Functional Ecology

British Ecological Society

Functional Ecology 2011, **25**, 1327–1338 doi: 10.1111/j.1365-2435.2011.01883.x

Do wood-grazing fishes partition their niche?: morphological and isotopic evidence for trophic segregation in Neotropical Loricariidae

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Summary

1. Morphic detritus, including coarse particulate organic matter such as terrestrial tree leaves and wood, is consumed by few fishes in temperate stream systems but is ingested by abundant and diverse groups of specialized fishes in tropical rivers; physiological assimilation and partitioning of morphic detritus by fishes remain poorly understood.

2. This study examines seven species of Neotropical suckermouth-armored catfishes (Loricariidae) that live among and feed on coarse woody debris. Five species represent two unrelated evolutionary lineages showing convergent morphological specializations for gouging into and eating wood, small particles of which fill their guts. Two morphologically distinct species unrelated to wood-eaters and to each other forage along the surface of wood.

3. We examined six jaw functional morphological characteristics of each loricariid species as well as C and N stable isotope ratios of blood plasma, red blood cells and fin tissue of three wood-eating species and muscle tissues of all seven species. Consumer isotopic signatures were compared among species and with isotopic signatures of potential food resources, including biofilm, seston and both bulk wood and holocellulose extracted from bulk wood.

4. Wood-eating species had robust jaws specialized for gouging wood, $\delta^{13}C$ signatures consistent with assimilation of cellulosic wood carbon (not bulk wood carbon or lignin) and elevated $\delta^{15}N$ values ($> 5{\cdot}8‰$) relative to wood that were consistent with assimilation of N from intermediate microbial decomposers in the environment rather than direct assimilation of N from wood or from endosymbiotic N-fixers. Two non-wood-eating species occupied divergent regions of jaw functional morphospace, and isotopic signatures were consistent with assimilation of C from biofilm and seston, respectively, and N from enriched sources such as microbes, macroinvertebrates or seston.

5. Food resources associated with the surfaces of coarse woody debris in Neotropical rivers are partitioned among at least three guilds of loricariid consumers with divergent jaw morphologies specialized for wood gouging, surface grazing and macroinvertebrate probing. Direct consumption of morphic detritus by specialized Neotropical fishes constitutes a potentially important but poorly understood component of detritus processing and nutrient cycling in tropical rivers.

Key-words: detritivory, detritus processing, durophagy, functional morphology, resource partitioning, shredders, wood-eating, xylivory

Introduction

Up to 80% of terrestrial and 50% of aquatic primary production enters pools of detritus that are trophically inaccessible to vertebrates because of their low nutritional quality and their richness in indigestible structural plant polymers (e.g. lignin, lignocellulose; Maltby 1994; Cebrian 1999; Kleber *et al.* 2010). In aquatic ecosystems, detritus is an important basal food resource upon which many metazoan food webs are highly dependent (Winemiller 1990; Depczynski & Bellwood 2003; Wilson *et al.* 2003). The molecular structure and nutritional quality of detritus, which strongly affect its availability as a food resource, are highly variable in aquatic systems, and much of this variation is related to its origin as

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either autochthonous (aquatic) or allochthonous (terrestrial). Morphic detritus, defined by having cell wall structure, is typically allochthonous, nutritionally poor and composed mostly of structural plant polymers that make it difficult for most animals to digest (D'Avanzo, Alber & Valiela 1991; Forsberg *et al*. 1993; Alber & Valiela 1994; Hedges *et al*. 1994; Maltby 1994). Amorphic detritus lacks cellular structure and is commonly associated with the epilithic algal complex – a loose assemblage of detritus, microbes, algae and diatoms that commonly collects on submerged surfaces in aquatic systems (Hoagland, Roemer & Rosowski 1982; Van Dam *et al*. 2002; Wilson *et al*. 2003; Klock *et al*. 2007). In comparison with morphic detritus, epilithic algal complexes are rich in protein (Bowen *et al*. 1984; Wilson *et al*. 2003; Crossman, Choat & Clements 2005) and are nutritionally valuable for a wide range of aquatic invertebrates and fishes (Bowen 1979; D'Avanzo, Alber & Valiela 1991; Forsberg *et al*. 1993; Alber & Valiela 1994; Maltby 1994; Wilson *et al*. 2003).

In both temperate and tropical aquatic systems, diverse and often locally abundant invertebrate and vertebrate detritivores are adept at selectively feeding on the most labile and nutritionally rich fractions of detritus (Arsuffi & Suberkropp 1985; Wallace *et al*. 1987; D'Avanzo, Alber & Valiela 1991; Maltby 1994; Ahlgren 1996; Wilson *et al*. 2003). Morphic detritus, including coarse particulate organic matter such as allochthonous leaves and wood, is consumed by few fishes in temperate stream systems – some Asian carps (*Ctenopharyngodon idella*, *Hypophthalmichthys nobilis* and *H. moltrix*) being exceptions (Cremer & Smitherman 1980; Prinsloo & Schoonbee 1987) – but is specialized on by diverse assemblages of macroinvertebrates collectively referred to as shredders (Cummins 1973; Peterson & Cummins 1974; Cummins & Klug 1979; Maltby 1994). Studies of macroinvertebrate shredders in temperate streams demonstrate that when morphic detritus is consumed, most consumer energy and nutrition are derived not from the detritus itself, but from microbes, especially fungi, that colonize morphic detritus and are most directly responsible for its decay (Bärlocher & Kendrick 1973; Swift, Heal & Anderson 1979; Arsuffi & Suberkropp 1989; Bucher *et al*. 2004; Berg & McClaugherty 2008). Shredders are adept at selectively consuming subsets of morphic detritus colonized by fungal species that are most easily digested (Bärlocher & Kendrick 1973; Cummins & Klug 1979; Bärlocher 1980; Arsuffi & Suberkropp 1984; Maltby 1994), although the extent to which this feeding selectivity yields partitioning of detrital food resources is unknown. Furthermore, specialized consumption of morphic detritus by macroinvertebrates and the relative contribution of detrital resources to food webs have received considerable attention in temperate stream systems (Bärlocher & Kendrick 1974; Peterson & Cummins 1974; Anderson & Sedell 1979; Cummins & Klug 1979; Cummins 1994; Maltby 1994), but remain poorly studied in tropical rivers (Benstead 1996; Tomanova, Goitia & Helesic 2006).

