

# Effects of native and invasive species on stream ecosystem functioning

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**Abstract** Native consumers play a vital role in maintaining ecosystem functioning, but species invasion may alter these processes. We hypothesized that the individual effects of large-bodied native and invasive consumers on ecosystem functioning and invertebrate community assemblages differ from the interactive effects. In the San Marcos River (Texas, USA), big claw river shrimp (*Macrobrachium carolinense*, Decapoda: Palaemonidae) is a large-bodied native freshwater shrimp species with low abundance, and armored catfish (*Hypostomus plecostomus*, Loricariidae) is an abundant, large-bodied invasive species. To examine natural distribution of these consumers, we conducted repeated field surveys of the river. Catfish had a wide range of distribution with high densities in the river, while shrimp with low densities had a patchy distribution in the open areas adjacent to openings and crevices. To investigate their individual and interactive effects, we performed a  $2 \times 2$  factorial mesocosm stream channel experiment cross-classifying the presence and absence of catfish and shrimp for assessing their effects on ecosystem engineering and ecosystem functioning. Presence of invasive catfishes in mesocosms showed a significant influence on ecosystem functioning by decreasing periphyton biomass, altering periphyton nutrient ratios, and facilitating detrital decomposition. Catfish presence altered invertebrate community composition in leaf packs and produced

ecosystem engineering effects by altering benthic habitat. The native big claw river shrimp had little effect on ecosystem functioning in mesocosms, but its presence appeared to mitigate the effects of catfish on periphyton and sediments. Our results suggest that native consumers can have the ability to mitigate the effects of invasive taxa, thus conservation of native species is critical to the preservation of ecosystem functioning in stream ecosystems.

**Keywords** Ecosystem engineers · Big claw river shrimp · Armored catfish · Community · River

## Introduction

Ecosystem functioning is linked to community composition and the functional roles of taxa (Covich et al. 2004; Zhang et al. 2004). Organisms which modify habitat structure and affect resource availability through mechanical and physiochemical alteration of resource materials and/or habitats are referred to as allogenic ecosystem engineers (Jones et al. 1994; Gutierrez and Jones 2006). In many ecosystems, native taxa often function as ecosystem engineers, playing critical roles influencing ecosystem functioning such as production, decomposition, and nutrient cycling (Webster and Benfield 1986; Vanni et al. 1997; McIntyre et al. 2007). Invasive species, often in competition with native species (Olsson et al. 2009), also alter ecosystem properties and habitat characteristics (Vitousek 1990; Parker et al. 1999; Crooks 2002; Atkinson et al. 2010). The individual effects of native and non-native ecosystem engineers on resource availability and ecosystem functioning have been widely investigated (Moore 2006), but relatively few studies have investigated interactions between native and invasive ecosystem engineers

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coexisting in the same ecosystems (but see Berkenbusch et al. 2007; Gribben et al. 2009). Thus, it is unclear how effects of native and invasive ecosystem engineers may be altered by each other.

Riverine ecosystems often support diverse assemblages of native organisms (Malmqvist 2002). However, populations of native taxa are declining from multiple anthropogenic disturbances (Dudgeon et al. 2006), including the establishment of invasive species (Lodge et al. 1998; Mooney and Hobbs 2000). Spring-fed river ecosystems are particularly relevant systems to examine the individual and interactive effects of native and invasive species on ecosystem functioning because hydrological and physiochemical constancy of these systems has led to the evolution of endemic spring-adapted taxa with limited geographic ranges (Hubbs 1995). This constancy in physiochemical conditions also makes spring-fed ecosystems highly susceptible to invasion by non-native taxa (Moyle and Light 1996).

Here, we present a study examining a native and an invasive species in the spring-fed San Marcos River (Texas, USA): the native big claw river shrimp (*Macrobrachium carolinense*, Decapoda: Palaemonidae; hereafter referred to as shrimp) and the invasive suckermouth catfish (*Hypostomus plecostomus*, Loricariidae; hereafter referred to as catfish or armored catfish). Big claw river shrimp are amphidromous and widely distributed throughout the Caribbean and the Gulf of Mexico, in which the northern end of their geographic range is in the San Marcos River (Bowles et al. 2000). Shrimp populations in the upper San Marcos River currently exhibit low densities, but these arthropods historically exhibited high abundances in the river (Bowles et al. 2000). Shrimp migrate over 320 km and cross multiple low-head dams ranging from approximately 1–4 m in height to reach the headwaters of the San Marcos River. Armored catfish, native to South America, have been introduced via the aquarium trade into subtropical and spring-fed ecosystems across North America (Nico and Martin 2001) and have been in the San Marcos River since the late 1990s (Perkin et al. 2010). Previous studies have compared the impacts of stream grazing fishes and macroarthropods relating to consumer biomass or identity (Bengston et al. 2008; Ludlam and Magoulick 2010), but this study examined the individual and combined effects of these consumers on stream ecosystem processes.

Macroarthropods play important roles in nutrient cycling, sediment transport, and organic matter processing in streams (Covich et al. 2004). Big claw river shrimp are large-bodied (up to 1 kg wet weight) omnivores (Bowles et al. 2000), which eat small fish, leaf litter, mollusks, and invertebrates (Crowl et al. 2001), and can be top predators in some streams (Covich et al. 1996). Loricariid catfishes

are efficient algivores and can increase sediment transport and turbidity through foraging and burrowing activities (Power 1984). Catfishes have relatively high body P content (high %P by mass) due to their bony armor plates containing Ca-PO<sub>4</sub>, and their growth can be P-limited when P is low in algae (Hood et al. 2005). Catfishes consuming algae with C:P ratios higher than their body C:P (e.g., a stoichiometrically imbalanced diet) can affect nutrient cycling, resource availability and quality (Sterner and Elser 2002; Knoll et al. 2009). Although catfish and shrimp have the potential to affect community and ecosystem functioning, the degree of diet overlap between big claw shrimp and armored catfish is likely to be limited.

We had two goals in this study: (1) examine the distribution of invasive armored catfish and native big claw river shrimp in the upper San Marcos River, and (2) examine the effects of catfish and shrimp on ecosystem functioning and benthic communities in stream mesocosms. We predicted that catfish are abundant and widespread distributed throughout the upper San Marcos River and that shrimp are relatively rare and exhibit a more patchy distribution. We tested the hypothesis that native and non-native consumers differently influence ecosystem functioning and invertebrate community composition and that the effect of each consumer will be modified by the other consumer species. We predicted that herbivorous catfish will reduce periphyton biomass, increase sediment transport and alter periphyton nutrient ratios (i.e., algal C:P and N:P). Specifically, we predicted that (1) catfish presence will lead to a depletion of P in periphyton (e.g., higher algal C:P and N:P) due to their low mass-specific P excretion rates; (2) shrimp presence will increase leaf litter decomposition, sediment transport, and alter invertebrate community composition; and (3) shrimp presence will mitigate the effects of catfish on ecosystem function and nutrient dynamics through antagonistic interactions and interference associated with its predatory tendencies.

## Materials and methods

### Study area

The San Marcos River is located along the Balcones Escarpment in central Texas, USA and is characterized by clear water, abundant macrophytes, and little temporal variation in temperature (~22 °C), flow, and water quality (Groeger et al. 1997). Like many spring-fed river systems in the western US, the San Marcos River is habitat for multiple endemic and endangered species (USFWS 1996; Bowles et al. 2000). Water from the Edwards Aquifer emerges in a small wetland area (Spring Lake) and subsequently creates the upper San Marcos River. Water in the

upper portion of the river is relatively elevated in N, almost exclusively in the form of  $\text{NO}_3^{2-}$ , with concentrations  $\sim 1,600 \mu\text{g/L}$ . In contrast, total P concentrations are much lower with  $\text{PO}_4^{3-}$  being the dominant form;  $\text{PO}_4^{3-}$  ranges from 10 to 30  $\mu\text{g/L}$ . TN:TP ratios ( $\sim 220:1$  by moles) and bioassays suggest that river algal communities are P-limited (Groeger et al. 1997).

### Field surveys

Monthly nighttime snorkel surveys were performed to determine and quantify longitudinal patterns of shrimp and catfish populations at two sites in the upper spring-influenced portion of the river. Preliminary observations indicated that both species were most active at night and that densities and behavioral differences between the two species necessitated different survey methods. Catfish surveys were determined with snorkel survey counts using dive lights, by swimming five cross-river transects at two sites in the upper San Marcos River. The upstream site was located just below the river headwaters and the downstream site was located approximately 1.2 km downstream. On each count occasion, five divers swam along each transect at a reach and counted catfish within a 1 m area along each transect line. Catfish were grouped into three size classes:  $<10$  cm total length (TL), 10–40 cm TL, and  $>40$  cm TL. Catfish surveys were conducted monthly from May to October 2008, and from April to May 2009.

