Trophic ecology of a nonnative population of suckermouth catfish (*Hypostomus plecostomus*) in a central Texas spring-fed stream

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Abstract Introduced suckermouth catfishes (Family Loricariidae) are now established in a number of spring-influenced streams in North America but their impacts on native biota are not well documented. Purposes of this study were to quantify gut contents of the loricariid *Hypostomus plecostomus* from the San Marcos River in central Texas and to evaluate the role of *H. plecostomus* in the San Marcos River food web using stable isotope analysis. Gut content analysis indicated that *H. plecostomus* (*N*=36) primarily consumed amorphous detritus (87% in biovolume), filamentous red algae (5.4%), and picoplankton (4.1%). Macrophytes, macroinvertebrates, and fish eggs were not found in gut contents. Stable isotopes demonstrate that *H. plecostomus* occupies a trophic position indicative of an herbivore and likely utilizes detritus of algal origin. The results from our study suggest that large populations of *H. plecostomus* in the San Marcos River may directly compete with several native herbivorous fishes and may be disrupting trophic flows and nutrient cycling in spring-influenced streams of central and west Texas.

Keywords Biological invasion · Herbivory · Stable isotopes · Aquarium releases · Endangered species management

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Introduction

Human-assisted introductions of exotics have resulted in unprecedented global changes (Ricciardi 2007), nearly worldwide biotic homogenization, and extinction of native or endemic taxa (Rahel 2000; Olden et al. 2004; Clavero and Garcia-Berthou 2005). Freshwater ecosystems are especially vulnerable to invasions because there are so many potential routes of introduction (Sala et al. 2000), including intentional pathways like stocking, and unintentional pathways like release of ballast water and aquarium releases. Billions of dollars are now spent every year to eradicate nonnative aquatic species (Pimentel et al. 2004).

Efforts to limit the introduction of invasive species or to manage established exotic populations are often hindered by insufficient understanding of the natural history of problematic species (Simberloff et al. 2005). The loricariid genera *Hypostomus* and *Pterygoplichthys*, which are native to Central and South America, are widely introduced into North American waters (Courtenay et al. 1974;

Ludlow and Walsh 1991; Page 1994; Edwards 2001; Hoover et al. 2004), yet little is known about their ecological impacts. Although suckermouth catfishes are commonly touted as algivores in the aquarium trade, the limited dietary data that are available indicate that diets in native habitats vary substantially among species, with some species consuming primarily amorphous detritus and others consuming periphyton, plants, and macroinvertebrates (Delariva and Agostinho 2001). With over 500 described species of loricariids (Hoover et al. 2004), very few of which have been subjects of intense study, it is difficult to predict the potential impact of introductions into non-native habitats. Indeed, though suckermouth catfishes have been established in North America for more than 40 years, we have found no published information on diets of suckermouth catfishes in introduced habitats.

Suckermouth catfish were first noted in the upper San Marcos River, central Texas, USA in the 1990s, and are thought to have been introduced through illegal aquarium releases (Perkin 2009; Perkin and Bonner 2010). Loricariid populations in the upper San Marcos River are composed of the species *Hypostomus plecostomus* (Hubbs et al. 2008), which are characterized by a sail-like dorsal fin (<9 rays), a snout with a smooth margin, fused opercular bones, and a spotted pigment pattern (Burgess 1989; Hoover et al. 2004). It is estimated that *H. plecostomus* composes 25–50% of the river ichthyomass (W. H. Nowlin, unpub. data). The San Marcos River contains several state and federally listed taxa that are likely to be impacted by this large nonnative fish population. Potential impacts include competition with native herbivorous macroinvertebrates and fishes, destruction of adhesive eggs of phytophilic-spawning fishes, dramatic alteration of habitat through foraging and burrowing activities, and interruptions of energy flows and trophic interactions (Hoover et al. 2004). The purpose of our study was to examine the potential impacts of *H. plecostomus* on native flora and fauna in the San Marcos River. Main objectives of this study were to quantify the diet of *H. plecostomus* in the San Marcos River, to determine if it consumes macroinvertebrates, fish eggs, or native vegetation (such as the federally-listed Texas wild rice *Zizania texana*), and also to assess the role of *H. plecostomus* in energy flow and trophic dynamics of the San Marcos River food web.