Herein, we investigate a syntopic assemblage of seven suckermouth armored catfish species (Loricariidae) that are endemic to Neotropical rivers and known to graze heavily upon the surfaces of coarse woody debris. The family Loricariidae is highly species rich (> 800 species) and is restricted to tropical Central and South America. Loricariids display extraordinary variation in jaw structures (Schaefer & Lauder 1996; Lujan & Armbruster 2011), but relatively little interspecific variation from a generalized diet of detritus and algae, for which their intestinal physiology is highly specialized (German & Bittong 2009; German *et al*. 2010). Five of the seven loricariid species we examined have a highly derived jaw morphology allowing them to gouge into wood and selectively consume wood particles (Schaefer & Stewart 1993; Armbruster 2003; German 2009; Lujan & Armbruster 2011). Wood consumption is a dietary specialization that is unknown in fishes outside the Neotropics. Indeed, among freshwater metazoans as a whole, specialization on wood as a dietary resource is relatively rare and appears largely restricted to a few aquatic insects (Trichoptera: Calamoceratidae, Coleoptera: Elmidae; Anderson *et al*. 1978) and beavers (Rodentia: Castoridae; Vispo & Hume 1995). The complex structural molecules in wood (e.g. cellulose and lignin) are physiologically unavailable as an energy source to most animals because they lack genes coding for the requisite digestive enzymes (Maltby 1994; Lo, Watanabe & Sugimura 2003). Hence, most metazoan wood-eaters are largely dependent on microbes, including fungi and bacteria, that are able to synthesize a much broader range of digestive enzymes, including cellulases, oxidases and peroxidases needed for wood decomposition (Maltby 1994; Abdel-Raheem & Ali 2004; Bucher *et al*. 2004). To subsist on diets with large portions of cellulose and lignin, vertebrate herbivores and detritivores must either adopt microbes as endosymbionts living in various regions of the gut – these include ruminants and beavers – or they must rely on predigestion of wood by microbes that are ubiquitous in the environment. Consumers pursuing this latter strategy directly consume and assimilate bacteria and fungi, as well as compounds liberated from plant detritus by microbial enzymes.

In rivers, the relative contribution of amorphic vs. morphic detritus to metazoan food webs can be an important predictor of ecosystem function (e.g. River Continuum Concept: Vannote *et al*. 1980; Flood Pulse Concept: Junk, Bayley & Sparks 1989; Riverine Productivity Model: Thorp & Delong 2002); however, partitioning of detritus among consumer species remains poorly understood, especially in tropical rivers where detritivorous fishes are both abundant and diverse (Bowen 1983). The pre-eminent contribution of microbes to the digestive physiology of many detritivores complicates traditional investigations of resource partitioning using only visual or volumetric analyses of gut contents, which cannot resolve the relative nutritional or energetic importance of heterogeneous epilithic algal complexes (Moore 1977). A nutritional ecological approach, however, incorporating knowledge of diet, functional morphology, intake, digestive physiology and dietary assimilation (Karasov & Martinez del Rio 2007) can provide robust information with which to resolve detrital food web linkages.

To investigate the potential for partitioning of detrital resources, we examined carbon (C) and nitrogen (N) stable isotopic signatures and jaw functional morphology among syntopic wood-grazing loricariids, the digestive physiology of which has already been described (German 2009; German & Bittong 2009; German & Miles 2010; German *et al.* 2010). We determined the stable C and N isotopic signatures of several potential food resources, including biofilm, bulk wood and purified holocellulose, and of four different consumer tissues differing in isotopic turnover rate (German & Miles 2010). Isotopic analyses are especially useful for investigations of trophic diversity among detritivores because, unlike gut content analyses that capture only a snapshot of foods recently ingested, isotopic analyses integrate dietary history over periods ranging from several days to several weeks, depending on tissue-specific isotopic turnover rates (German & Miles 2010).

To better understand the potential mechanistic basis of trophic resource partitioning among these consumers, we also examined several functional morphological aspects of their jaw. We hypothesize that analysis of stable isotopes of C and N will reveal resource partitioning among wood-grazing loricariid catfishes, especially those grazing the surface of wood and those that actively ingest wood. Specifically, we expect that wood-eating loricariids will show stable C signatures consistent with the assimilation of microbial decomposers and more labile components of wood detritus (e.g. cellulose) as opposed to those of bulk wood, which includes chemically recalcitrant lignin. We also predict that wood-eating catfish will be enriched enough in nitrogen isotopes relative to bulk wood to indicate an intermediate trophic level between them and wood substrates, thereby supporting their selective assimilation of microbial decomposers and wood degradation products, as opposed to the direct assimilation of wood. For those species that lack specialized durophagous jaw morphologies and that do not actively ingest wood, we predict that stable C and N signatures will be consistent with assimilation of either biofilm or the flocculant, amorphic detritus that accumulates on wood surfaces. Given that digestive physiological characteristics are similar among wood-eating and wood-grazing loricariids (German 2009; German & Bittong 2009), we hypothesize that variation in jaw functional morphology will correspond with variation in resource assimilation.

Materials and methods

SPECIMEN AND TISSUE COLLECTION

Loricariid catfishes were collected in August 2006 by electrofishing among aggregations of coarse woody debris in middle reaches of the Marañon River, a medium-gradient whitewater tributary of the upper Amazon River in northern Peru (Fig. 1). Water physicochemical parameters at our main collecting site (approximately 4°35′22″S, 77°51′10″W) were as follows: temperature, 23·5 °C; specific conductivity, 155 μS cm^{-1}; dissolved oxygen, 7·7 mg L^{-1}, 92% saturation. Consumers and resources sampled for the isotopic component of this study were collected from a single site (Fig. 1), whereas jaw morphological data were gathered from specimens from multiple sites. In addition to the seven loricariid species examined herein (Table 1), 15 non-loricariid species and eight other loricariid species were collected syntopically. Additional loricariids not examined in this study were Ancistrini sp. (new genus, new species; $n = 9$), *Chaetostoma lineopunctatum* ($n = 1$), *Hypostomus emarginatus* ($n = 8$), *H. nicefori* ($n = 3$), *H. unicolor* ($n = 26$), *Lasiancistrus schomburgkii* ($n = 17$), *Loricaria clavipinna* ($n = 5$) and *Sturisoma nigrirostrum* ($n = 1$). Specimens were assigned to species using species checklists (Reis, Kullander & Ferraris 2003; Ortega *et al.* 2011) and a wide range of original descriptions and taxonomic revisions.