Shrimp are rare in the river and often observed in rocky crevices, but occasionally observed in the main channel. In addition, shrimp were frequently observed under the full moon, which is consistent to the movement pattern of other freshwater migratory macroarthropods (Kikkert et al. 2009). Due to low densities of shrimp, we did not limit our searches to 50-m reaches within each site, but instead performed counts of all shrimp observed in each larger section of the river. Searches were performed on a monthly basis from April to November 2008 and from April to July 2009, typically on nights of or within 1–2 days of the full moon. Snorkelers divided the search area into approximately equal sections and searched the open channel, all openings and crevices, and macrophyte stands with dive lights for shrimp. Counts at a site typically lasted for 1–2 h. Shrimp were enumerated and categorized as adult ( $>13$  cm) or juvenile ( $<13$  cm).

### Stream channel experiment

We investigated the effects of shrimp and catfish in a replicated stream-channel experiment, which consisted of a  $2 \times 2$  factorial design in which the presence and absence of shrimp was cross-classified with the presence and absence of armored catfish. The design consisted of the

following treatment combinations: a control (catfish absent and shrimp absent;  $-C, -S$ ), catfish present (catfish present and shrimp absent;  $+C, -S$ ), shrimp present (catfish absent and shrimp present;  $-C, +S$ ), and catfish and shrimp present ( $+C, +S$ ). Shrimp presence treatments consisted of one shrimp and catfish presence treatments consisted of two catfish. Due to the low densities of shrimp and its conservation status (e.g., high priority status by the Texas Parks and Wildlife Comprehensive Wildlife Conservation Strategy), we limited the number of replicates of each treatment to four. Experimental mesocosms, such as artificial stream channels are frequently used and appropriate model systems for the examination of ecological interactions, but some community diversity and environmental heterogeneity are sacrificed with their use (Drenner and Mazumder 1999).

Sixteen stream channels were created by modifying eight existing concrete raceways located in a covered outdoor facility, which were divided in half with a PVC-plastic mesh frame which was fully lined with 6-mil black polyethylene. Each original raceway had a single valve that discharged water into it; in order to ensure equal flow from the single valve to each of the two stream channels within each raceway, we created a single PVC and plastic reservoir that discharged equal amounts of water over a small spillway into each stream channel. Water feeding stream channels came from an outdoor artesian well from the Edwards Aquifer, providing stream channels the same water as the San Marcos River. Water inflow rates to channels were sufficient to create a residence time of  $\sim 10$  min. Channel dimensions were  $4.0 \times 0.3 \times 0.3$  m ( $l \times w \times d$ ). The ends and tops of all channels were fenced off with 3-cm aperture mesh to prevent escape of shrimp or catfish. Forty-watt full-spectrum florescent lights were hung  $\sim 70$  cm above each channel in an orientation parallel to flow. Lights were kept on a 16/8 h light/dark cycle, with mean light intensity of  $\sim 100 \mu\text{mol/m}^2/\text{s}$  immediately above the water surface (using a Li-Cor  $2\pi$  quantum sensor; Li-Cor Environmental, Lincoln, Nebraska, USA). Light intensity in stream channels were within the range of intensities observed in closed-canopy sections of the San Marcos River (W. H. Nowlin, unpublished data). Stream channel bottoms were covered with sand, gravel, and cobble (cover = 50 % cobble, 50 % sand and gravel); proportions are comparable to the upper San Marcos River. One cinderblock was added to each channel as a refuge site for shrimp and catfish; cinderblocks were typically occupied during daytime. Channels were checked daily to note location and status of catfish and/or shrimp.

Prior to the start of the experiment, periphyton from the San Marcos River was collected by scrubbing rocks with a nylon bristle brush into a bucket of river water. Equal aliquots of this periphyton slurry were added to each stream channel four times over a 3-week period. The

brushed rocks were also added to channels in equal densities to promote periphyton growth. Macroinvertebrates collected with a kick net from the upper San Marcos River were placed into a bucket of river water. One of equal aliquots from the bucket was added to each channel; three aliquots were kept to determine baseline densities of invertebrates added to channels. A multivariate analysis of variance (MANOVA) was run to determine differences between subsamples for all weeks and all invertebrate functional feeding groups (both abundance and richness; based on Merritt and Cummings 2007), total taxon richness, total taxon abundance and abundance for each taxon present. Differences between subsamples were found to be non-significant (Wilks  $\lambda = 0.065$ ,  $F_{2,24} = 14.72$ ). Because mesocosm source water was from the underground aquifer (containing few invertebrates) and macroinvertebrates were allowed to 'drift' downstream out of stream channels, addition of river macroinvertebrates was repeated every 7 days to simulate incoming macroinvertebrate drift. Each week we added  $438 \pm 69$  invertebrates to each channel. Invertebrate taxa added to stream channels were reflective of the community in the river, which was mostly composed of amphipods, ephemeropterans, dipterans, trichopterans, and gastropods.

After a 3 week equilibration period, the start of the experiment was initiated by addition of shrimp and catfish. Shrimp and catfish were collected from the upper San Marcos River by hand or dip nets. Shrimp lengths (rostrum tip to tail) ranged from 19.5 to 25.0 cm (mean  $\pm$  1 SE;  $20.9 \pm 1.9$  cm), with wet mass ranging from 126.0 to 299.0 g ( $184.9 \pm 57.8$  g). Catfish total lengths (TL) ranged from 23.0 to 33.0 cm ( $28.2 \pm 3.6$  cm), and individual wet mass ranged from 130.0 to 382.0 g ( $250.1 \pm 90.9$  g). Observations of shrimp and catfish indicated that they had adequate room to move about stream channels. After the experiment, all shrimp were released back into the San Marcos River, with the exception of one shrimp (from one of the shrimp only treatments) which died on day 15 of the experiment. We chose not to replace this individual because of the shrimp's conservation status and instead removed that stream channel data from analyses. The experiment began on August 24, 2007 and ran for 28 days.

Previous work in tropical systems indicated that big claw river shrimp are omnivorous (Crowl et al. 2001). However, shrimp in the San Marcos River occupy a fairly high trophic position (trophic level  $\sim$ 4, with algae occupying trophic level 1; Pound et al. 2011) and have been observed eating live and dead fish. Thus, to ensure that the shrimp in our stream channels occupied a similar trophic role as in the San Marcos River, we added one small dead fish (*Lepomis* spp. 70–120 mm TL) to each stream channel once per week, as a potential food source. Fish were added to all channels each week to prevent differences associated

with addition of fish. Fish were collected from the San Marcos River with nets, pithed, submerged, and weighted down within the stream channel to allow shrimp access. Remaining fish material was removed from each stream channel after a 24-h period and weighed (wet mass) and measured to determine the amount consumed. Fish in channels containing shrimp were entirely consumed in all but four instances; each instance involved a different shrimp.

To assess ecosystem responses to shrimp and catfish, we measured periphyton biomass, sediment and organic matter transport and accumulation, periphyton nutrient ratios, and organic matter decomposition. All ecosystem response variables were measured on days 14 and 28. To estimate periphyton biomass and the amount of organic and inorganic matter on surfaces, four ceramic tiles ( $16.2 \times 16.2$  cm) were placed in the downstream section of each stream channel. Two tiles were enclosed within a 2-cm aperture wire cage and two were open to direct activities of shrimp and catfish. All tiles were placed in channels 3 weeks before the experiment was started. One 'caged' and one 'uncaged' tile was removed from each stream channel on each sampling date. Upon being pulled from a stream channel, the upper surfaces of tiles were cleaned with a soft bristled nylon brush and rinsed into an acid-washed HDPE beaker with Milli-Q water. Chlorophyll *a*, organic matter (OM), inorganic matter (IM), and C, N and P content of materials on tiles were determined from this slurry. A portion of the slurry was filtered onto a Pall A/E filter and filters were frozen at  $-4$  °C. Chl*a* was extracted using 99 % HPLC grade acetone for 4 h in the dark and measured on a Turner Trilogy<sup>TM</sup> Lab Fluorometer (Turner Designs Inc., Sunnyvale California). OM and IM mass on tiles (mg OM or IM/cm<sup>2</sup>) were determined by filtration onto pre-weighed Pall A/E filters and determination of dry mass before and after ignition at 450 °C for 4 h. To estimate C and N content of periphyton (mg nutrient/cm<sup>2</sup>), tile material was filtered onto pre-ashed Whatman GF/F filters (nominal pore size 0.7  $\mu$ m), dried at 60 °C for 48 h, and analyzed on a CE Elantech Carbon–Nitrogen analyzer. We did not remove or correct for inorganic C on filters used in analyses; thus, values of C content of filters include some inorganic C. In order to measure P content of periphyton (mg P/cm<sup>2</sup>), materials on tiles were filtered onto Whatman GF/F filters, digested with HCl at 100 °C, and measured as PO<sub>4</sub><sup>3-</sup> using the molybdenum blue method (Wetzel and Likens 2000).

