate food to exhibit growth over the 60-day experimental period. Catfish lost weight in both enriched and unenriched stream channels, but catfish in channels with nutrient enrichment lost less weight than in catfish in unenriched channels, although these differences were not significant. In addition, catfish in enriched channels had greater lipid content. Less mass loss and higher lipid content of catfish in enriched stream channels is likely due to increased food availability. Although I did not detect increases in periphyton production and biomass in the presence of nutrient additions, periphyton growth responses or changes in quality in response to nutrient additions may have been too small to detect, but adequate to affect catfish growth.

Catfish in nutrient enriched channels exhibited significantly lower mass-specific excretion rates of P, but mass-specific N excretion rates did not differ among catfish in enriched versus unenriched channels. These results are contradictory to findings that well-fed fishes tend to exhibit greater mass-specific nutrient excretion rates than under-fed fishes (Mather et al. 1995, Roy and Lall 2003, Glaholt and Vanni 2005). However, decreased P excretion by catfish in enriched channels may be due to allocation of nutrients (especially P) to growth. Although catfish lost weight in both enriched and unenriched stream channels, catfish in enriched lost less mass and had higher lipid content. Liess and Hillebrand (2006) found that snails in nutrient enriched conditions exhibited increased P retention due to higher growth rates and RNA production. Thus, it is possible that catfish in enriched channels were able to allocate more P to growth (albeit

not much) than catfish in unenriched channels, leading to significantly lower mass-specific P excretion rates. A finding of increased P retention in catfish also supports my hypothesis that P accumulation or retention in catfish led to increased periphyton community P-limitation.

4.3 *Conclusions and Implications for Invasive Species Management in the San Marcos River*

Past studies have found that increased nutrients may contribute to the success and establishment of invasive species in ecosystems (Vitousek et al. 1997, Davis et al. 2000, Thompson et al. 2001, Romanuk and Kolasa 2005). Although nutrient enrichment affected some aspects of catfish growth and condition in the stream channel experiment, data from the field survey portion of this study did not find that catfish densities were higher at more enriched sites in the San Marcos River. Therefore, the results from this study suggest that the influence of increased enrichment and productivity on the densities and biomass of invasive herbivores may not be particularly strong when food is not likely to be limiting and local abiotic habitat conditions have a greater effect on the distributions and abundance of the invasive species in question.

This study additionally lends support to a growing body of evidence that, while both nutrients and grazers are fundamentally important in structuring primary producer communities, the interaction of these two factors is less common than once thought (Hillebrand 2002, Gruner et al. 2008). In the present study, the effects of nutrient additions were largely limited to the detrital portion of the food web, but the effects of invasive catfish were more far-reaching, affecting periphyton biomass, benthic sediment distribution, rates of terrestrial OM decomposition, and the nutrient limitation status of

periphyton communities. These results imply that the invasion of catfish has much greater implications for the dynamic San Marcos River ecosystem than nutrient enrichment, at least at the levels used in this study. Ecologists have identified invasive species as one of the most substantial threats to the integrity of aquatic ecosystems (Sala et al. 2000) and the presence of suckermouth catfish in the San Marcos River has the potential to disrupt primary productivity, trophic flows, nutrient dynamics, and habitat quality and quantity in the river (Cohen et al. in review, Scott et al in review, this study). Future population control efforts for suckermouth catfish in the San Marcos River system are clearly required.

Table 1. Two-way, repeated measures ANOVA summary statistics for the effects of catfish and nutrients on various response variables in the stream channel experiment.

Response	Effect	df_n	df_d	F	p
Tile Chlorophyll *a*					
Open	(Intercept)	1	45	1292.163	<.0001
	date	3	45	2.5707	0.0659
	catfish	1	16	93.1075	<.0001
	nutrients	1	16	0.2544	0.6209
	date × catfish	3	45	0.2607	0.8533
	date × nutrients	3	45	4.9965	0.0045
	catfish × nutrients	1	16	0.1446	0.7088
	date × catfish × nutrients	3	45	1.6705	0.1868
Closed	(Intercept)	1	46	473.5994	<.0001
	date	3	46	2.1176	0.1109
	catfish	1	16	0.9892	0.3347
	nutrients	1	16	0.2534	0.6216
	date × catfish	3	46	1.1469	0.3403
	date × nutrients	3	46	0.9832	0.409
	catfish × nutrients	1	16	0.7846	0.3888
	date × catfish × nutrients	3	46	1.2824	0.2916
Tile IM					
Open	(Intercept)	1	41	641.8332	<.0001
	date	3	41	4.3239	0.0097
	catfish	1	16	18.2187	0.0006
	nutrients	1	16	0.8271	0.3766
	date × catfish	3	41	1.2728	0.2964
	date × nutrients	3	41	0.9651	0.4184
	catfish × nutrients	1	16	0.4165	0.5278
	date × catfish × nutrients	3	41	0.8341	0.4829
Closed	(Intercept)	1	47	95.48151	<.0001
	date	3	47	1.07526	0.3687
	catfish	1	16	53.41543	<.0001
	nutrients	1	16	0.00273	0.959
	date × catfish	3	47	0.86092	0.468
	date × nutrients	3	47	1.48483	0.2308
	catfish × nutrients	1	16	0.20589	0.6561
	date × catfish × nutrients	3	47	0.14088	0.935

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
Tile OM					
Open	(Intercept)	1	42	2192.727	<.0001
	date	3	42	3.8421	0.0162
	catfish	1	16	21.3272	0.0003
	nutrients	1	16	0.1563	0.6978
	date × catfish	3	42	0.3756	0.7711
	date × nutrients	3	42	0.0909	0.9647
	catfish × nutrients	1	16	0.4336	0.5196
	date × catfish × nutrients	3	42	1.2207	0.3141
Closed	(Intercept)	1	46	661.0482	<.0001
	date	3	46	6.2443	0.0012
	catfish	1	16	177.8609	<.0001
	nutrients	1	16	0.6716	0.4245
	date × catfish	3	46	1.1848	0.3259
	date × nutrients	3	46	0.8918	0.4526
	catfish × nutrients	1	16	0.3604	0.5567
	date × catfish × nutrients	3	46	0.3238	0.8081
Tile Nutrient Ratios					
Open C:N	(Intercept)	1	39	119.6671	<.0001
	date	3	39	4.97134	0.0051
	catfish	1	16	0.11218	0.742
	nutrients	1	16	0.71394	0.4106
	date × catfish	3	39	1.27969	0.2948
	date × nutrients	3	39	0.27703	0.8416
	catfish × nutrients	1	16	0.00066	0.9799
	date × catfish × nutrients	3	39	0.07177	0.9747
Open C:P	(Intercept)	1	39	1556.795	<.0001
	date	3	39	2.0377	0.1244
	catfish	1	16	1.0964	0.3106
	nutrients	1	16	0.2956	0.5941
	date × catfish	3	39	0.4638	0.7092
	date × nutrients	3	39	0.2191	0.8825
	catfish × nutrients	1	16	0.5831	0.4562
	date × catfish × nutrients	3	39	0.6039	0.6164