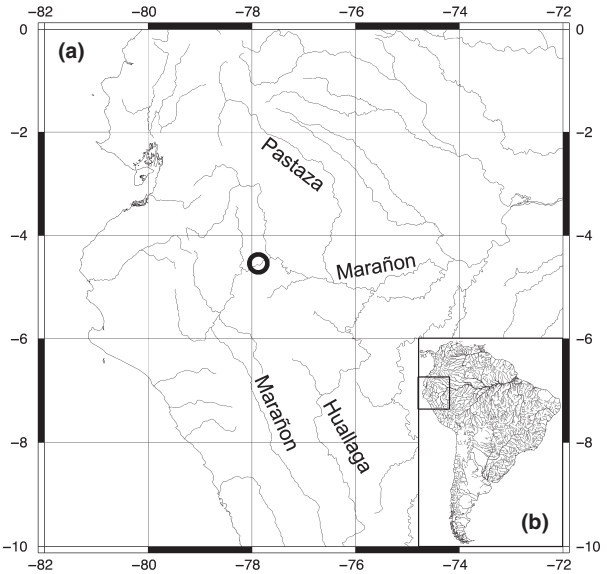

Fig. 1. Location of the study site (a, ○) in north-western South America (b).

Specimens from which plasma, red blood cell (RBC), fin and muscle tissue were collected were held in coolers of aerated river water until sampled. For *Panaque* cf. *bathyphilus*, *P. nocturnus* and *Hypostomus pyrineusi*, approximately 300 μL of blood was drawn with a 23-gauge needle from the haemal arch just posterior to the anal fin of each fish, transferred to a sterile centrifuge vial and immediately centrifuged at 13 000 ***g*** for five min in an Eppendorf 5415R desktop centrifuge (Eppendorf Inc., Hauppauge, New York) powered by a 12V car battery via a power inverter; this separated RBCs, white blood cells and plasma fractions of the blood (Reich, Bjorndal & Martínez del Rio 2008; German & Miles 2010). Following separation, RBCs and plasma were placed into separate, sterile centrifuge vials, and white blood cells were discarded. Fin clips (approximately 0·5 g wet weight) were taken with sterile scissors by cutting membranous tissue and soft, branched rays (not ossified unbranched rays) from the left or right pelvic fin and placed in separate sterile centrifuge vials.

Because these fishes were used for analyses of gastrointestinal tract structure and function (German 2009; German & Bittong 2009), they were then euthanized in buffered water containing 1 g L^{-1} tricaine methanesulfonate (MS-222, Argent Chemicals Laboratory, Inc., Redmond, WA, USA) and measured (standard length). Upon dissection, epaxial white muscle samples (approximately 0·5 g wet weight) were taken and placed in sterile centrifuge vials. Epaxial muscle samples were also taken in the same manner from *Panaque gnomus*, *P. albomaculatus*, *Lamontichthys filamentosus* and *Spatuloricaria puganensis* (Table 1). A separate but complementary set of epaxial muscle tissues were dissected from different individuals of each fish

Table 1. Total number of loricariid individuals collected from a single coarse woody debris dam in the Marañon River of northern Peru, and the number of individuals sampled for respective portions of this study. The jaw morphology data set included specimens from multiple sites within the Marañon River, and the mean, minimum (Min.) and maximum (Max.) standard lengths (SL) refer to these individuals. All individuals from which tissues for isotope analyses were sampled were at the high (adult) end of these ranges

Sample	Total Collected	Individuals sampled					No. of samples	Mandibles examined	Mean SL (mm)	Min. SL (mm)	Max. SL (mm)
		Plasma	RBC	Fin	Muscle-f	Muscle-s					
Hypostominae: Hypostomini											
Hypostomus pyrineusi	14	6	6	6	5	8		19	131	63	195
Hypostominae: Ancistrini											
Panaque albomaculatus	5				5	2		13	89	62	115
Panaque cf. *bathyphilus*	13	4	5	5	4	6		11	122	67	162
Panaque gnomus	34				4	7		30	63	51	69
Panaque nocturnus	59	7	7	5	5	7		83	103	65	145
Loricariinae											
Lamontichthys filamentosus	21				6	7		18	141	94	174
Spatuloricaria puganensis	21				3	2		9	142	100	175
Invertebrates											
Crab					3						
Shrimp					3						
Resources											
Biofilm							4				
Cellulose							4				
Seston							4				
Wood							9				

species listed above and preserved in salt according to the methods of Arrington & Winemiller (2002; Table 1).

Biofilm was sampled from pieces of wood in the same habitat from which fishes were collected. Surfaces of the wood were gently brushed, and the loosened material was collected in a ziplock bag that subsequently was sealed and shook to mix the contents. One millilitre of the resulting slurry was pipetted into 1·5-mL centrifuge vials and centrifuged at 10 000 ***g*** for 5 min. The supernatant was discarded, and the pellet was defined as 'biofilm'. Five individual biofilm subsamples (consisting of 3 mL of pooled sample each) were collected and analysed separately. Seston was collected by filtering river water through a 0·25-mm glass fibre filter. Wood that had been heavily grazed upon by wood-eating catfishes (i.e. wood from which fish were collected and which had abundant visible grazing scars) was sampled by scraping its surface with a razor blade, knife or machete. Invertebrates and wood were rinsed with deionized water. Salt-preserved muscle tissues were processed at Auburn University. Seston samples were dried in a field oven at 70 °C for 3 h and transported (dry) back to the laboratory. All other tissue samples (including blood, fin and muscle that were not preserved in salt), biofilm, wood and invertebrates were frozen in liquid nitrogen in the field and transported to the University of Florida on dry ice. Voucher specimens of all fish species collected were deposited at the Natural History Museum of San Marcos University in Lima, Peru, and at the Auburn University Museum Fish Collection in Auburn, Alabama.