To assess sediment downstream movement and accumulation, sediment traps were placed mid-channel and allowed to collect sediments (Statzner and Peltret 2006). Sediment traps consisted of shallow plastic trays ( $12.7 \times 12.7$  cm); two sediment traps were placed mid channel 2.3 m from the downstream end of the channel. One sediment trap was pulled from each stream channel on

each sampling date. Each sediment trap was washed with DI water into an aluminum weigh boat and contents were allowed to dry at 60 °C for 48 h. Dry mass (g) was measured. Samples were homogenized, ashed at 500 °C for 4 h, and IM was determined by difference. Accumulation of IM was expressed as mg in trays on each sampling date (days 14 and 28).

We quantified organic matter decomposition by measuring leaf litter mass loss. Four pre-weighed dry leaf packs, each containing 10 leaves of Texas Oak (*Quercus texana*), a common riparian tree species, were placed in each stream channel. Two leaf packs were enclosed within bags consisting of 3-cm aperture plastic mesh, and two were left open. Leaves were enclosed in mesh bags of this aperture size in order to substantially reduce the direct access of shrimp and catfish to leaves while still allowing other macroinvertebrates and microbes access to them. Leaves were tied together with monofilament fishing line around the petioles and weighted with metal washers to ensure submersion. One 'bagged' and one 'unbagged' leaf pack were removed on each sampling date. Leaf packs were subsequently washed with DI water to remove organic matter and organisms and were dried for 48 h at 60 °C. Leaf litter dry mass (g) was determined for calculating decomposition rate as percent change in mass over the period each pack was in a channel.

At the end of the experiment, we examined nutrient recycling by catfish and shrimp by estimating nutrient excretion. Each shrimp or catfish from channels was quantified for excretion rates of  $\text{N-NH}_4^+$  and  $\text{P-PO}_4^{3-}$ . Live organisms were placed in filtered (Pall A/E) stream water in acid-washed plastic tubs and allowed to excrete for ~1 h (Mather et al. 1995; Schaus et al. 1997; Higgins et al. 2006). Organism's N and P excretion were measured as  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  accumulation over the time interval. Ammonium was analyzed with the phenate method (Solorzano 1969) and  $\text{PO}_4^{3-}$  with the molybdenum blue method (Wetzel and Likens 2000).

To investigate effects of shrimp and catfish on benthic community, we examined invertebrates in unbagged leaf packs and in the benthos of stream channels. We chose to analyze only invertebrate communities with which catfish and shrimp had direct contact. When leaf packs were removed on each sampling date (days 14 and 28), invertebrates were removed by rinsing with DI water and picking with forceps and preserved in 95 % EtOH. To assess the influence of shrimp and catfish on benthic invertebrate communities, two basket samplers were placed within the substrate at the end of each stream channel prior to the start of the experiment. Basket samplers were constructed with 15.2 cm diameter, 3.8 cm depth plastic baskets filled with cleaned river cobble and gravel. Basket samplers were buried in stream channel substrate with the

upper lip of the basket flush with the benthic surface. On days 14 and 28, one basket sampler was collected from each stream channel. Invertebrates from leaf packs and basket samplers were identified to the lowest necessary taxonomic group (Thorpe and Covich 2001; Merritt and Cummings 2007).

#### Data analysis

For the field survey portion of the study, difference in the abundance of catfish between upstream and downstream sites was assessed with repeated-measures ANOVA. The mean of densities of transect counts at each site on each sampling date (8 dates total) were compared between the upstream and downstream site, with site serving as the independent (categorical) variable, total catfish density (number/m<sup>2</sup>) as the dependent variable, and sampling date as the repeated measure. The Greenhouse–Geisser correction was applied if the assumption of sphericity was not met. Due to low shrimp densities and the count method we used, we did not compare shrimp numbers between sites using statistics. To calculate density of shrimp at the two sites, we utilized ArcGIS 10 (ESRI, Inc., Redlands, California) to calculate the surface area (m<sup>2</sup>) of the surveyed upstream and downstream sites.

In the stream channel experiment, we examined the main and interactive effects of shrimp and catfish on periphyton biomass, OM and IM on tiles, and periphyton nutrient ratios (molar C:N, C:P, and N:P) by calculating the mean of each response variable across both sampling dates and analyzing with two-way analysis of variance (ANOVA) for cross-classified factors. We utilized the mean of the two sampling dates of these response variables in analyses because the experimental period was relatively short (28 days), treatment effects were apparent by the first sampling date (14 days after start of the experiment), and we were more interested in examining the overall effect of treatments on this set of response variables rather than how effects might vary in a relatively short time period. For this set of analyses, the main effects are the independent effect of each factor (catfish or shrimp) and the interaction effect is the amount of measured variation in the response variable due to the interdependence of catfish and shrimp. All invertebrate community response variables (invertebrates in unbagged leaf packs and in basket samplers) were analyzed for total invertebrate abundance, taxon abundance, taxon richness, abundance of the various functional feeding groups, and taxonomic richness of the various functional feeding groups. Again, means were taken across both dates for each response variable and analyzed with two-way ANOVA. In the case of response variables where time is clearly a factor (sediment and organic matter accumulation in sediment traps and mass loss of leaf litter), we

performed a two-way analysis of covariance (ANCOVA) using sampling date as the covariate. This approach allowed us to account for the variance in sediment accumulation and leaf litter mass loss associated with time and to examine the main and interaction effects of shrimp and catfish. Due to the uneven number of replicates in each treatment combination, Type III sums of squares were used in all ANOVAs. Data not meeting assumptions of normality and homoscedasticity were  $\log_{10}$  transformed. If a significant catfish  $\times$  shrimp interaction was detected, we performed an analysis of simple effects with Tukey HSD tests to determine how the effects of each treatment may differ in the presence and absence of the other treatment.

Although the experiment initially had four replicates of each treatment, we were forced to omit two stream channels from analyses. One replicate of the 'only shrimp present' ( $-C$ ,  $+S$ ) treatment was omitted because the shrimp died (see above) and we omitted one replicate of the control treatment ( $-C$ ,  $-S$ ) because a shrimp in an adjacent channel crawled over the dividing fence and was in the control channel for  $\sim 24$  h before it was removed and placed back in its original channel. The shrimp in the control stream channel produced a noticeable effect in this short amount of time; thus, we elected to omit this channel from analyses. For all analyses, we set  $\alpha$  at 0.05, and all data were analyzed with SPSS 15.0 for Windows (SPSS<sup>®</sup> Inc.).

## Results

### Field surveys

Catfish densities in the San Marcos River exhibited substantial spatial variation. The upstream site had significantly higher ( $0.49$  individuals/ $m^2$ ) catfish densities than the downstream site ( $0.22$  individuals/ $m^2$ ), and catfish densities at both sites were lower in early summer and increased as summer progressed, but this seasonal variation was not significant (two-way repeated measures ANOVA, site:  $F_{1,4} = 10.59$ ,  $P < 0.05$ ; time:  $F_{7,4} = 3.37$ ,  $P > 0.05$ ; site  $\times$  time:  $F_{7,4} = 2.19$ ,  $P > 0.05$ ) (Fig. 1a, b). The upstream site had more even proportions of the three catfish size classes in the population, with small ( $<10$  cm), medium ( $10$ – $40$  cm) and large ( $>40$  cm) individuals composing approximately 28, 49 and 23 % of the individuals throughout the period of observation (Fig. 1a). In contrast, the downstream site had fewer large individuals in the population (approximately 6 % of the population) (Fig. 1b).

Shrimp were less abundant than catfish in the San Marcos River (Fig. 1c, d) and were virtually non-existent in the upstream site ( $0.0001$  individuals/ $m^2$ ; Fig. 1c). In the downstream site, both large ( $>13$  cm length) and small ( $<13$  cm) individuals were observed, resulting in 5–12

total individuals being observed at the downstream site on each count night ( $0.0031$  individuals/ $m^2$  in 2009; Fig. 1d). Shrimp distribution was patchy within each site and the shrimp were often observed in the open but in areas adjacent to openings and crevices.