Materials and methods

The San Marcos River originates in Spring Lake and flows 120 km southeast toward its confluence with the Guadalupe River. The headwaters are spring-fed by the Edwards Aquifer, resulting in year-round physiochemical stability (~23°C year-round) in the upper 5 km of the river (Groeger et al. 1997). There are several endemic species in this reach (Ono et al. 1983), with some species listed as endangered or threatened, including the San Marcos salamander *Eurycea nana*, Texas wild rice *Zizania texana*, the fountain darter *Etheostoma fonticola*, and the Comal Springs riffle beetle *Heterelmis comalensis*. The current study was conducted in the upper reaches of the San Marcos River, starting just downstream from the impounded headwaters (Spring Lake) and continuing downstream for ~300 m. This segment of the river is characterized by high water clarity, abundant macrophytes, and cobble/sand substrates.

To examine the diet of exotic *H. plecostomus* populations in the San Marcos River, up to 10 individual fish were collected with gigs each month from January to December 2005 at various times during the day and night. Immediately upon collection, fish were pithed, measured for total length (TL) to the nearest 0.01 mm, and preserved in formalin. The gut (stomach and first intestinal loop) of each preserved fish was excised, slit lengthwise, and contents were initially examined under a dissecting scope. Contents of each gut were then washed with 4% formalin into individual containers and sub-sampled three times for triplicate examination. Each sub-sample was drawn by re-suspending contents in a vortex mixer and pipetting 1 ml of the suspension into a Palmer-Maloney Counting Cell (Palmer and Maloney 1954; Wildco, Saginaw, MI). Thirty fields of view were examined with a compound scope at 40× magnification. Discernable items were identified taxonomically (to genus when possible), classified into a dietary category, measured, and counted. Dietary categories were as follows: amorphous detritus (complex aggregates of amorphous material), filamentous red algae, filamentous green algae, filamentous cyanobacteria, picoplankton (i.e., algae <2 μm in diameter), diatoms, plant material, and sand.

After the gut contents of all fish had been examined, the volumetric contribution of each indi-

vidual item was calculated using linear dimensions of the item according to the procedures of Hyslop (1980) and Hillebrand et al. (1999), with the exception that the contribution of sand was measured directly by volumetric displacement. Mean biovolume for each dietary item category was calculated as the sum of the volumetric contributions of all items in the category across all fish, and dividing by the total number of occurrences of the category across all fish. Total count per milliliter was determined for each diet item category in a fish according to the procedure of Wetzel and Likens (2000), and this count was converted to count per category for that fish based on the total volume of its gut sample. This count per category in a fish was multiplied by the mean biovolume for that category to estimate the biovolume contribution of each dietary category to the gut content of each fish. Biovolume contribution of each category in a fish was divided by the sum of the biovolume contributions of all the dietary categories to determine the percent biovolume per category for each fish. Mean percent biovolume for each dietary item category was then calculated across all fish sampled in the study.

To supplement gut content data, we also performed stable isotope analyses on *H. plecostomus* and several major constituents of the upper San Marcos River food web, including periphyton, coarse particulate organic matter (CPOM), macroinvertebrates, and several other fish species. Periphyton collections consisted of both microalgae and filamentous algae collected from slow runs and riffle habitats (Findlay et al. 2002). Microalgae were sampled in duplicate from each habitat type. Each sample was a composite of material scrubbed off of several rocks selected from the habitat. For each sample, rocks were scrubbed with a clean nylon brush, and material was rinsed with Milli-Q water into an acid-washed high density polyethylene (HDPE) centrifuge tube. Filamentous algae were collected as a single composite sample by removing algae from several rocks selected from each habitat type, and combining the algae from these rocks into an acid-washed HDPE vial. Samples were stored in a cooler and transported to the laboratory for further processing. Duplicate samples of CPOM were gathered by hand and placed into plastic bags. CPOM consisted of terrestrial leaves (mostly sycamore, *Platanus occidentalis*) gathered from the river bed. Macroinvertebrates were collected from riffle and run