HOLOCELLULOSE ISOLATION

Wood is composed of several carbon compounds, including cellulose, hemicellulose and lignin (Berg & McClaugherty 2008). Sugar products released during microbial degradation of cellulose and hemicellulose, and microbial polymers found in wood detritus (e.g. chitin), are largely metabolizable by detritivorous fishes (German & Bittong 2009). However, lignin is composed of diverse monomers, which are not metabolizable by fishes, or vertebrates in general (Karasov & Martinez del Rio 2007). Thus, from an isotopic standpoint, detritivorous fishes should not be capable of directly assimilating carbon from lignin in wood or detritus. Cellulose and hemicellulose tend to have $\delta^{13}C$ signatures about 2‰ enriched over bulk wood, whereas lignin tends to be ~4‰ depleted relative to bulk wood (Gaudinski *et al.* 2005; Bowling *et al.* 2008). Hence, assimilation of C from cellulose and/or lignin is possible to discern with stable isotopes.

To address the potential for differential assimilation of different wood C fractions, we isolated holocellulose (Leavitt & Danzer 1993; Gaudinski *et al.* 2005), which comprises the cellulosic and hemicellulosic compounds of wood, following the procedure described by German & Miles (2010). Briefly, wood was dried at 60 °C and ground to pass through a 1-mm screen, and 200–500 mg samples of the ground wood were placed in polyester solvent bags (Ankom Technology, Macedon, NY, USA). The samples were extracted in 2 : 1 toluene/ethanol in a Dionex Accelerated Solvent Extractor (ASE®), followed by extraction in 100% ethanol. The samples were then boiled for 4 h in deionized water and allowed to dry in a drying chamber at room temperature. The samples were then soaked in an aqueous bleach solution at 70 °C for 5 days. Following the bleaching, the samples were rinsed and dried at 60 °C. The remaining material was holocellulose as determined by Gaudinski *et al.* (2005).

SAMPLE PREPARATION FOR ISOTOPE ANALYSIS

Blood (RBCs and plasma solutes), fin clip and muscle samples from fish, and wood, holocellulose, invertebrate, biofilm and seston (on a glass fibre filter) samples from the habitat, were dried to a constant weight for 24–48 h at 60 °C and ground to a fine powder (Reich, Bjorndal & Martínez del Rio 2008). To eliminate the potential confounding effects of lipids on $\delta^{13}C$ values (Post *et al.* 2007), and to be consistent with a controlled laboratory study of isotopic incorporation in tissues of the loricariid catfish *Pterygoplichthys disjunctivus* (German & Miles 2010), lipids were extracted from fin and frozen muscle tissues and all resource samples using petroleum ether in a

Dionex ASE (R) [= registered trademark] (Reich, Bjorndal & Martínez del Rio 2008; German & Miles 2010). Plasma solutes and RBC samples were too small to extract lipids (German & Miles 2010). Salt-preserved muscle tissue samples were rinsed and soaked in DI water, dried and ground following the methods of Arrington & Winemiller (2002). Subsamples of all dried and ground samples were weighed to approximately 10^{-5}g and pressed into pre-cleaned Ultra-Pure tin capsules (Costech).

Wood, resources and all animal tissues except salt-preserved muscle were combusted in a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT ConFlow III device (Finnigan MAT, Bremen, Germany) to a Finnigan-MAT DeltaPlus XL (Finnigan MAT) isotope ratio mass spectrometer in the light stable isotope laboratory at the University of Florida, Gainesville. Encapsulated salt-preserved muscle tissues were dry-combusted (micro Dumas technique) with a Carlo Erba CHN elemental analyzer and passed with purified gases (CO_2 and N_2) into a Finnigan Delta C mass spectrometer at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens. Stable isotope abundances for all tissues are expressed in delta notation (δ) and defined as parts per thousand (‰) relative to a standard as follows:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively. R_{standard} for ^{13}C was Vienna Pee Dee Belemnite (VPDB) limestone formation international standard. R_{standard} for ^{15}N was atmospheric N_2. IAEA CH-6 ($\delta^{13}C = -10{\cdot}4$) and IAEA N1 ammonium sulphate ($\delta^{15}N = +0{\cdot}4$), calibrated monthly to VPDB and atmospheric N^2, respectively, were inserted in all runs at regular intervals to calibrate the system and assess drift over time. The analytical accuracy of our measurements, measured as the SD of replicates of standards, was 0·14 for $\delta^{13}C$ and 0·11 for $\delta^{15}N$ ($N = 120$).

JAW FUNCTIONAL ANALYSIS

The right lower jaw ramus (mandible; consisting of the fused dentary, mentomeckelium and anguloarticular; Geerinckx *et al.* 2007) was dissected from voucher specimens (Table 1)