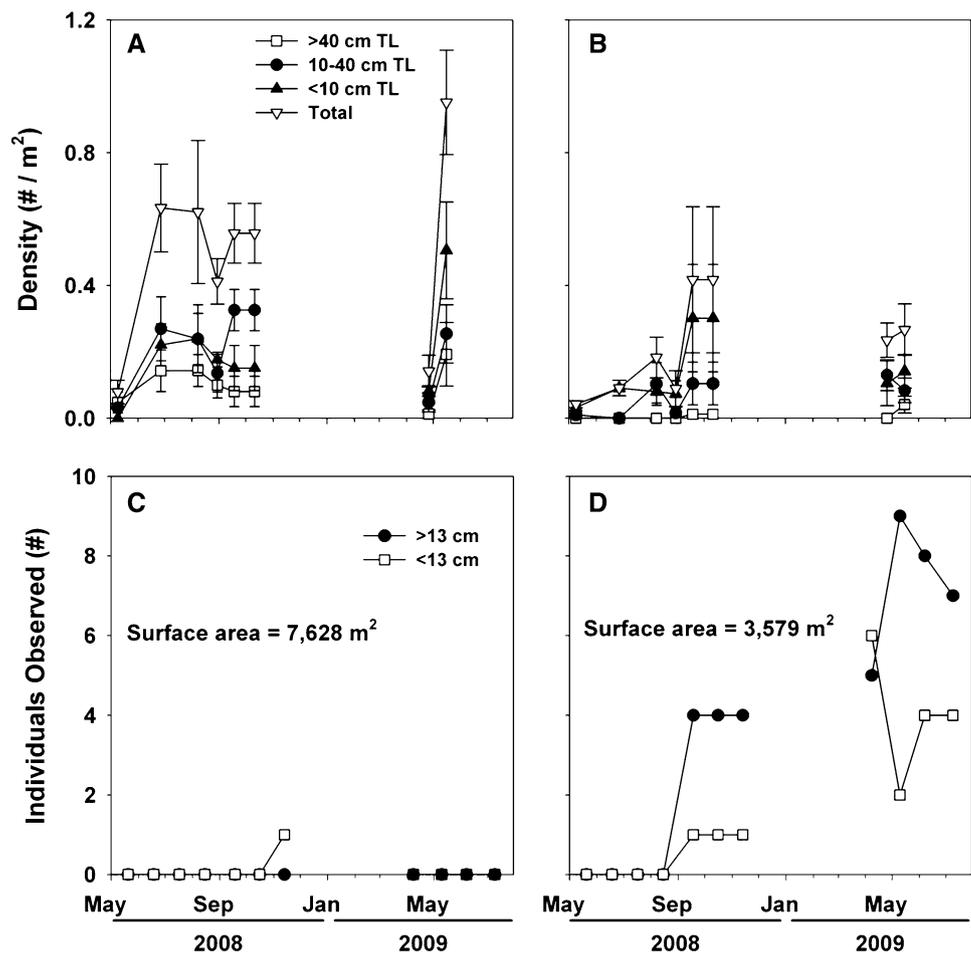
### Stream channel experiment

Catfish caused a significant reduction in periphyton biomass (Chl $a$ ) on uncaged tiles, whereas shrimp had little effect on periphyton biomass on uncaged tiles (Fig. 2a; Table 1). There was a marginally non-significant ( $P = 0.052$ ) catfish  $\times$  shrimp interaction indicating interdependence between the effects of catfish and shrimp on periphyton Chl $a$  on uncaged tiles. Analysis of simple effects indicated that catfish led to a significant reduction in Chl $a$  when shrimp absent (comparison of  $-C$ ,  $-S$  and  $+C$ ,  $-S$  treatments:  $P < 0.001$ ), but the effect of catfish on Chl $a$  was not detected when shrimp were present (comparison of  $-C$ ,  $+S$  to  $+C$ ,  $+S$ :  $P = 0.148$ ). In contrast, catfish did not modify the effects of shrimp on periphyton (comparison of  $-C$ ,  $-S$  and  $-C$ ,  $+S$ :  $P = 0.188$ ; comparison of  $+C$ ,  $-S$  and  $+C$ ,  $+S$ :  $P = 0.188$ ). Neither catfish or shrimp had a significant effect on periphyton of caged tiles (Table 1; Fig. 2b).

The presence of both catfish and shrimp reduced the amount of organic matter and inorganic matter on uncaged tiles (Table 1; Fig. 2c, e). There was a significant catfish and shrimp interaction for these two response variables (Table 1). Analyses of simple effects indicated that catfish led to a significant reduction in IM and OM on uncaged tiles when shrimp were not present ( $-C$ ,  $-S$  vs.  $+C$ ,  $-S$ :  $P < 0.001$  for both response variables), but these effects were not detected when shrimp were present ( $-C$ ,  $+S$  vs.  $+C$ ,  $+S$ :  $P \geq 0.940$  for both variables) (Fig. 2c, e). In turn, catfish modified the effects of shrimp on IM ( $-C$ ,  $-S$  vs.  $-C$ ,  $+S$ :  $P = 0.006$ ;  $-C$ ,  $-S$  vs.  $-C$ ,  $+S$ :  $P = 0.318$ ), but catfish did not alter the effects of shrimp on uncaged tile OM ( $-C$ ,  $-S$  vs.  $-C$ ,  $+S$ :  $P = 0.199$ ;  $-C$ ,  $-S$  vs.  $+C$ ,  $+S$ :  $P = 0.310$ ). Catfish or shrimp did not affect OM and IM on caged tiles (Fig. 2d, f).

Catfish significantly reduced periphyton C:N, C:P, and N:P on uncaged tiles, whereas shrimp had no effect on those nutrient ratios on uncaged tiles (Fig. 3a, c, e; Table 1). A significant catfish  $\times$  shrimp interaction effect was detected for uncaged tile periphyton C:P and N:P. Catfish led to a significant reduction in C:P and N:P when shrimp were absent ( $-C$ ,  $-S$  vs.  $+C$ ,  $-S$ :  $P \leq 0.002$  for both ratios), but these effects were not apparent when shrimp were present ( $-C$ ,  $+S$  vs.  $+C$ ,  $+S$ :  $P \geq 0.869$  for both ratios). Similarly, catfish modified the effects of shrimp on C:P and N:P of open tiles ( $-C$ ,  $-S$  vs.  $-C$ ,  $+S$ :

**Fig. 1** Densities (number/m<sup>2</sup>) of invasive catfish and native shrimp in the San Marcos River over the period of field observations. Densities of total catfish, large catfish >40 cm TL, intermediate-sized catfish 10–40 cm TL, and small catfish at the upstream (a) and downstream (b) sites are presented. Each point represents the mean density of transect counts on each data and error bars  $\pm 1$  SE. The number of large (>13 cm) and small (<13 cm) shrimp counted on each observation night are presented for the upstream (c) and downstream (d) sites