habitats with a combination of kick-nets and picking from rocks. Macroinvertebrates were placed into plastic bags containing stream water, maintained for 2 h to allow elimination of gut contents, and then preserved in 70% EtOH. Fish were collected by seining or spear-fishing at night, pithed, placed into plastic bags, and frozen. The large-bodied (~1 kg wet mass) bigclaw river shrimp *Macrobrachium carcinus* were also captured by hand. Upon capture, a front claw was removed from each shrimp and placed into a plastic bag and frozen. Immediately afterward, shrimp were returned to the river alive.

In the laboratory, microalgae were filtered onto pre-combusted glass fiber filters (Whatman GF/F). Filamentous algae were rinsed with Milli-Q water, and detritus was removed. Macroinvertebrate samples were sorted into taxonomic groups and rinsed of attached algae or detritus. Tissue samples of snails (Pleuroceridae: *Elimia comalensis*; Thiaridae: *Tarebia granifera* and *Melanoides tuberculatus*) were removed from the foot region with a clean scalpel. Macroinvertebrate samples were prepared as composite samples of multiple organisms within a taxon (76 *Hyalella azteca*, 29 Baetidae, 3 Naucoridae, and 5 snails). Fish were individually analyzed using filleted muscle. Bigclaw river shrimp were individually analyzed for stable isotopes using soft tissue removed from frozen appendages. All samples were dried at 60°C for 48 h. There is a large amount of calcium carbonate in San Marcos River water, which potentially affects the ^{13}C: ^{12}C ratios of periphyton (W.H. Nowlin, unpubl data). Therefore, dried filamentous algae and microalgae on filters were placed in a fuming HCl chamber for 24 h to remove inorganic carbon. All samples except microalgae filters were homogenized with a clean mortar and pestle before encapsulation. Samples were sent to University of California-Davis for analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ and duplicates were run approximately every 10 samples with a mean standard error of <0.15‰. All stable isotope values are reported with δ notation, where $\delta^{13}C$ and $\delta^{15}N$ values are equivalent to $([R_{SAMPLE}/R_{STANDARD}] - -1)*1000$, where R is the ^{13}C: ^{12}C or the ^{15}N: ^{14}N of the sample and standards. PeeDee Belemnite (for $\delta^{13}C$) and atmospheric N (for $\delta^{15}N$) were used as standards.

Results of $\delta^{15}N$ analysis were used to estimate trophic position of consumers, where each organism

is considered ~1 trophic position above its direct prey. $\delta^{15}N$ values of consumers become enriched with each trophic transfer, thus $\delta^{15}N$ can be used to estimate trophic position of consumers (Post 2002). Because algal $\delta^{15}N$ values can be highly variable in space and time, we utilized an approach in which the organism with the lowest $\delta^{15}N$ value in the community was designated as the baseline consumer with a trophic position = 2 (Post 2002; Anderson and Cabana 2007). The $\delta^{15}N$ of the baseline organism was subsequently used to estimate trophic position for all other invertebrate and vertebrate consumers in the food web using the equation:

$$\text{Trophic position}_{Consumer} = \left(\left[\delta^{15}N_{Consumer} - \delta^{15}N_{Baseline} \right] / f \right) + 2$$

where $\delta^{15}N_{Consumer}$ is the $\delta^{15}N$ value for consumer for which trophic position is estimate, $\delta^{15}N_{Baseline}$ is the $\delta^{15}N$ value of baseline organism, 2 is the expected trophic position of the organism used to estimate baseline $\delta^{15}N$, and f is the $\delta^{15}N$ fractionation factor (3.4‰) expected between a predator and its direct prey (Post 2002; Anderson and Cabana 2007).