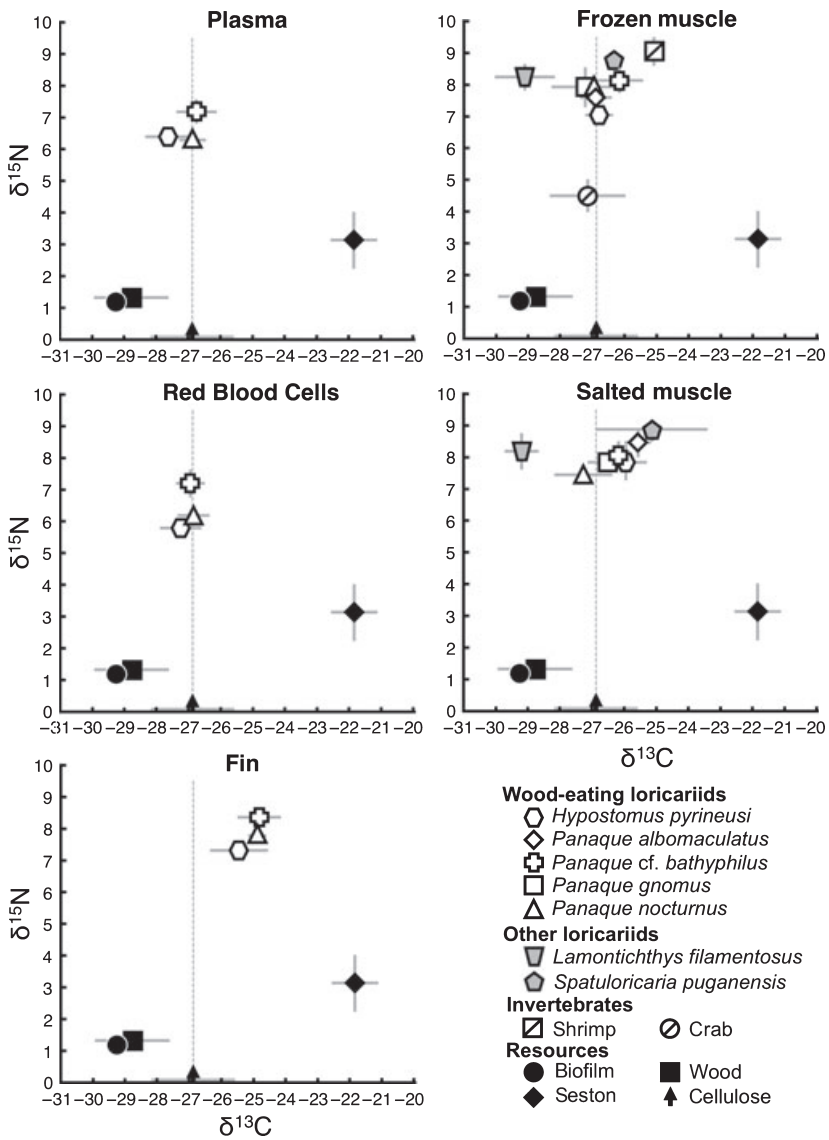

Fig. 2. Distributions in $\delta^{13}C$ vs. $\delta^{15}N$ biplot space of various tissues sampled from individuals of seven loricariid species, shrimps, crabs, biofilm scraped from wood, bulk wood, seston and holocellulose purified from bulk wood. Vertical dashed line marks the mean position along the $\delta^{13}C$ axis of purified holocellulose. Values represent mean ± standard deviation. Numbers of sampled individuals given in Table 1.

of each of the species for which we obtained isotope data. Bodies of all dissected voucher specimens are catalogued at the Auburn University Museum. Following dissection, mandibles were individually cleared and stained, and all soft tissue was removed; the stained, ossified elements were then allowed to air dry. Digital images were captured of each lower jaw element in two orthogonal perspectives using a Nikon Coolpix 990 digital camera mounted to a Leica MZ6 stereomicroscope. Jaw orientations were arbitrarily standardized using the broad anguloarticular/dentary coronoid flange as a reference, ensuring that this flange was either parallel or perpendicular to the field of view.

Five linear distances and one area (parameters) were measured from digital images of each mandible. Length and area measurements were made digitally using tpsDIG2 software (Rohlf, 2008, v. 2.12) and were individually standardized to a scale bar visible in each frame. Three of the linear distance parameters were analogous with lever arms for mandibular adduction in the majority of actinopterygians (Westneat 2004). These were measured from a midpoint along the surface of the anguloarticular condyle (AAC) to respective distalmost and proximalmost tooth insertions (output lever arms), and from a midpoint along the AAC surface to the centre of the adductor mandibulae (AM) insertion area (input lever arm).

Three parameters (two linear distance parameters and one area parameter) not typically examined in other studies of fish jaw mechanics were also measured. Distance from the most proximal to the most distal tooth insertions (tooth row length or TRL) was measured to provide an indication of the area across which force transmitted through the mandible may be instantaneously distributed. A distance perpendicular to the line between the anguloarticular condyle and the most distal tooth and from that line to the apex of the coronoid arch was also measured to quantify interspecific variation in the height or maximum excursion of the coronoid arch. Finally, area across which the AM muscle inserts (AM_{area}) was measured. AM_{area} correlates with adductor mandibular volume (Lujan & Armbruster 2011) and is interpreted as being proportional to maximum force deliverable to the mandible. Morphometric methods follow those of Lujan & Armbruster 2011) and a more complete description of methods and discussion of the functional relevance of measured parameters can be found therein.

STATISTICAL ANALYSIS

Differentiation of loricariid species along $\delta^{13}C$ and $\delta^{15}N$ axes was statistically examined by first applying nonparametric Kruskal–Wallis rank sum test to each tissue data set and then conducting *post hoc* pairwise comparison of means using a Wilcoxon signed-rank test. Tissue–diet discrimination factors empirically determined for the loricariid *Pterygoplichthys disjunctivus*, as well as those predicted by equations designed for fish (Caut, Angulo & Courchamp 2009), were combined with gut content analysis (German 2009) to make dietary inferences. Principle component analysis (PCA) was used to examine the multivariate differentiation of jaw morphologies quantified by the six parameters defined earlier. Loricariids span a wide range of body shapes, from long and slender to short and stout, thereby preventing standardization of jaw morphometrics to any comparable measure of body size (e.g. body mass and standard length). We therefore conducted a PCA on raw morphometric data and examined distributions of taxa in mandibular morphospace using PCs 2–4. PC1 eigenvectors were entirely positive (Table 2), which is interpreted as a gradient of body size variation, whereas PCs 2–4 span a range of positive and negative values (Fig. 3, Table 2) indicative of variation in shape (Cadima & Jolliffe 1996). Statistical analyses were performed using JMP software (v. 5.0.1; SAS Institute Inc.).

Results

STABLE ISOTOPES

Most tissues of wood-eating loricariids (all samples except *H. pyrineusi* plasma) were significantly enriched in ^{13}C relative to bulk wood ($P < 0{\cdot}02$, Kruskal–Wallis test; $P < 0{\cdot}05$, Wilcoxon test). In contrast, $\delta^{13}C$ signatures of most tissues of wood-eating species were statistically indistinguishable from that of cellulose extracted from recently grazed wood. $\delta^{13}C$ signatures of plasma and RBCs of the wood-eating loricariids *H. pyrineusi*, *P.* cf. *bathyphilus* and *P. nocturnus* were statistically indistinguishable from each other and from cellulose (Fig. 2). Frozen and salt-preserved muscle tissues from these