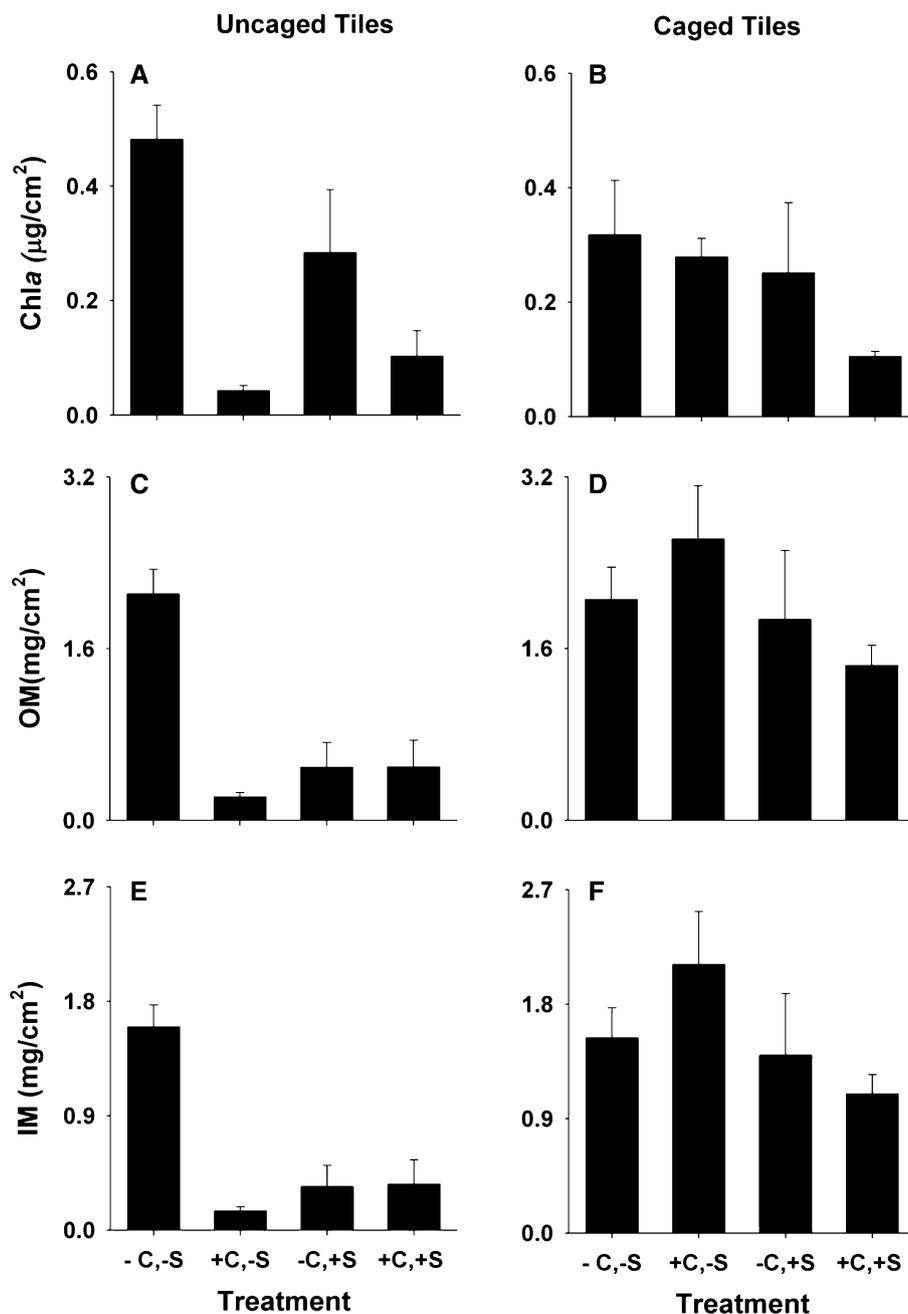
$P < 0.020$  for both ratios;  $-C, -S$  vs.  $+C, +S$ :  $P \geq 0.343$  for both ratios). Catfish and shrimp had no effect on periphyton C:N, C:P, and N:P on caged tiles (Fig. 3b, d, f; Table 1).

Over the experimental period, there was a downstream accumulation of total and inorganic sediments in stream channels and catfish significantly increased this downstream accumulation (ANCOVA; total sediment: time:  $P_{time} = 0.0001$ , catfish:  $P_{catfish} = 0.005$ ; inorganic sediment:  $P_{time} = 0.004$ ,  $P_{catfish} = 0.013$ ) (Table 2). By the end of the experiment, treatments containing catfish accumulated at least two times more sediment as treatments without catfish (Fig. 4a, b; Table 2). Shrimp did not have a significant effect on downstream transport of sediments ( $P > 0.05$  for total sediment and inorganic sediments). Leaf litter lost mass in both bagged and unbagged leaf packs over the experimental period ( $P_{time} < 0.001$  for bagged and unbagged leaf packs) (Table 2; Fig. 4c). Catfish led to faster mass loss of open leaf packs ( $P = 0.016$ ), but had no effect on decomposition of bagged leaf packs ( $P = 0.616$ , Table 2; Fig. 4d). In contrast to predictions, shrimp did not have a significant effect on leaf litter mass loss of both bagged and unbagged leaf packs (Table 2).

Dominant taxonomic groups found in unbagged leaf packs consisted of amphipods, gastropods, ostracods, ephemeropterans, and trichopterans. Catfish elicited a significant reduction in collector-gatherer abundance in unbagged leaf packs (Table 3). Although catfish and shrimp did not exhibit significant main effects on scraper taxon richness in leaf packs, a significant catfish  $\times$  shrimp interaction was detected for this response variable. However, analysis of simple effects indicated that the effects of catfish and shrimp did not differ in the presence of each other ( $P \geq 0.054$ ). There was no significant effect of catfish or shrimp on the abundance or richness of all other taxonomic or functional feeding groups (Fig. 5a; Table 3).

Basket samplers contained relatively low densities of invertebrates (Fig. 5b) and dominant taxa were chironomids, amphipods, and ostracods. Across treatments, the mean number of invertebrates per basket was  $4.8 \pm 0.8$  individuals. We did not detect a significant treatment effect on abundance and richness of total invertebrates and virtually all functional feeding groups and taxonomic groupings; however, catfish led to a significant reduction in the abundance of ostracods (Table 3). However, ostracod densities were low in all treatments (0–2 individuals per

**Fig. 2** Composition of periphyton biomass, organic and inorganic matter on tiles in stream channels for control (-C, -S), catfish (*Hypostomus* sp.) only (+C, -S), shrimp (*Macrobrachium carcinus*) only (-C, +S) and catfish and shrimp present (+C, +S) treatments. **a** Mean concentration of periphyton on uncaged tiles; **b** mean concentration of periphyton on caged tiles; **c** mean mass organic matter on uncaged tiles; **d** mean mass organic matter on caged tiles; **e** mean mass inorganic matter on uncaged tiles; **f** mean mass inorganic matter on caged tiles. Error bars  $\pm 1$  SE. The statistical results of ANOVAs are listed in Table 1



basket sampler), thus we view this significant result with caution.

At the end of the experiment, we determined nutrient excretion rates of catfish and shrimp to examine differences in nutrient recycling by these two consumers. We first examined whether P and N excretion by both catfish and shrimp differed among treatments. We 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 we 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:  $F_{1,4} = 1.07$ ,  $P = 0.377$ ). Thus, we 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 ( $F_{1,10} = 17.5$ ,  $P < 0.001$ ) (Fig. 6a); however, due to high variability in P excretion, we did not detect a significant difference between catfish and shrimp in mass-specific P excretion rates or the N:P of nutrients excreted (P:  $F_{1,10} = 0.22$ ,  $P = 0.65$ ; N:P:  $F_{1,10} = 2.3$ ,  $P = 0.15$ ) (Fig. 6b, c).

**Table 1** Summary of *F* values from ANOVAs (Type III sum of squares) for the main and interaction effects of shrimp (S) and catfish (C) on *Chla*, inorganic matter (IM), organic matter (OM) on open and caged tiles

Treatment	<i>df</i>	Tiles—open			Tiles—caged		
		<i>Chla</i>	IM	OM	<i>Chla</i>	IM	OM
S	1	1.37 (0.268)	14.04 ( <b>0.004</b> )	10.62 ( <b>0.009</b> )	3.14 (0.107)	2.78 (0.126)	2.78 (0.126)
C	1	27.89 (< <b>0.001</b> )	21.78 (< <b>0.001</b> )	21.78 (< <b>0.001</b> )	1.86 (0.202)	0.16 (0.699)	0.024 (0.460)
S × C	1	4.85 (0.052)	19.77 ( <b>0.001</b> )	15.68 ( <b>0.003</b> )	0.62 (0.449)	1.64 (0.230)	1.13 (0.574)
Error	10						

	<i>df</i>	Tiles—open			Tiles—caged		
		C:N	C:P	N:P	C:N	C:P	N:P
S	1	1.20 (0.300)	2.26 (0.164)	2.43 (0.150)	0.22 (0.651)	0.01 (0.998)	0.01 (0.917)
C	1	13.72 ( <b>0.004</b> )	8.94 ( <b>0.014</b> )	7.44 ( <b>0.021</b> )	0.07 (0.803)	0.06 (0.816)	0.11 (0.917)
S × C	1	0.31 (0.593)	7.48 ( <b>0.021</b> )	9.22 ( <b>0.013</b> )	0.04 (0.85)	4.72 (0.055)	4.66 (0.056)
Error	10						

Lower panel is a summary of *F* values from ANOVA examining the effects of shrimp and catfish on molar nutrient ratios of periphyton in open and caged tiles

S Shrimp, C Catfish

*P* values are given in parentheses. *P* values in bold are considered significant at  $\alpha \leq 0.05$  level