Results of $\delta^{13}C$ analysis are often used to identify sources of organic matter (OM) used by consumers in aquatic food webs, because terrestrial (CPOM) and algal organic matter sources often exhibit distinct $\delta^{13}C$ values (Findlay et al. 2002; Kennedy et al. 2005). In addition, $\delta^{13}C$ values are conserved through food webs, with little trophic fractionation (Post 2002). Thus, we used $\delta^{13}C$ values of periphyton and CPOM to determine the percent contribution of potential OM sources (algae *versus* terrestrially-derived CPOM) to consumers in the San Marcos River food web (Fry 2006). Results from $\delta^{13}C$ analysis of filamentous algae (*Cladophora* sp.), microalgae from faster flow areas, and microalgae from run habitats did not significantly differ from each other (one-way ANOVA, $F_{2, 5}=1.00$, $P=0.464$). Consequently, we used the mean $\delta^{13}C$ values for all algae (-34.77 ± 1.10‰) and CPOM (-29.38 ± 0.23‰) as end points in a two-source mixing model (Fry 2006), which provides estimates of the percent contribution of the two potential food sources to consumers in the San Marcos River food web. Mean and error estimates for the mixing model were made according to Phillips and Greg (2001) using IsoError (http://www.epa.gov/wed/pages/models/stableIsotopes/

isotopes/isoerror1_04.htm). $\delta^{13}C$ values for fish and macroinvertebrates were corrected for trophic enrichment of 0.5‰ per trohic level (Findlay et al. 2002). Because we calculated error estimates in the mixing model, only consumers that had >1 replicate sample were used to determine the percent contribution of algal *versus* terrestrial organic matter sources to their diet. These consumers were *H. plecostomus*, bigclaw river shrimp, sunfishes (*Lepomis*), largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), and Rio Grande cichlid (*Cichlasoma cyanoguttatus*). We additionally pooled the $\delta^{13}C$ results for bateid mayflies and snails into an invertebrate 'scraper/collector/gatherer' group for mixing model analysis.

Results

Gut contents

Thirty-six *H. plecostomus* were collected for gut content analysis, ranging in total length from 65 to 428 mm. Amorphous detritus and picoplankton were the most common food items found in guts (occurrence in *H. plecostomus* = 100%), followed by diatoms (83%), filamentous bluegreen algae (50%), and filamentous red algae (Batrachospermaceae; 30%)

Table 1 Percent occurrence and mean percent biovolume (± 1 SE) of food items found in 36 suckermouth catfish (65–428 in TL) taken from the San Marcos River, January through December 2005

Taxa	% Occurrence	% Biovolume
Amorphous Detritus	100	86.5±3.3
Filamentous Red Algae	30.6	5.4±2.7
Filamentous Bluegreen Algae	50.0	<1.0
Filamentous Green Algae	8.3	<1.0
Picoplankton	100	4.1±0.9
Sand	2.8	1.5±1.5
All Diatoms	83.3	1.3±0.3
Cocconeis	58.3	<1.0
Fragilariaceae	72.2	<1.0
Naviculoids	83.3	<1.0
Aulacoseira	25.0	<1.0
Plant Material	5.6	<1.0

(Table 1). Filamentous green algae, aquatic plant material, and sand were each found in <10% of *H. plecostomus*. Amorphous detritus of likely algal origin was the most abundant food item consumed (mean±1 SE; 87%±3.3) by biovolume, followed by filamentous red algae (5.4%±2.7), and picoplankton (4.1%±0.9). All other food items comprised <2% of the total biovolume in catfish. We additionally assessed whether *H. plecostomus* size (grouped into size categories ≤180 mm TL and >180 mm TL based on minimum length at sexual maturity; Cook-Hildreth 2009) or the month in which fish were collected influenced the dietary composition by performing a MANOVA on the percent biovolume of the three most abundant food items found in guts (algal detritus, red algae, and picoplankton). Neither fish size (Wilks' Lambda= 0.955; $F_{3, 32}=0.499$; $P=0.686$) nor collection month (Wilks' Lambda=0.486; $F_{27, 70}=0.734$; $P=0.813$) exhibited a significant influence on the dietary composition of *H. plecostomus*.