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
Open N:P	(Intercept)	1	39	307.2565	<.0001
	date	3	39	5.22049	0.004
	catfish	1	16	0.9138	0.3533
	nutrients	1	16	0.87114	0.3645
	date × catfish	3	39	0.25817	0.855
	date × nutrients	3	39	0.31959	0.8111
	catfish × nutrients	1	16	0.4019	0.5351
	date × catfish × nutrients	3	39	0.49751	0.6862
Closed C:N	(Intercept)	1	29	74.73562	<.0001
	date	2	29	10.27389	0.0004
	catfish	1	16	1.67047	0.2146
	nutrients	1	16	0.00771	0.9311
	date × catfish	2	29	0.43967	0.6485
	date × nutrients	2	29	0.02659	0.9738
	catfish × nutrients	1	16	0.25287	0.6219
	date × catfish × nutrients	2	29	0.19922	0.8205
Closed C:P	(Intercept)	1	29	144.7599	<.0001
	date	2	29	0.92116	0.4094
	catfish	1	16	2.12926	0.1639
	nutrients	1	16	1.05931	0.3187
	date × catfish	2	29	2.72148	0.0826
	date × nutrients	2	29	1.67171	0.2055
	catfish × nutrients	1	16	0.81335	0.3805
	date × catfish × nutrients	2	29	1.56892	0.2254
Closed N:P	(Intercept)	1	29	118.3882	<.0001
	date	2	29	1.88305	0.1703
	catfish	1	16	16.74162	0.0009
	nutrients	1	16	3.35798	0.0856
	date × catfish	2	29	1.06423	0.3581
	date × nutrients	2	29	1.93763	0.1622
	catfish × nutrients	1	16	1.53556	0.2331
	date × catfish × nutrients	2	29	0.97605	0.3888

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
Leaf Pack CPOM					
open	(Intercept)	1	57	1205.148	<.0001
	date	4	57	38.6373	<.0001
	catfish	1	16	114.0102	<.0001
	nutrients	1	16	4.4517	0.051
	date × catfish	4	57	5.1109	0.0014
	date × nutrients	4	57	0.0678	0.9913
	catfish × nutrients	1	16	0.4562	0.5091
	date × catfish × nutrients	4	57	1.3251	0.2717
closed	(Intercept)	1	62	1462.037	<.0001
	date	4	62	5.8193	0.0005
	catfish	1	16	4.0009	0.0627
	nutrients	1	16	0.5761	0.4589
	date × catfish	4	62	0.3235	0.8612
	date × nutrients	4	62	0.7028	0.593
	catfish × nutrients	1	16	0.6302	0.4389
	date × catfish × nutrients	4	62	0.6441	0.6331
Leaf Pack Nutrient Ratios					
open C:N	(Intercept)	1	61	6951.908	<.0001
	date	4	61	2.819	0.0326
	catfish	1	16	6.492	0.0215
	nutrients	1	16	2.807	0.1133
	date × catfish	4	61	5.165	0.0012
	date × nutrients	4	61	0.848	0.5004
	catfish × nutrients	1	16	1.488	0.2402
	date × catfish × nutrients	4	61	0.598	0.6656
open C:P	(Intercept)	1	61	394.9893	<.0001
	date	4	61	6.3803	0.0002
	catfish	1	16	1.0504	0.3207
	nutrients	1	16	7.8956	0.0126
	date × catfish	4	61	0.7578	0.5568
	date × nutrients	4	61	0.2649	0.8994
	catfish × nutrients	1	16	0.5398	0.4731
	date × catfish × nutrients	4	61	0.5445	0.7037

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
open N:P	(Intercept)	1	61	469.5707	<.0001
	date	4	61	7.7014	<.0001
	catfish	1	16	0.1714	0.6844
	nutrients	1	16	7.6016	0.014
	date × catfish	4	61	0.7012	0.5941
	date × nutrients	4	61	0.3655	0.8323
	catfish × nutrients	1	16	0.1793	0.6776
	date × catfish × nutrients	4	61	0.4962	0.7385
closed C:N	(Intercept)	1	61	6021.819	<.0001
	date	4	61	1.826	0.1354
	catfish	1	16	1.758	0.2035
	nutrients	1	16	0.174	0.6822
	date × catfish	4	61	1.302	0.2795
	date × nutrients	4	61	0.025	0.9987
	catfish × nutrients	1	16	0.009	0.9242
	date × catfish × nutrients	4	61	0.094	0.984
closed C:P	(Intercept)	1	61	878.9575	<.0001
	date	4	61	14.3548	<.0001
	catfish	1	16	1.346	0.263
	nutrients	1	16	9.0499	0.0083
	date × catfish	4	61	1.1547	0.3397
	date × nutrients	4	61	1.3664	0.2561
	catfish × nutrients	1	16	0.5657	0.4629
	date × catfish × nutrients	4	61	0.812	0.5224
closed N:P	(Intercept)	1	61	1001.183	<.0001
	date	4	61	14.5218	<.0001
	catfish	1	16	0.2204	0.645
	nutrients	1	16	6.8444	0.0187
	date × catfish	4	61	0.7941	0.5336
	date × nutrients	4	61	1.3321	0.2683
	catfish × nutrients	1	16	0.5061	0.4871
	date × catfish × nutrients	4	61	0.4485	0.7731

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
Periphyton Production	(Intercept)	1	47	77.86731	<.0001
	date	3	47	17.45731	<.0001
	catfish	1	16	0.62396	0.4411
	nutrients	1	16	0.04022	0.8436
	date × catfish	3	47	0.29622	0.8279
	date × nutrients	3	47	1.27751	0.293
	catfish × nutrients	1	16	1.64751	0.2176
	date × catfish × nutrients	3	47	0.44424	0.7225
Community Metabolism					
pre-dawn	(Intercept)	1	32	323.054	<.0001
	date	2	32	59.8739	<.0001
	catfish	1	16	2.1856	0.1587
	nutrients	1	16	1.3381	0.2643
	date × catfish	2	32	4.0592	0.0268
	date × nutrients	2	32	1.9177	0.1634
	catfish × nutrients	1	16	0.0063	0.9376
	date × catfish × nutrients	2	32	0.4195	0.6609
pre-dusk	(Intercept)	1	32	1737.185	<.0001
	date	2	32	0.0411	0.9598
	catfish	1	16	0.028	0.8691
	nutrients	1	16	0.5293	0.4774
	date × catfish	2	32	1.4308	0.254
	date × nutrients	2	32	1.7106	0.1969
	catfish × nutrients	1	16	0.1694	0.6861
	date × catfish × nutrients	2	32	0.5562	0.5789