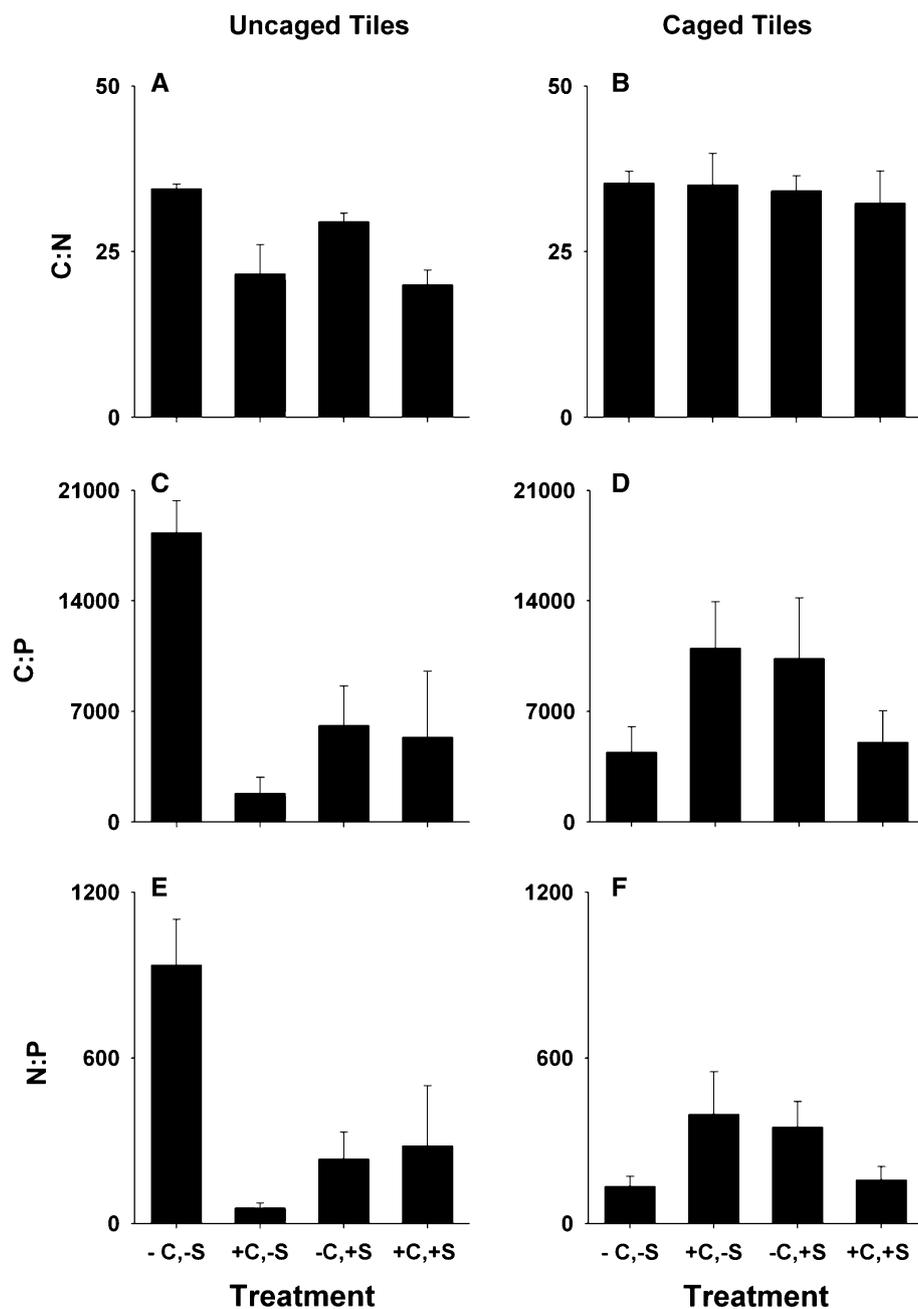
## Discussion

Invasive armored catfish were abundant in the San Marcos River and affected ecosystem functioning in mesocosm stream channels. In the experiment, catfish significantly reduced periphyton biomass, OM and IM on uncaged tiles, and increased the downstream transport of sediments. In the absence of catfish, OM, IM, and *Chla* on uncaged tiles was on average 4–5 times higher than when catfish were present. In addition, catfish increased leaf litter decomposition rates and altered periphyton nutrient ratios, but had relatively minor effects on invertebrate community structure. In contrast, the presence of native shrimp had little effect on ecosystem functioning and invertebrate community structure. Our results indicate that armored catfish can act as allogenic ecosystem engineers in the San Marcos River through mechanical modification of benthic habitat (i.e., redistribution and transport of sediments) and alteration of resource availability (i.e., periphyton biomass, periphyton nutrient content, OM availability) (Jones et al. 1994). Results also indicate that native shrimp can mitigate effects of invasive catfishes, potentially lessening their impacts on ecosystem functioning.

It is likely that catfish removed periphyton and sediments from uncaged tiles through movement and foraging. Grazing by herbivorous fishes can affect multiple structural and functional properties of stream ecosystems, including periphyton biomass, periphyton height and composition, primary productivity, and nutrient dynamics (Flecker 1996; Flecker et al. 2002; Evans-White et al. 2003; Taylor et al. 2006). Our study found that catfish substantially reduced

periphyton biomass on uncaged tiles. In addition, catfish increased leaf litter decomposition in unbagged leaf packs, presumably through increasing litter fragmentation and mass loss. Bertrand and Gido (2007) similarly found that herbivorous *Phoxinus* minnows decreased the size of benthic particulate organic matter (POM) in stream ecosystems. In the current study, the observed increase in leaf litter decomposition in the presence of catfish may be due to several possible, but not mutually exclusive mechanisms. First, increased rates of decomposition may be due to catfish directly grazing biofilms on leaf litter. Biofilms grow on leaf litter during decomposition (Webster and Benfield 1986) and grazing of these biofilms can facilitate fragmentation. Second, armored catfish graze benthic surfaces and swim close to the benthos (Power 1984; Power et al. 1989). Thus, incidental contact and fragmentation of leaf litter through their movements may have also increased decomposition. In contrast to their impact on ecosystem functioning, catfish had little effect on invertebrates. However, catfish led to a decrease in the abundance of collector-gatherers in unbagged leaf packs. Few studies have investigated the effects of grazing fish on stream invertebrate community composition. Bertrand and Gido (2007) found that herbivorous redbelly dace (*Phoxinus erythrogaster*) had no impact on invertebrate community structure. However, Flecker (1992) found that grazing tropical fishes reduced abundances of ephemeropterans, invertebrate collector-gatherers, and chironomids. Rosemond et al. (1998) observed that presence of consumers (including fish and shrimp) in a tropical stream decreased collector-gatherer abundance on leaf packs, but they were

**Fig. 3** Nutrient ratios (C:N, C:P, N:P) of periphyton in caged and uncaged tiles in stream channels for all treatments. *Error bars*  $\pm 1$  SE. The statistical results of ANOVAs are listed in Table 1



unable to determine the individual impacts of each consumer on invertebrate community structure. In this study, we observed a decrease in density and diversity of invertebrates in the presence of catfish, which may be due to increased disturbance of leaf litter through catfish feeding and movement.

Catfish affected nutrient dynamics of periphyton by decreasing C:P and C:N on uncaged tiles. Catfish reduced C:P three-fold (from  $\sim 18,000:1$  to  $\sim 3,500:1$ ) and reduced C:N from nearly 34:1 to approximately 21:1. These C:nutrient ratios are relatively high (especially in the 'both

catfish and shrimp absent' treatment) but fall within the range of C:nutrient ratios reported in the literature (Cross et al. 2005). A decrease in algal C:nutrient ratios in grazed periphyton is consistent with meta-analyses which have indicated that grazing on periphyton tends to decrease C:nutrient ratios through an increase periphyton N- and P-content (Hillebrand et al. 2008). Periphyton biofilms often contain a large detritus component (Frost et al. 2005) and decreases in grazed periphyton C:nutrient ratios may be due to non-selective removal of detritus and algae and subsequent re-growth of relatively more P- and N-rich

**Table 2** Summary of  $F$  values from ANCOVAs (Type III sum of squares) examining the effects of time, shrimp (S) and catfish (C), and the interaction of shrimp and catfish ( $S \times C$ ) on leaf break-down rate (LR) and CPOM of open and mesh enclosed leaf packs

Treatment	$df$	Open		Mesh	
		LR (%)	CPOM	LR (%)	CPOM
Time	1	15.14***	31.37***	26.68***	4.81*
S	1	0.61	1.06	1.05	1.54
C	1	6.72**	0.00	0.26	0.378
$S \times C$	1	0.80	0.04	0.37	1.13
Error	23				