Table 2. Eigenvectors and per cent variance explained by each principle component (PC) in a PC analysis of six morphometric variables measured from the mandibles of seven loricariid species (Fig. 2, Table 1). Measured aspects of each mandible included height of the coronoid arch (H1), adductor mandibular insertion area (AM_{area}), length of the input lever arm (In), length of an output lever arm to the distalmost tooth (Out_{dist}), length of an output lever arm to the proximalmost tooth (Out_{prox}) and tooth row length (TRL). Maximum and minimum eigenvectors for each PC in boldface

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	5·3	0·4	0·2	0·1	0·0	0·0
% variance	88·2	6·7	2·8	1·3	0·7	0·4
Cumulative %	88·2	94·9	97·6	99·0	99·6	100·0
Eigenvectors						
H1	0·414	−0·300	−0·173	**0·743**	**0·386**	−0·080
AM_{area}	0·410	−0·007	**0·766**	−0·270	0·383	−0·160
In	0·415	**−0·379**	0·225	0·068	**−0·689**	0·392
Out_{dist}	**0·427**	0·070	**−0·289**	−0·188	−0·330	**−0·765**
Out_{prox}	0·417	−0·139	−0·499	**−0·537**	0·336	**0·395**
TRL	**0·363**	**0·861**	−0·012	0·216	−0·085	0·270

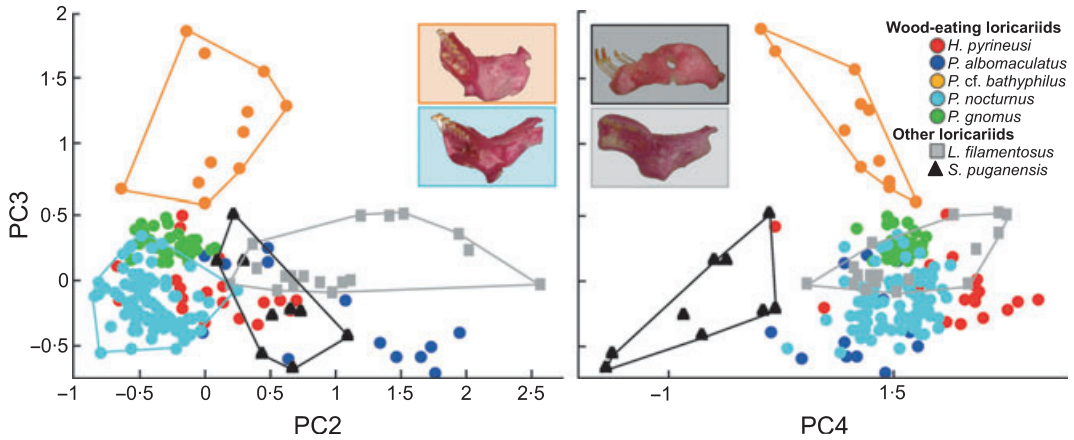

Fig. 3. Distributions of loricariid mandibles in multivariate morphospace described by a principle component (PC) analysis of six functionally relevant parameters measured from each mandible. Species sample sizes given in Table 1 and eigenvectors describing the relative contribution of each morphometric parameter given in Table 2.

species plus the wood-eating *Panaque albomaculatus* and *P. gnomus* likewise yielded $\delta^{13}C$ signatures indistinguishable from each other and from cellulose (Fig. 2). In contrast to muscle and blood, fin tissues of wood-eating loricariids were significantly ^{13}C-enriched relative to purified cellulose (Fig. 2, $P < 0{\cdot}05$, Wilcoxon test), which is consistent with previous laboratory studies demonstrating relatively high $\Delta^{13}C_{tissue\text{-}diet}$ discrimination between food resources and loricariid fin tissue, and a difference among fin and other tissues sampled from the same individuals (German & Miles 2010).

Of the loricariids examined herein, only *L. filamentosus* was statistically distinguishable from other loricariids in $\delta^{13}C$ ($P < 0{\cdot}02$, Kruskal–Wallis test). Both frozen and salt-preserved muscle tissues from *L. filamentosus* were significantly depleted in $\delta^{13}C$ relative to other loricariids ($P < 0{\cdot}05$, Wilcoxon test), and closely matched $\delta^{13}C$ values measured for biofilm brushed from wood at the field site.

In contrast to considerable homogeneity in $\delta^{13}C$, loricariid consumers showed significant $\delta^{15}N$ differentiation in each of the examined tissues ($P < 0{\cdot}02$, Kruskal–Wallis test). Among wood-eating loricariids, plasma, RBC and fin tissues of *P.* cf. *bathyphilus* were more ^{15}N-enriched than those of *P. nocturnus* ($P < 0{\cdot}05$, Wilcoxon test). *Panaque* cf. *bathyphilus* plasma, RBC, fin and frozen muscle tissues were also more ^{15}N-enriched than those of *H. pyrineusi* ($P < 0{\cdot}05$, Wilcoxon test), as were fin and frozen muscle tissues of *Panaque nocturnus*, and frozen muscle tissues of both *P. gnomus* and the non-wood-eaters *L. filamentosus* and *S. puganensis*