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
Water Column Nutrients					
nitrates	(Intercept)	1	64	88297.01	<.0001
	date	4	64	4.53	0.0027
	catfish	1	16	0.06	0.8163
	nutrients	1	16	0.92	0.3514
	date × catfish	4	64	0.53	0.7142
	date × nutrients	4	64	1.22	0.3113
	catfish × nutrients	1	16	2.37	0.1431
	date × catfish × nutrients	4	64	0.46	0.7632
total nitrogen	(Intercept)	1	64	3741.286	<.0001
	date	4	64	15.018	<.0001
	catfish	1	16	3.134	0.0957
	nutrients	1	16	0.248	0.625
	date × catfish	4	64	1.85	0.1301
	date × nutrients	4	64	0.044	0.9963
	catfish × nutrients	1	16	0.74	0.4025
	date × catfish × nutrients	4	64	0.466	0.7602
ammonium	(Intercept)	1	64	158.422	<.0001
	date	4	64	8.74372	<.0001
	catfish	1	16	0.34658	0.5643
	nutrients	1	16	0.13732	0.7158
	date × catfish	4	64	0.09469	0.9838
	date × nutrients	4	64	0.35905	0.8368
	catfish × nutrients	1	16	1.04439	0.322
	date × catfish × nutrients	4	64	0.32045	0.8633
SRP	(Intercept)	1	63	601.6264	<.0001
	date	4	63	299.4466	<.0001
	catfish	1	16	1.4575	0.2449
	nutrients	1	16	0.2512	0.6231
	date × catfish	4	63	0.233	0.9188
	date × nutrients	4	63	0.7398	0.5684
	catfish × nutrients	1	16	0.0022	0.9633
	date × catfish × nutrients	4	63	0.3598	0.8363

Table 1 (continued).

Response	Effect	df_n	df_d	F	p
total phosphorus	(Intercept)	1	64	793.4213	<.0001
	date	4	64	265.4609	<.0001
	catfish	1	16	0.0226	0.8825
	nutrients	1	16	1.9932	0.1772
	date × catfish	4	64	0.2942	0.8807
	date × nutrients	4	64	2.3429	0.0642
	catfish × nutrients	1	16	0.9798	0.337
	date × catfish × nutrients	4	64	1.0546	0.3863

Table 2. Two-way ANOVA summary statistics for the effects of catfish and nutrients on periphyton nutrient deficiency. Dates were analyzed separately.

Response	Effect	*df*	*F*	*p*
First Date				
N	nutrients	1	6.5759	0.02079
	catfish	1	0.8489	0.37055
	nutrients × catfish	1	0.0044	0.94775
	Residuals	16		
P	nutrients	1	0.6464	0.433195
	catfish	1	13.7529	0.001908
	nutrients × catfish	1	0.1529	0.700904
	Residuals	16		
Second Date				
N	nutrients	1	0.0625	0.8058
	catfish	1	0.1801	0.6769
	nutrients × catfish	1	0.012	0.9143
	Residuals	16		
P	nutrients	1	0.3357	0.57039
	catfish	1	8.2764	0.01095
	nutrients × catfish	1	0.0168	0.89839
	Residuals	16		

Table 3. T-test summary statistics for the effects of nutrient enrichment on catfish.

Response	*df*	*t*	*p*
NH_4^+	5.375	-0.1318	0.9
SRP	6.395	-2.6423	0.03619
final vs initial weight	29	6.8442	1.619×10^{-7}
mass loss	7.792	1.739	0.1212
% lipid	7.738	1.3453	0.2166
C:N	5.113	1.1701	0.2936
C:P	7.986	0.4441	0.6687
N:P	7.977	2.24E-01	0.828

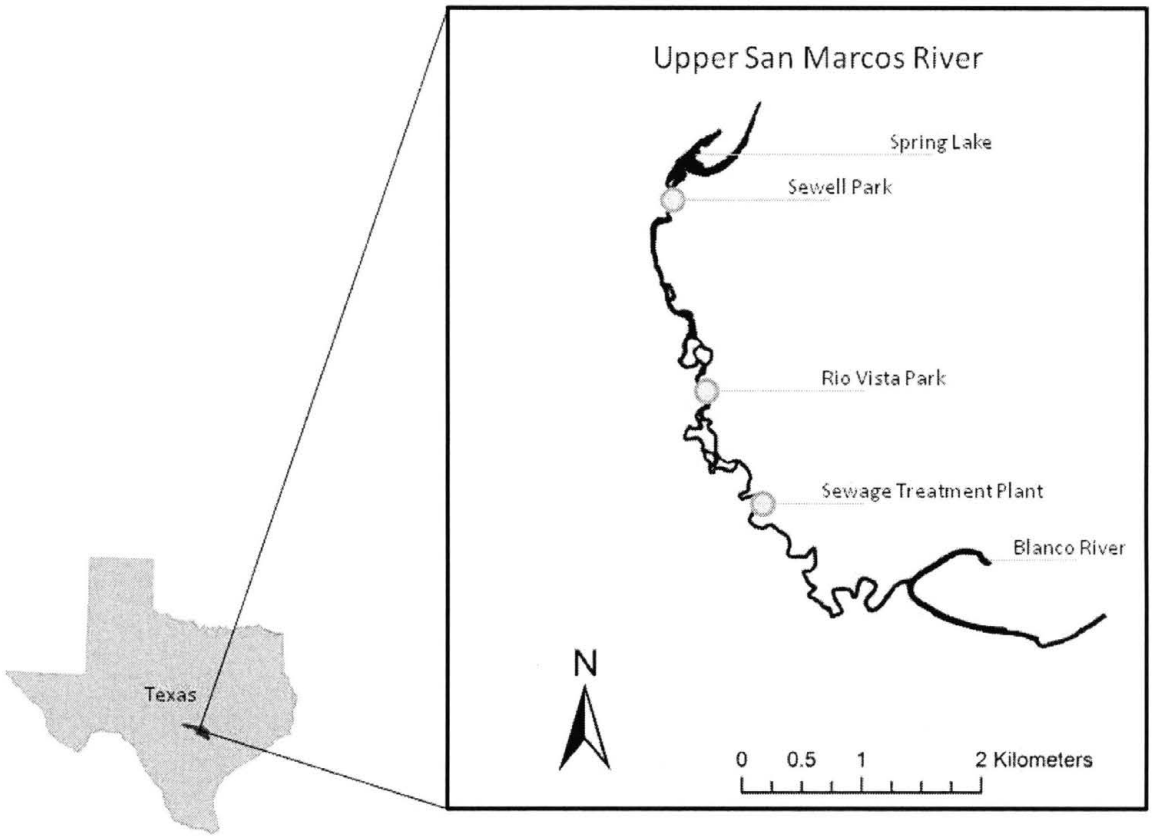

Figure 1. Map of the upper portion of the San Marcos River indicating the three sites for the catfish habitat association study.