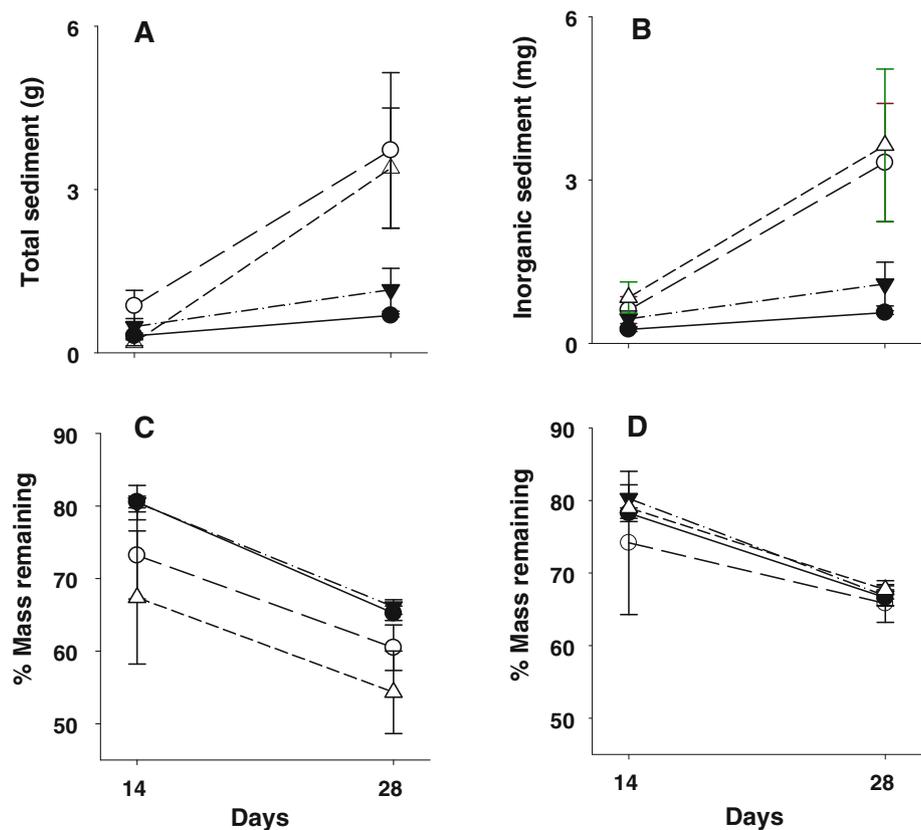
	$df$	Sediment accumulation	
		Total (mg)	IM (mg)
Time	1	22.03***	10.28**
S	1	1.30	0.32
C	1	9.41**	7.30*
$S \times C$	1	0.10	0.01
Error	23		

Lower panel contains  $F$  values from ANCOVAs for total sediment and inorganic matter accumulated in traps

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

algae (Hillebrand et al. 2008). Indeed, armored catfish within the San Marcos River were largely non-selective grazers whose diets are composed of detritus of algal origin (Pound et al. 2011). Significantly lower C:P and C:N of periphyton biofilms in the presence of catfish may also be due to removal of carbonates and/or inorganic sediments; water from the San Marcos River comes from a limestone aquifer and river waters are high in calcium carbonate. As previously stated, we did not correct periphyton C:nutrient ratios for inorganic C within periphyton, thus removal of IM from surfaces may remove a substantial amount of C, causing a decrease in C:nutrient ratios. In addition, the relative enrichment of periphyton in N and P in the presence of catfish grazing may be due to the alteration of periphyton architecture and composition leading to faster nutrient uptake rates and enrichment (Burkholder et al. 1990; Hillebrand and Kahlert 2001; Hillebrand et al. 2002). Finally, excretion of nutrients on surfaces by catfish as they graze may increase nutrient supply, thereby lowering periphyton C:nutrient ratios (Hillebrand et al. 2008). All of these mechanisms may simultaneously act to alter periphyton C:nutrient ratios in the presence of catfish and we cannot determine which mechanism(s) were most important.

**Fig. 4** Results of response variables for four treatments: **a** total sediment deposition, **b** inorganic sediment deposition in sediment traps, **c** detrital breakdown rates in open leaf packs, and **d** detrital breakdown rates in mesh leaf packs. Closed circles (solid line) represent control ( $-C, -S$ ), open circles (long dash line) represent catfish only ( $+C, -S$ ), closed triangles (dash dot line) represent shrimp only ( $-C, +S$ ), and open triangles (short dash line) represent catfish and shrimp ( $+C, +S$ ) treatments. Error bars  $\pm 1$  SE



**Table 3** Summary of *F* values of two-way ANOVAs examining the effects of time, shrimp (S) and catfish (C), and the interaction of shrimp and catfish (C × S) on invertebrate communities

Treatment	<i>df</i>	Total Invertebrates		Shredders		Scrapers		Predators		Collector-gatherers	
		Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich
Leaf packs											
S	1	0.03	2.60	0.00	0.00	0.94		2.12	3.26	0.94	0.27
C	1	4.13	2.19	0.68	0.00	3.05		0.82	1.51	9.06*	0.27
S × C	1	1.18	0.31	2.00	2.40	6.35*	0.56	0.26	1.37	0.51	
Error	10										
	<i>df</i>	Ephem.	Diptera	Amph	Trichop	Gast					
S	1	0.48	0.05	0.00	0.62	0.38					
C	1	0.41	1.55	0.81	0.05	0.01					
S × C	1	0.04	0.05	2.37	0.03	0.17					
Error	10										
Baskets	<i>df</i>	Total invertebrates		Shredders		Scrapers		Predators		Collector-gatherers	
		Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich
S	1	2.92	0.61	0.21	0.07	0.01	0.01	1.75	0.60	1.39	1.18
C	1	0.78	0.06	0.71	0.18	4.03	3.18	0.04	0.04	0.00	0.71
S × C	1	0.70	1.20	1.89	3.25	0.24	0.54	0.04	0.12	0.52	1.18
Error	10										
	<i>df</i>	Ephem.	Coleop.	Diptera	Amph	Trichop	Gast	Ostrocooda			
S	1	1.63	0.31	2.29	1.31	1.62	0.04	0.77			
C	1	0.01	2.76	1.12	1.11	0.07	3.86	5.10*			
S × C	1	0.34	0.31	1.26	2.23	0.07	0.97	0.77			
Error	10										

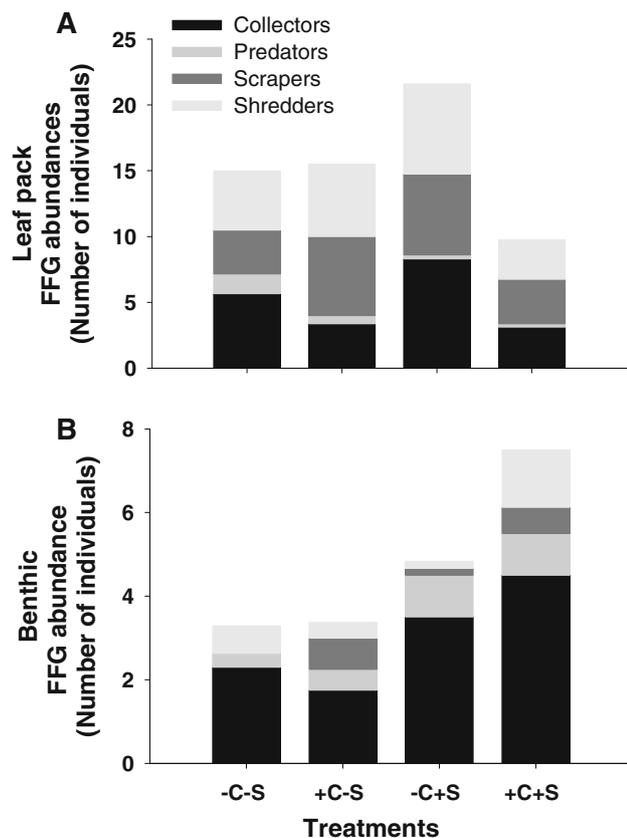
Upper 2 panels are the effects of shrimp and catfish on open leaf pack invertebrates. Lower two panels are effects of shrimp and catfish on invertebrate composition of basket samplers. Response variables are invertebrate abundance (Abund), taxon richness (Rich), Ephemeroptera (Ephem), Coleoptera (Coleop), Diptera, Arthropoda (Amph), Trichoptera (Trichop), Gastropoda (Gast), and Ostrocooda. No data is available for shredder richness in leaf packs because shredder richness = 1 in all treatments

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

In addition to the effects of catfish on C:nutrient ratios, we found that catfish decreased periphyton N:P on uncaged tiles. Although catfish increased periphyton N and P content (as indicated by decreased periphyton C:N and C:P), the observed decrease of periphyton N:P in the presence of catfish indicates that catfish increased P content of periphyton more than N content. These findings are in disagreement with stoichiometric theory, which predicts that grazers with low body C:P (like loricariid catfishes; Vanni et al. 2002) would retain P from food, thereby decreasing availability of P in the environment and causing depletion of P in primary producers (Sterner 1990; Sterner and Elser 2002). However, meta-analysis of grazer-periphyton interactions found that grazers with low body C:P tended to increase periphyton P content, in apparent contradiction to stoichiometric predictions (Hillebrand et al. 2008). This trend may be a consequence of complex relationships between plasticity in grazer P content, grazer

growth rates, and the relationship between grazer elemental ratios and physiological demands (Hillebrand et al. 2008). Periphyton in the San Marcos River are P-limited and grazing by catfishes may cause changes in periphyton architecture, turnover, and composition (e.g., Flecker et al. 2002; Hillebrand et al. 2002), leading to increased P uptake and enrichment. However, we did not assess these aspects of the periphyton and do not know if this led to the observed responses.