Stable isotope analysis

Five macroinvertebrate taxa (baetid mayflies, naucorids, *Hyalella azteca*, snails, and big claw river shrimp) and five fish taxa were used for stable isotope analysis (Fig. 1). Baetid mayflies had the lowest $\delta^{15}N$ value of all consumers, and were consequently selected as the baseline organism and assigned a trophic position of 2.0. Trophic positions of naucorids and *Hyalella azteca* were slightly >2, followed by snails (2.7) and *H. plecostomus* (2.8±0.4). Trophic position of Rio Grande cichlid, rock bass, big claw river shrimp, and sunfishes ranged between 3 and 4. Largemouth bass occupied the highest trophic position (4.13) of fishes collected from the San Marcos River.

Algal and terrestrial CPOM $\delta^{13}C$ values exhibited distinct differences (algae=−34.8‰, CPOM=−29.4‰), thus we utilized a two-source mixing model to determine the percent contribution of these two OM sources to consumer diets. Several taxa (e.g., baetids, naucorids, Rio Grande cichlids, and suckermouth catfish) exhibited mean $\delta^{13}C$ values slightly more deplete than that of algae; however, $\delta^{13}C$ values of these organisms fell within the range of $\delta^{13}C$ values observed in algae. Based on our two-source mixing model, a majority of consumers in the river (invertebrate scraper/collector gatherers, suckermouth catfish, Rio
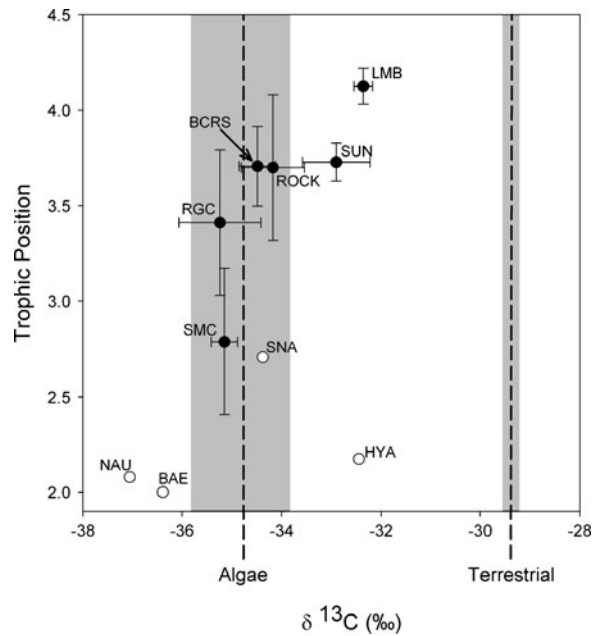

Fig. 1 Dual isotope plot of consumer $\delta^{13}C$ and trophic position of the San Marcos River food web. Values for macroinvertebrates and fishes represent mean values and ± SE for replicate samples. *Staggered vertical lines* represent mean algal $\delta^{13}C$ and mean CPOM $\delta^{13}C$ with ± 1 SE shown in *gray*. Abbreviations are: *NAU* naucoridae; *BAE* baetid mayflies; *HYA Hyalella azteca*; *SMC* suckermouth catfish; *SNA* snails; *RGC* Rio Grande cichlid; *ROCK* rock bass; *BCRS* big claw river shrimp; *SUN* sunfishes; and *LMB* largemouth bass

Grande cichlids, rock bass, big claw river shrimp, and sunfishes) obtain >65% of their OM from algal-derived sources (Table 2). Largemouth bass appeared to derive a greater percentage of its food sources from terrestrial sources, but still derived a majority (55%) of its OM from algal-derived sources.