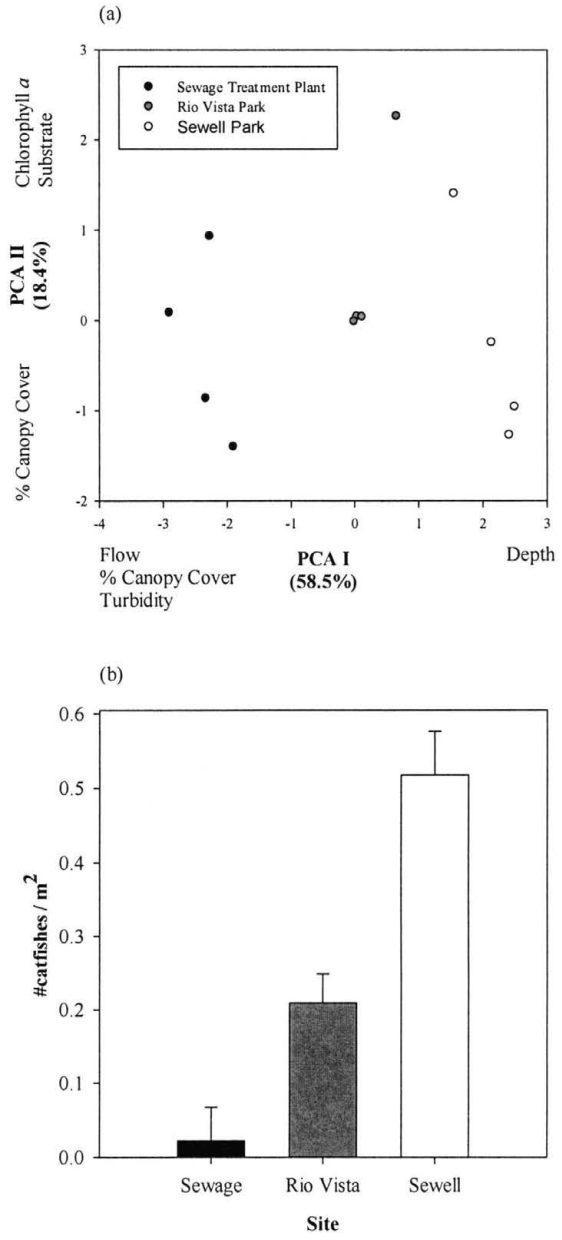

Figure 2. (a) Principal component analysis habitat plots of PC axes I and II for three sites on the San Marcos River. Variables were averaged by site for each season. (b) Snorkel surveys of *Hypostomus* catfish in the San Marcos River. Number of catfishes per unit area were averaged over sampling date by site.

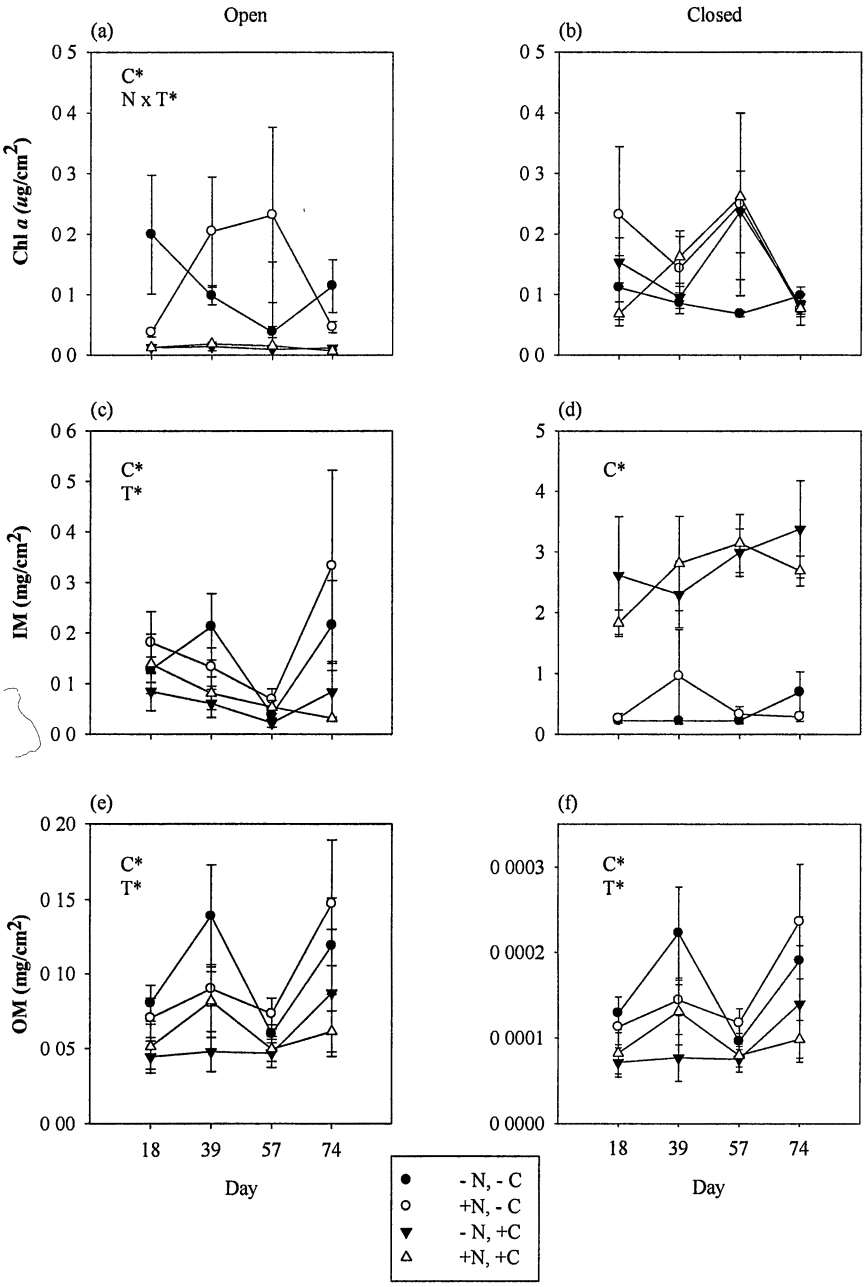

Figure 3. Responses of (A-F) open (accessible to catfish) and closed (inaccessible) tiles to the effects of nutrient enrichment and catfish presence over time. Note differences in scale of the *y*-axes. Only significant effects of each factor and interaction term are indicated on the graphs for each response variable. Error bars are ± 1 SE.