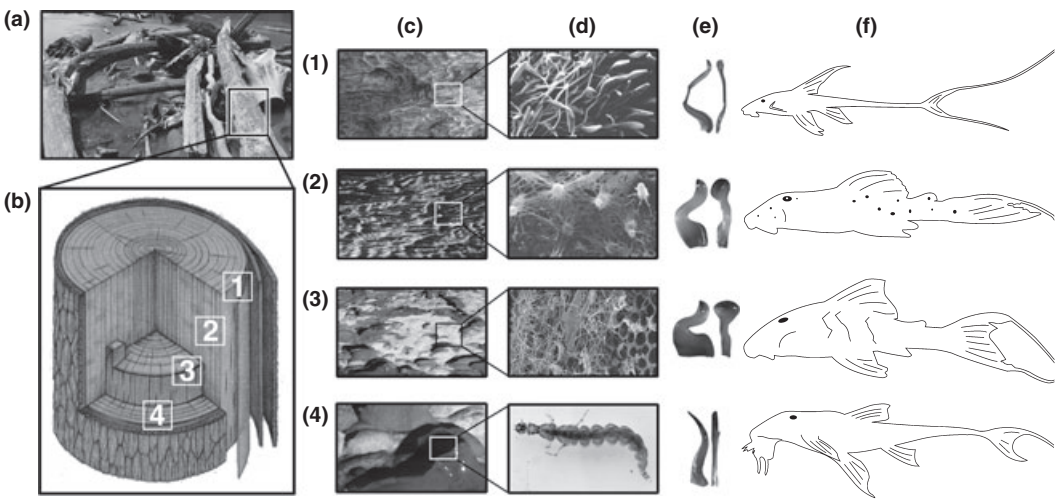

Fig. 4. Summary of trophic segregation observed among syntopic loricariid catfishes occupying coarse woody debris (a) in the upper Amazon Basin (Fig. 1). We conclude, based on C and N stable isotope data (Fig. 2) and mechanical properties of the mandible (Fig. 3), that loricariids partition wood-associated food resources in a manner corresponding to the approximate depth (b) of wood surfaces being grazed or browsed. *Lamontichthys filamentosus* (f1) uses relatively weak mandibles with numerous, gracile teeth (e1) to graze biofilm (d1) that grows on wood surfaces (c1). Several *Panaque* species, including *P. albomaculatus* (f2), use stronger mandibles and stouter teeth (e2) to scrape and ingest shallow layers of wood (c2) and associated microbes (d2), whereas *P.* cf. *bathyphilus* (f3) has robust mandibles and teeth (e3) that it uses to gouge and ingest deeper wood layers (c3) and associated microbes (d3). *Spatuloricaria puganensis* (f4) uses medial clusters of stout, elongate teeth (e4) to probe and browse crevices (c4) for detritus and insect larvae (d4). Images (d1) and (d2) from Hoagland, Roemer & Rosowski (1982) and (d3) from Moskal-del Hoyo, Wachowiak, & Blanchette (2010), used with permission. Fish illustrations by Jason German.

($P < 0{\cdot}05$, Wilcoxon test). Frozen muscle tissues of *S. puganensis* were also more ^{15}N-enriched than those of *P. albomaculatus*, and salted muscle tissues of *S. puganensis* and *L. filamentosus* were more ^{15}N-enriched than those of *Panaque nocturnus* ($P < 0{\cdot}05$, Wilcoxon test).

Overall, ^{15}N tissue–diet discrimination factors ($\Delta^{15}N_{tissue\text{-}diet}$) of wood-eating catfishes were high ($> 5{\cdot}8‰$) in comparison with values obtained from a laboratory study of the loricariid *Pterygoplichthys disjunctivus* (4·1–5·2‰; German & Miles 2010), which suggests that some of these catfishes may have assimilated N from a unknown basal resource or, alternatively, existence of an intermediate trophic level between wood and certain catfish species. Total $\delta^{15}N$ range of the loricariids examined herein spanned $< 1{\cdot}5‰$, suggesting that significant differences in $\delta^{15}N$ signatures likely reflect variation in the relative protein content of foods being ingested (Kelly & Martinez del Rio, 2010), but do not indicate distribution of these consumers across more than one trophic level. None of the loricariids revealed strong evidence of having assimilated carbon from seston, which was significantly enriched in ^{13}C relative to all consumers.

JAW FUNCTIONAL MORPHOLOGY

Principal component analysis revealed jaw morphological variation and inferred functional differentiation among loricariid species (Fig. 3). Eigenvectors and % variance explained by the PCA of mandibular functional parameters are given in Table 2. Interspecific morphological differences in loricariid jaws corresponded to a large degree with interspecific differences in isotope biplot space. *Panaque* cf. *bathyphilus*, which was consistently $\delta^{15}N$-enriched relative to other wood-eating loricariids, occupied a unique region of jaw morphospace, particularly with respect to PC axis 3. This pattern was strongly influenced by the large AM area of insertion (AM_{are}) in *P.* cf. *bathyphilus* (Table 2), which indicates a larger AM muscle and a more forceful jaw. The other wood-eating loricariids examined here revealed little separation in mandibular morphospace.

Lamontichthys filamentosus, which was the only species showing $\delta^{13}C$ values consistent with the assimilation of biofilm growing on the surface of wood, segregated from most other species in jaw morphospace by having high PC2 values, which were strongly influenced by the presence of long tooth rows (TRL, Table 2). The teeth of *L. filamentosus* are also more gracile and flexible relative to those of the specialized wood-eating loricariids examined here (Fig. 4). *Spatuloricaria puganensis*, which has distinctively elongated teeth (Fig. 4), segregated from most other species in mandibular morphospace by having low PC4 values. These were driven mostly by high Out_{prox} values, indicating relatively greater distances between the AAC and the proximalmost tooth, and a more medially displaced tooth cup. Medial displacement of the tooth cup, in combination with the long teeth of *S. puganensis*, suggests that this loricariid is able to insert its jaws and teeth deep into crevices to remove aquatic insects. Moreover, observations of aquatic insects in the gut contents of *Spatuloricaria* species from other locations in South America (Melo, Machado & Pinto-Silva 2004) are consistent with this foraging mode and with the relatively enriched $\delta^{15}N$ values observed for *S. puganensis*.

Discussion

Stable isotope data suggest that trophic resources associated with the surfaces of coarse woody debris in Neotropical rivers are partitioned among at least three guilds of loricariid consumers with divergent jaw morphologies, respectively specialized for wood gouging, surface grazing and macroinvertebrate probing (Fig. 4). Species known to be selective consumers of wood based on previously published gut contents data (Schaefer & Stewart 1993; Armbruster 2003; German 2009) had $\delta^{13}C$ signatures closely matching the mean signature of holocellulose extracted from bulk wood collected from the fishes' habitat (Fig. 2). Although wood particles compose 70–75% of wood-eater gut contents, lesser fractions of other items, including amorphic detritus, diatoms and algae, are also ingested (German 2009). $\delta^{13}C$ values of biofilm and seston, respectively depleted and enriched in ^{13}C relative to cellulose (Fig. 2), suggest that differential assimilation of these carbon sources might provide an alternative hypothesis for wood-eater $\delta^{13}C$ signatures. Although such mixing would not require assimilation of wood-degrading microbes (which largely reflect the $\delta^{13}C$ of holocellulose; Boström, Comstedt & Ekblad 2008), examination of this hypothesis with a linear mixing model did not fully account for the observed $\delta^{13}C$ enrichment of wood-eater tissues (D. P. German, unpublished data). Our findings suggest that wood-eating loricariids are indeed assimilating microbially derived C, and this is further supported by fish tissues having $\delta^{15}N$ values $> 5{\cdot}8‰$ larger than bulk wood, which is greater than the range for tissue–diet discrimination (4·1–5·2‰) predicted from a controlled laboratory study of the loricariid *Pterygoplichthys disjunctivus* (German & Miles 2010) or from regression equations designed specifically for fish tissues (Caut, Angulo & Courchamp 2009). Our conclusion is that wood-eating loricariids, like many other detritivores, assimilate carbon from microbial sources and are not capable of direct assimilation of wood carbon.