Table 2 Two-source carbon mixing model for contributions of algal and CPOM derived food sources to macroinvertebrates and fishes collected from the San Marcos River in July 2007. Mean values and ± 1 SE are reported for replicated samples

Species	N	Percent algae	Percent CPOM
Invertebrate scrapers	2	100±27.9	0±27.9
Suckermouth catfish	5	100±20.5	0±20.5
Rio Grande cichlid	2	100±25.4	0±25.4
Rock bass	4	88.9±20.3	11.1±20.3
Big claw river shrimp	2	94.7±18.9	0.53±17.5
Sunfishes	5	65.6±17.5	35.4±17.5
Largemouth bass	2	55.3±11.0	44.7±11.0

Discussion

Gut content assessment and stable isotope analysis collectively indicated that *Hypostomus plecostomus* in the San Marcos River is herbivorous and consume algal-derived, amorphous detritus. Their trophic position also suggested a more omnivorous feeding strategy than gut content assessment. Aquatic detritus typically is an amalgam of algal and animal materials (Ray and Straškraba 2001; Moore et al. 2004). Therefore, our results suggest that higher trophic position of *H. plecostomus* is likely attributed to consumption of amorphous detritus containing indistinguishable animal material rather than selective or incidental consumption of live invertebrates, vertebrates, or vertebrate eggs.

Gut contents of *H. plecostomus* from the San Marcos River were similar to loricariids taken from native environments (Bowen 1983; Fugi et al. 1996; Delariva and Agostinho 2001). Percent volume of amorphous detritus ranged from 10% to 96% among three genera and six species (*N* per species=18 to 26) of loricariids taken from the Parana River, Brazil, whereas percent volume ranged from 0% to 7% for plant material (Delariva and Agostinho 2001). Detritivorous fishes usually ingest smaller particles (<100 μm) which are amorphous in structure, as opposed to larger morphous fragments, because amorphous detritus contains less refractory organic matter, is more digestible, and supports higher growth production in detritivores than morphous plant detritus (Bowen 1984; Sinsabaugh and Linkins 1990). Ingestion of small, amorphous particles is consistent with feeding-associated morphologies of detritivorous fishes, in general, and of detritivorous loricariids, specifically. Long and thin branchial filaments and wide oral cavity of loricariids enable straining of detrital particles or suctioning of flocculent detrital matter from substrates, and trapping of the particles in mucus on gillrakers (Odum 1968; Bowen 1983; Ahlgren 1996; Delariva and Agostinho 2001). In addition, suckermouth catfishes in general have less developed pharyngeal teeth and poorly developed stomachs, which are characteristic of fishes that consume amorphous detritus (Bowen 1983; Delariva and Agostinho 2001).

A goal of invasive species management is the identification of ecological and evolutionary traits that allow certain animals to become successful invaders.

In the absence of other life history constraints, detritivorous and omnivorous fishes feeding at lower trophic levels are predicted to be successful invaders because they utilize food sources that are rarely limiting (Moyle and Light 1996; Gido and Frannsen 2007). Small amounts of detritus is usually present in the guts of most fishes and is likely ingested incidentally with other prey items, but few fishes are actually specialized in consuming and deriving nutrition from this low quality food source (Bowen 1983). Unlike omnivorous fishes that use detritus to sustain metabolic demands when other food is limited (Bowen et al. 1995), loricariids can support growth and reproduction on a diet of detritus. As tropical fishes require waters warmer than 20°C, water temperature is the primary life history constraint that will inhibit range expansion. Thermally stable spring-fed environments such as the San Marcos River are, therefore, ideal habitats for suckermouth catfishes, such as *H. plecostomus*. The prediction of *H. plecostomus* as successful invaders in the San Marcos River is confirmed by numerous underwater fish counts (W.H. Nowlin, unpublished data) and observations made during repairs of a low-head dam in 2005, where >150 kg of suckermouth catfish were removed from a 100-m stretch of the dewatered river channel (V. Cantu, National Fish Hatchery and Technology Center-San Marcos). We hypothesize that large *H. plecostomus* populations will increase or remain relatively stable because of their ability to utilize detritus.