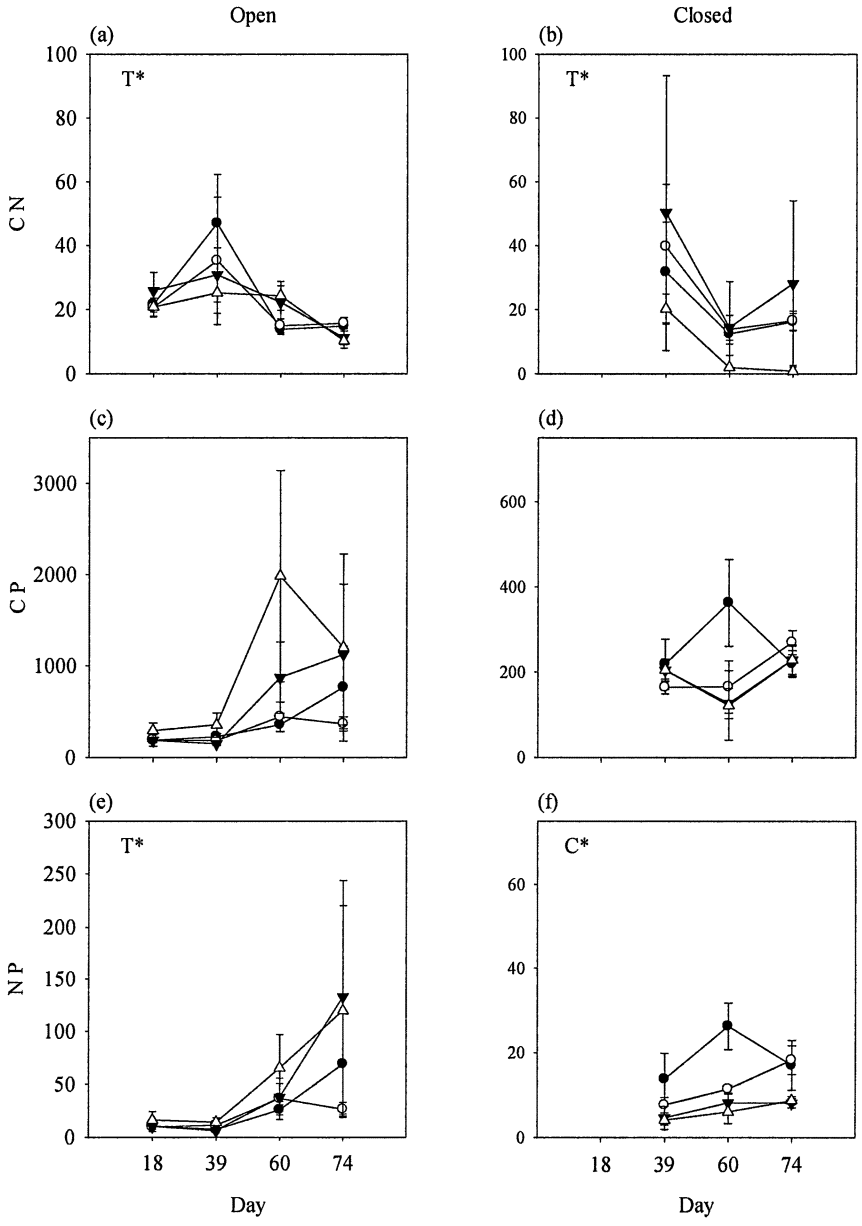

Figure 4. Responses of C:N, C:P, and N:P of periphyton on open (a, c, e) and closed (b, d, f) tiles to the effects of nutrient enrichment and presence of catfish over time. Legend corresponds to Figure 3. Note differences in scale of the *y*-axes. Due to problems with laboratory equipment, the first date for the closed tiles had to be excluded from analysis. Error bars are ± 1 SE. Only significant effects are indicated on the graphs.

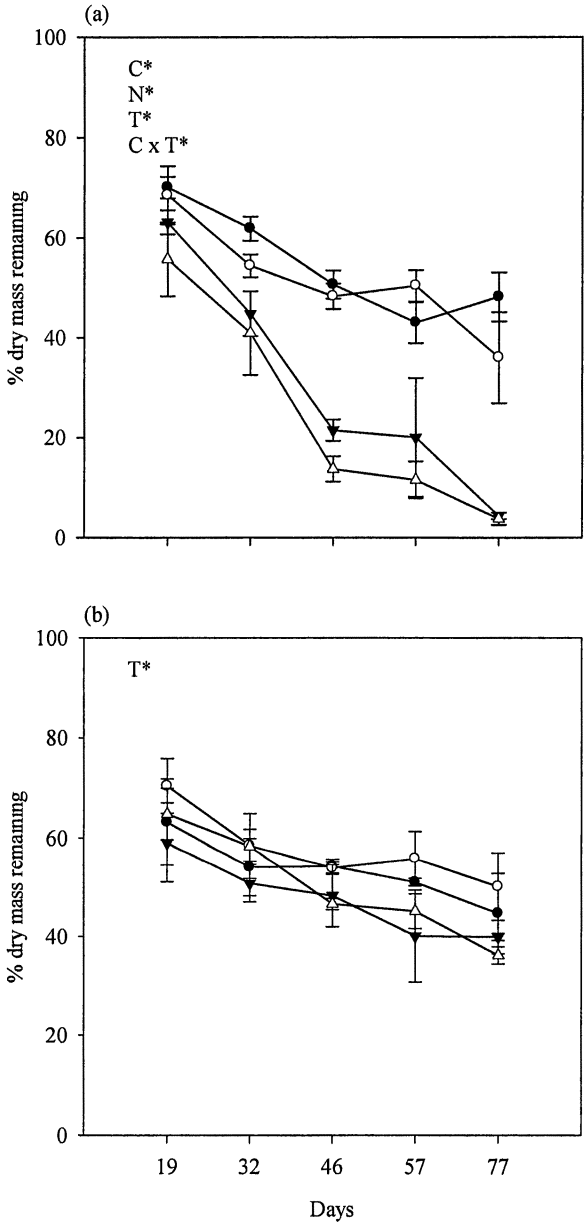

Figure 5. Percent mass remaining of (a) open and (b) closed leaf coarse particulate organic matter. Legend corresponds to Figure 3. Only significant effects of each factor and interaction terms are indicated in the graphs. Error bars are ±1 SE.