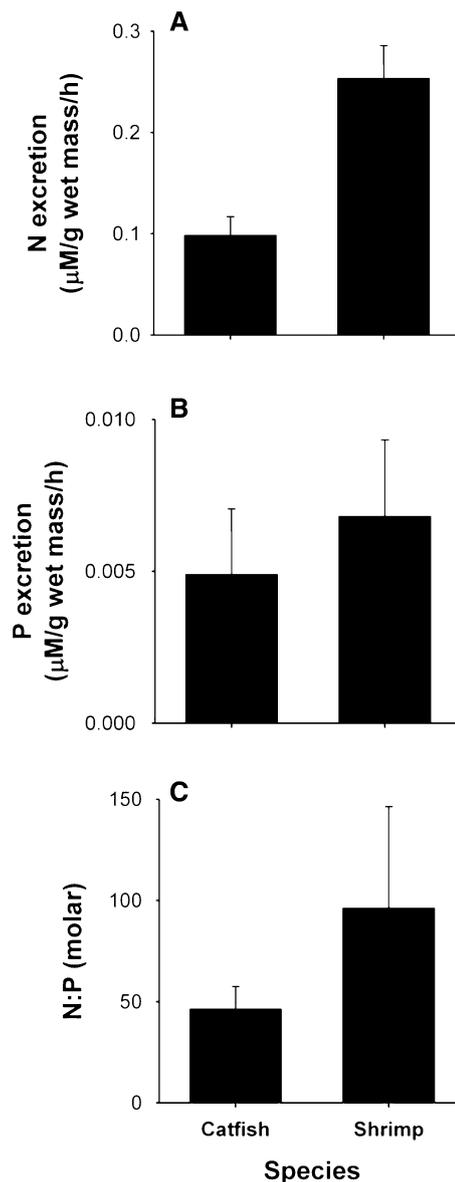
Grazers in lotic systems often have strong effects on nutrient cycling (Flecker et al. 2002; Hillebrand et al. 2008; Knoll et al. 2009). We found that catfish had larger effects on ecosystem functioning and nutrient cycling at sites where they had foraging access (i.e., uncaged tiles). Catfish did not affect periphyton biomass, organic matter, inorganic matter, or nutrient ratios on caged tiles, as well as bagged leaf litter decomposition. These results indicate catfish effects on periphyton had a substantial spatial



**Fig. 5** Mean invertebrate functional feeding group (FFG) abundances for **a** open leaf packs and **b** benthic basket samplers in stream channels. Means were averaged across both sampling dates

component and did not propagate outside of locations where they had direct foraging access. The lack of observed indirect effects may be due to the short experimental duration (28 days); indirect nutrient-mediated effects may require longer transmittance through food webs and ecosystems (e.g., Arango et al. 2009). In addition, a lack of wide-spread indirect effects may be because water residence times in experimental stream channels were relatively brief. Other studies which have observed significant, indirect nutrient-mediated effects of fishes were conducted in systems with longer effective water residence times, such as pool mesocosms (Knoll et al. 2009) or experimental streams with recirculating water (Hargrave 2006). Indirect effects of the invasive catfishes on ecosystem functioning in the San Marcos River may be evident downstream from the headwater reach where catfishes are abundant and maintain a high biomass.

In contrast to the effects of catfish, shrimp had little effect on ecosystem function and invertebrate community structure. Although there was little direct effect of shrimp on periphyton biomass, organic and inorganic matter on uncaged tiles were 1–2 times higher than those in the absence of shrimp. Contrary to our predictions, shrimp did



**Fig. 6** Mass specific excretion rates for shrimp and catfish. Rates for each species were averaged across all treatments. Error bars  $\pm 1$  SE

not affect rates of leaf litter decomposition or invertebrate communities. These large-bodied shrimp are thought to be omnivorous and can consume leaf litter (Covich and McDowell 1996). However, big claw river shrimp in the San Marcos River exhibit a tendency to be predacious; stable isotopes indicate that its trophic position is  $\sim 4$  in this river (Pound et al. 2011). In addition, use of dead fish to supplement shrimp diets may have dampened their consumptive effects on leaf litter and invertebrates because fish resource subsidy throughout the experiment may have been sufficient to alleviate the need for shrimp to use detritus or small-bodied invertebrates as food sources. Dead fish are likely to be less abundant in the San Marcos River than in the stream channel experiment due to

competition with other scavengers (i.e., crayfish) for this resource. It is possible that when given a choice, fish are a preferred food source because of its higher quality.

As predicted, a significant catfish  $\times$  shrimp interaction was detected for a number of response variables, including periphyton biomass, organic matter and inorganic matter, and the C:P and N:P of periphyton on uncaged tiles. Shrimp mitigated or lessened the effects of catfish on all of these response variables. Similarly, the presence of *M. carcinus* in tropical streams slowed litter decomposition rates through lowering detritivory by other decapods (March et al. 2001). We hypothesize that the responses observed in our experiment are due to non-fatal but aggressive behavior by shrimp limiting catfish foraging time in a particular location. It is important to note that the sizes of catfish used in this experiment are commonly found in the upper San Marcos River and were too large to be consumed by shrimp. Interference of foraging activities of invasive catfish by shrimp may be present in the San Marcos River as both consumers compete for habitat space. However, whether this interaction occurred and to what extent remains unknown. We additionally hypothesize that if we had used smaller-sized catfish in the experiment, shrimp might have caused substantial catfish mortality and subsequently had a stronger role in mediating catfish impacts. Inversely, if we had used smaller-sized shrimp in the experiment, then shrimp may have little effect in mediating catfish effects.

#### Implications of native-invasive interactions on the San Marcos River ecosystem

Our results indicate that the current ecosystem engineering role of big claw river shrimp in the San Marcos River is likely minimal. However, big claw river shrimp are large-bodied consumers, can reach relatively high densities, and can play structuring roles in stream communities (Covich et al. 1991; Crowl and Covich 1994). Thus, the ecosystem engineering role of shrimp in the river is likely to be density dependent. Our field survey data show that shrimp are currently rare in the San Marcos River; however, shrimp densities were much higher in the past, to the extent that populations were commercially harvested (Bowles et al. 2000). Density of shrimp in our stream channels was much higher than densities in the San Marcos River and it is likely we observed the maximum potential effect of shrimp on ecosystem functioning at relatively small spatial scales (i.e., at the scale of a few meters). If we were to calculate shrimp density based upon the local habitat areas they consistently utilize or occupy, then densities per  $m^2$  within the river would be higher than our reach-based estimates. Although shrimp had little direct effect on lower trophic levels and ecosystem functioning in this study, their effects may be most intense at the top of the food web

because they are large-bodied predators (Polis and Strong 1996). Thus, their extirpation from the San Marcos River might have effects not observed at the scale of this study.

Armored catfish were first reported in the San Marcos River in the late 1990s (Perkin et al. 2010). Our results indicate that catfish densities in the upper portion of the river are on average 0.22–0.50 individuals/ $m^2$ , which were comparable to the densities used in our experiment (0.59 individuals/ $m^2$ ). Catfishes currently represent 20–50 % of the upper San Marcos River ichthyomass (Pound et al. 2011). The effects we detected of catfish on sediment redistribution and transport are consistent with observations in other systems (Hoover et al. 2006). We predict that armored catfish with high densities and larger body size (>40 cm TL) are likely to have strong allogenic ecosystem engineering impacts in the upper San Marcos River by affecting habitat structure through sediment redistribution and resource availability and quality through alteration of periphyton biomass and stoichiometry.

Invasive species are a major concern for freshwater conservation and management (Mooney and Hobbs 2000), causing biodiversity loss, alteration of ecosystem functioning, and extinction of native taxa (Clavero and Garcia-Berthou 2005). Riverine ecosystems are facing widespread extinctions and extirpations of native species (Revenga et al. 2005; Dudgeon et al. 2006). This study observed that a native shrimp species facing substantial conservation concerns had the ability through non-trophic effects to mitigate some of the impacts of an invasive species on ecosystems. We also show that a non-native consumer, which can obtain high densities and biomass and has the ability to utilize a wide range of habitats, can have strong impacts on ecosystem functioning.

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