Because lower trophic level and detritivorous fishes typically are successful invaders (Peterson et al. 2006; Gido and Frannsen 2007; Gergs et al. 2008), invading fishes in general and suckermouth catfishes specifically are expected to compete with, and perhaps ultimately displace, native herbivorous fishes within central Texas drainages (Hubbs et al. 1978; Lopez-Fernandez and Winemiller 2005). Indeed, preliminary analysis of endemic Guadalupe round-nose minnow *Dionda nigrotaeniata* and central stone-roller *Campostoma anomalum* in central Texas rivers suggests moderate to high dietary similarities with *Hypostomus plecostomus* (Cohen 2008). However, dietary similarities between native and invasive herbivorous or detritivorous fishes do not necessarily equate to high levels of competition, especially because the main food resource (algae or detritus of algal origin) is typically very abundant.

Although the ability of *H. plecostomus* to competitively exclude native taxa remains unknown, introduced species in aquatic environments can have substantial impacts on nutrient cycling and ecosystem functioning (Hall et al. 2003; Gido and Frannsen 2007). *H. plecostomus* in the San Marcos River is almost exclusively supported by OM of algal origin, but algal-derived OM appears to be the dominant OM source for the entire river food web, with most consumers in the river receiving a majority of their carbon from algae. Populations of *H. plecostomus* in the San Marcos River represent a substantial trophic pathway not previously present prior to their introduction, and despite their relatively low trophic position (2.8), the likely invulnerability of *H. plecostomus* to native predators due to their armor plating and large spines might cause these populations to be in a trophic 'dead end' in the food web. Likewise, *H. plecostomus* influence nutrient cycling by disproportionately retaining and excreting nutrients (Hood et al. 2005; Higgins et al. 2006; Zimmer et al. 2006). Rates and ratios by which nutrients are recycled by fishes are a function of body nutrient composition (i.e., stoichiometry) and nutrient composition of their food (Schindler and Eby 1997; Vanni et al. 2002). Bodies of armor-plated loricariids are rich in phosphorous, resulting in high retention and low excretion of the nutrient (Vanni et al. 2002; Hood et al. 2005). If populations of *H. plecostomus* continue to increase in the San Marcos River, they might function as a phosphorous 'sink' with the potential to limit primary productivity, alter algal community composition, and diminish the quality of periphyton as a food source for algivores (Hood et al. 2005).

Aquarium and ornamental trade are significant vectors of species introductions throughout North America and are likely dominant vectors of introduction in areas with warm climates suitable for the majority of subtropical and tropical species found in these markets (Padilla and Williams 2004). In Texas, the aquarium trade is the second most significant vector for introduction of nonnative fishes, after deliberate introductions by federal and state agencies (Karatayev et al. 2009). Many of these introduced nonnative fishes occur in thermally stable spring-fed rivers (Howells 1992; Thomas et al. 2007), which are not only suitable habitats for these invaders, but also provide a refuge from cold winter temperatures. These same spring-fed rivers contain numerous

endemic species, including federally and state-listed species (Thomas et al. 2007). Indeed, the San Marcos River has a long history of successful invasions by aquarium trade species, including Mozambique tilapia *Oreochromis mossambicus*, the giant ramshorn snail *Marisa cornuarietis*, red-rimmed melania snails *Melanoides tuberculatus*, elephant ear taro *Colocasia esculenta*, and Beckett's water trumpet *Cryptocoryne beckettii* (Akridge and Fonteyn 1981; Hubbs et al. 2008; Howells 1992; Owens et al. 2001; Thomas et al. 2007). Legislation and public education (Hodge 2006) are evidently ineffective in preventing aquarium releases into the San Marcos River, but limiting transport of these kinds of organisms across state lines, such as through the Harmful or Potentially Harmful Fish, Shellfish, and Aquatic Plants legislation (21 TexReg 12414) may be a more successful measure to prevent illegal introductions. Regardless of alternatives, protecting the biotic integrity of spring-influenced aquatic systems from current and future exotic taxa is essential to long-term sustainability of the native flora and fauna and to reversing the current trends of biotic homogenization.

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