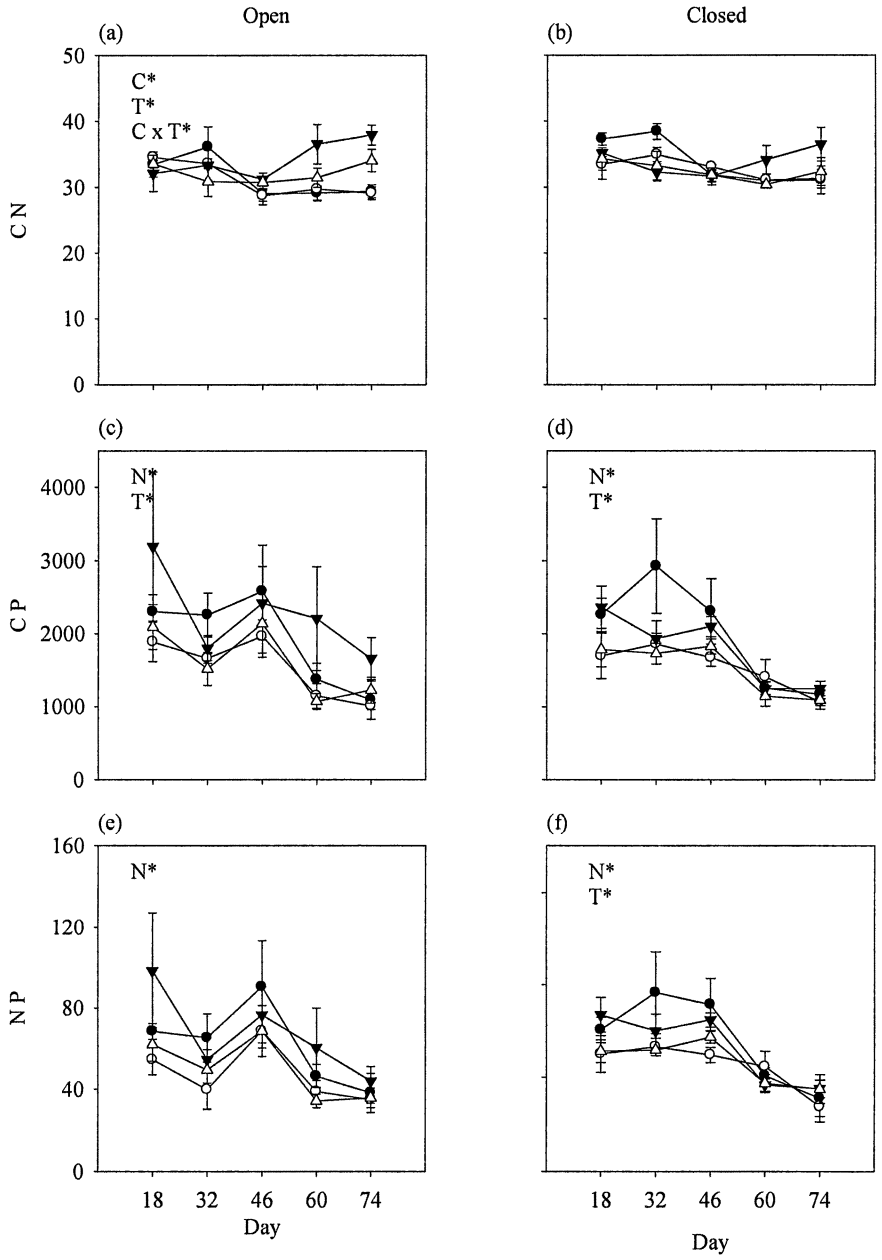

Figure 6. Responses of leaf litter C:N, C:P, and N:P in open (a, c, e) and closed (b, d, f) leaf packs to the effects of nutrient enrichment and presence of catfish over time. Legend corresponds to Figure 3. Only significant effects are indicated in graphs. Error bars are ± 1 SE.

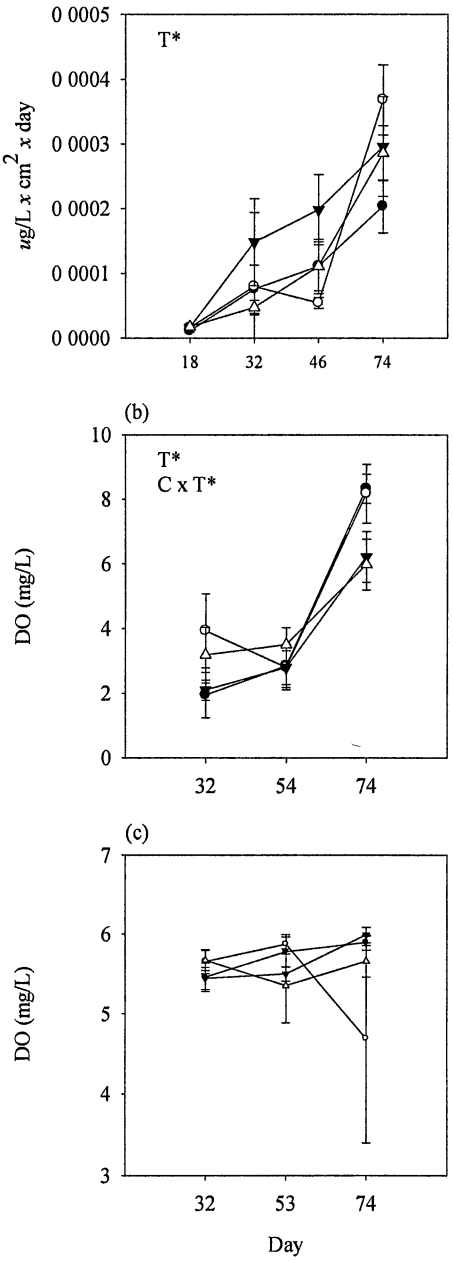

Figure 7. (a) Periphyton production on floating glass slides, (b) pre-dawn community metabolism, and (c) pre-dusk community metabolism. Legend corresponds on Figure 3. Only significant effects are shown in graphs. Error bars indicated ±1 SE.

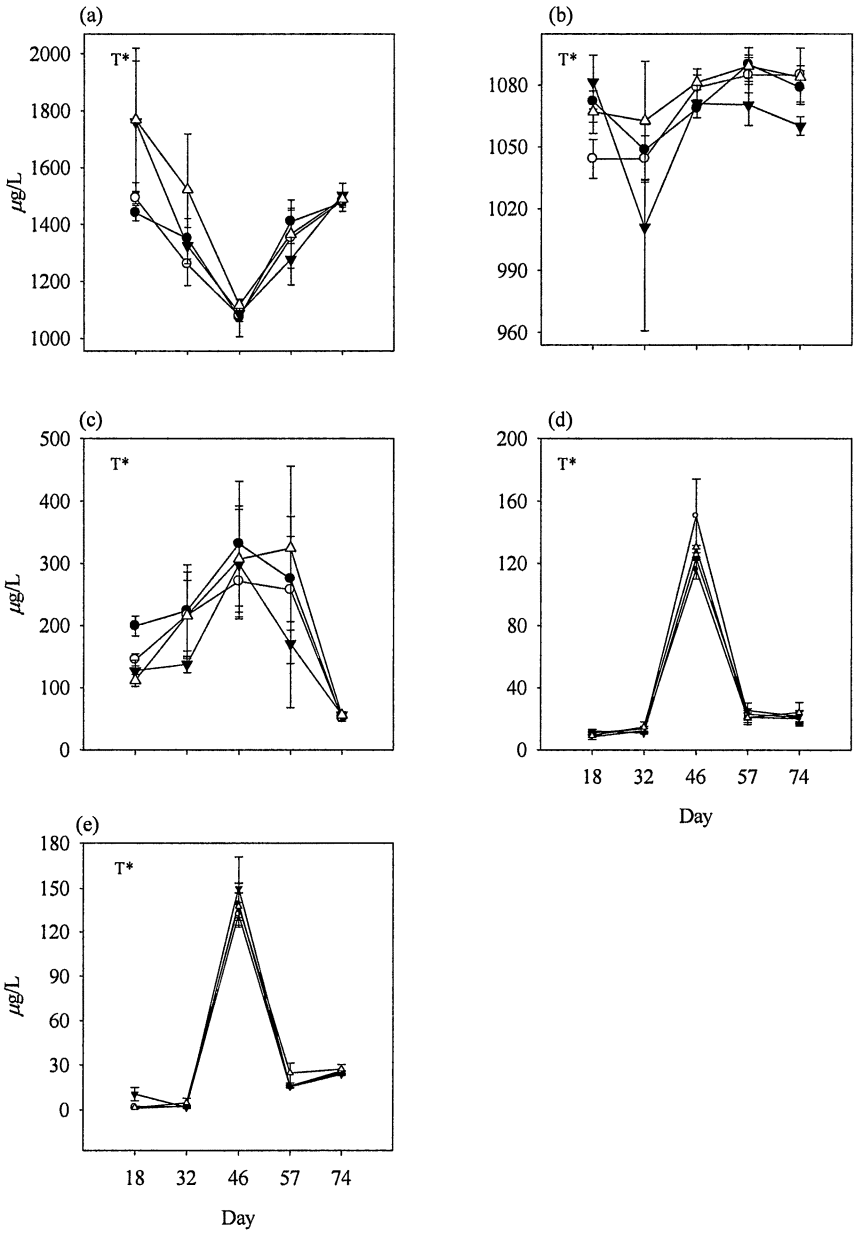

Figure 8. Water column nutrients: (a) TN, (b) NO_3^-, (c) NH_4^+, (d) TP, and (e) SRP. Legend corresponds to Figure 3. Please note differences of scale of *y*-axes. The September 1 sample date showed an anomaly in the data that can possibly be accounted for by a pulse of nutrients from the aquifer. Error bars are ± 1 SE.

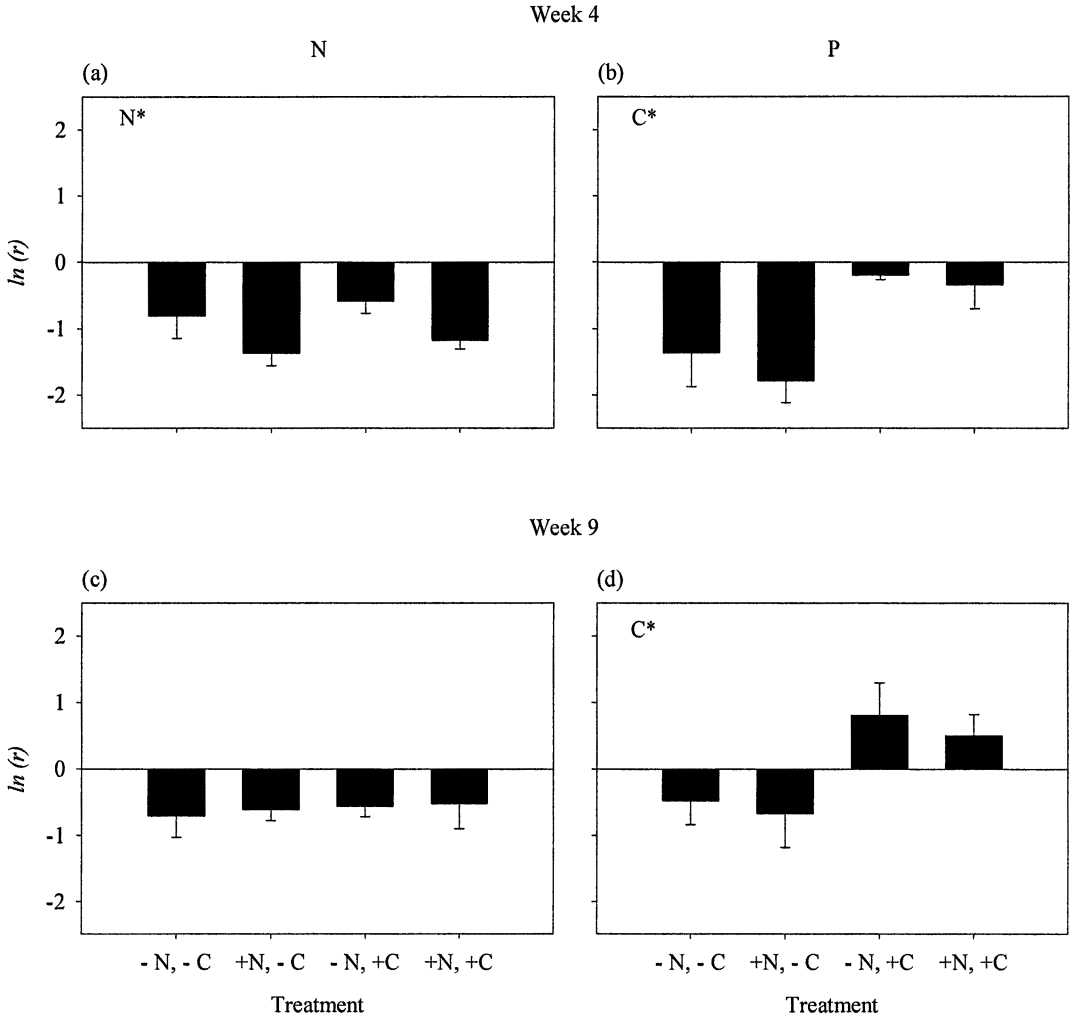

Figure 9. Periphyton Nutrient Deficiency. (a, c) N enrichment, (b, d) P enrichment. Only significant effects are shown. Error bars are ± 1 SE.

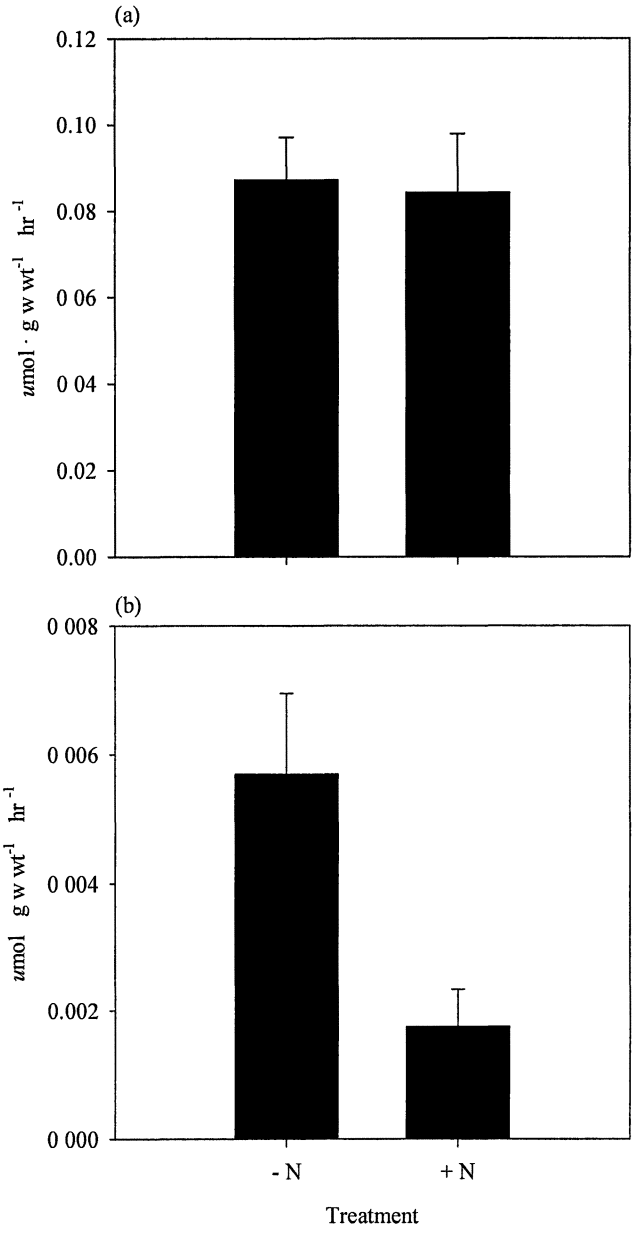

Figure 10. Excretion rate of NH_4^+ (a) and PO_4^{3-} (b) of catfish at end of the experiment. Error bars are ± 1 SE.

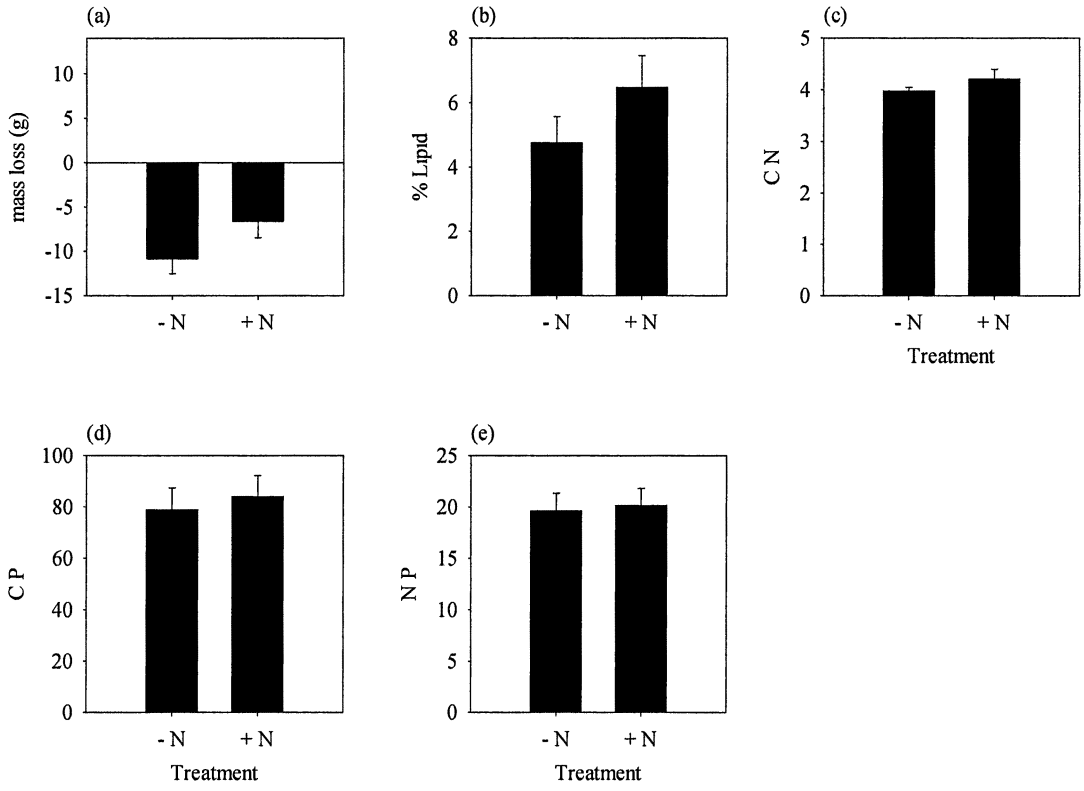

Figure 11. Responses of catfish to nutrient enrichment presence. Catfishes body nutrient ratios of C:N, C:P, and N:P (a-c). Catfishes % body lipid content (d), and catfishes weightloss (e).

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VITA

Crystal LeBoeuf attended The University of Texas at Austin where she received the degree of Bachelor of Science in Biology (Ecology, Evolution, and Behavior) in December 2007. During the pursuit of her undergraduate degree, she developed an interest in bats and other cave fauna. She became certified in bat conservation and management and volunteered for the rehabilitation and care of ill and injured bats. Her interest in caves led her to an internship and ultimately employment at Zara Environmental, L.L.C. There she shifted her focus to hydrogeology and biological issues related to water. In January 2009, she entered the Aquatic Resources Graduate Program at Texas State University-San Marcos. Since her time at Texas State, she has taught laboratory courses in Modern Biology for non-majors students and Organismal Biology for majors students.

Permanent Address: 300 Mockingbird Lane
Austin, TX 78745

This thesis was typed by Crystal LeBoeuf