The primary microbial decomposers of wood that is submerged under aerobic conditions are non-fruiting, ascomycete fungi commonly known as aquatic or Ingoldian hyphomycetes (Révay & Gönczöl 1990; Maltby 1994; Gönczöl & Révay 1997). Although tissue–substrate discrimination factors of hyphomycetes are unavailable, related groups of basidomycete fungi, which are more common terrestrial decomposers of wood, exhibit $\Delta^{15}N_{tissue\text{-}diet}$ enrichment rates from $+0{\cdot}9 \pm 0{\cdot}4‰$ (Gebauer & Taylor 1999) to $-0{\cdot}6 \pm 0{\cdot}7‰$ (Kohzu *et al.* 1999). Assuming that hyphomycetes have similar ranges of $\Delta^{15}N_{tissue\text{-}diet}$ enrichment, the assimilation of fungal material by loricariids could easily explain the ~0·6–1·7‰ difference between expected $\delta^{15}N$ signatures of loricariid consumers, given wood as a source for N, and those observed. German & Bittong (2009) measured

the digestive enzyme activities of three of the wood-eating loricariid species examined in this study and assayed for chitinase activities needed for digestion of fungal cell walls. They found elevated (>1 mM) concentrations of *N*-acetyl-glucosamine, the monomer of chitin and elevated *N*-acetyl-β-D-glucosaminiase activities in the fishes' guts, both of which suggest efficient chitin digestion. Fungal hyphae are typically too small to see with a light microscope, which may explain why they have generally escaped the attention of previous gut content studies, but SEM images of wood-eater gut contents (German 2009) confirm that fungal hyphae are ingested with wood. Moreover, the entire digestive strategy of wood-eating loricariids – high intake, rapid gut transit, low cellulose digestibility, as well as elevated chitin, protein and soluble polysaccharide-degrading enzyme activities (German 2009; German & Bittong 2009) – suggests that these fish cannot efficiently digest wood in their digestive tracts, but instead efficiently digest microbes and microbial digestive by-products produced during wood decomposition.

The specialized wood-eating loricariids we examined include representatives of two different evolutionary lineages, separated from each other at the taxonomic rank of tribe, and convergent in mandibular functional morphology, dentition and diet (Armbruster 2004, 2008). Four of the examined species are members of the genus *Panaque* (tribe Ancistrini), which is broadly distributed in tropical South America (Lujan, Hidalgo & Stewart 2010) and features a number of morphological synapomorphies that likely enhance the production and transmission of force during feeding (Schaefer & Stewart 1993). *Hypostomus pyrineusi* is a member of the monophyletic *H. cochliodon* group, which is also broadly distributed in tropical South America (Armbruster 2003), and shares with *Panaque* the presence of short, highly angled rows of a few, stout teeth, each having a unicuspid crown with the concave, adze-like shape of a carpentry instrument (Figs 3 and 4, Table 3). In a broad comparison of phylogenetically diverse loricariids (Lujan & Armbruster 2011), the morphometric parameters measured herein revealed further evidence that wood-eating loricariids are derived and specialized within their respective tribes and are convergent in aspects of mandibular functional morphology that likely serve to enhance force production, concentration and mechanical advantage. Among the examined species, *P.* cf. *bathyphilus* appears to have extended these specializations to such an extreme that it occupies a unique region of mandibular morphospace relative to all other species investigated (Fig. 2) and, indeed, a wide range of loricariids not examined in this study (Lujan & Armbruster 2011). Eigenvectors for the PC3 axis (Table 2) indicate that distinctiveness of the *P.* cf. *bathyphilus* mandibles is mostly due to enlargement of the AM insertion area (AM_{area}), which predicts a larger adductor muscle (Lujan & Armbruster 2011) and an increased maximum force deliverable to the mandible.

The convergence of durophagous jaw morphologies among wood-eating loricariids together with gut contents and stable isotope data provides strong support for the hypothesis that wood-eating is an adaptative specialization as opposed to a facultative foraging tactic. The $\delta^{15}N$ enrichment of wood-eating loricariids beyond what would be expected from direct assimilation of N from wood or from endosymbiotic N-fixers (i.e. reliance on N-fixers would result in low $\delta^{15}N$ signatures; Tayasu *et al.* 1997), combined with the role that fungi commonly play in decomposing submerged wood, suggest that loricariids derive this fitness advantage by accessing energy and nutrients not from wood *per se*, but from more labile forms of detritus, fungi and bacteria embedded in the wood matrix. Consistent $\delta^{15}N$ enrichment of *P.* cf. *bathyphilus*, even beyond the levels of other wood-eating loricariids (Fig. 2), combined with its extreme morphological specialization, suggests that its stronger jaws likely enable the consumption of a distinctive component of the wood surface. The stronger jaws of *P.* cf. *bathyphilus* may enable it to gouge deeper and/or more forcefully into wood than other loricariids (Fig. 4). Although more research is needed, available data on the spatial distribution of aquatic hyphomycetes on submerged wood suggest that there may be selective advantages to gouging deeper into wood. In a study of the spatial dynamics of hyphomycete fungi colonizing submerged wood, Gönczöl & Révay (1997) found that cut surfaces of heartwood supported significantly higher fungal activity than outer layers. Therefore, by having a mandible capable of gouging deeper into wood, *P.* cf. *bathyphilus* may be able to gain access to greater densities of nutritious fungi.

In contrast to specialized wood-eaters, *L. filamentosus* had a $\delta^{13}C$ signature closely matching the signatures for biofilm and bulk wood (Fig. 1). Gut contents of *Lamontichthys*

Table 3. Characteristics of the teeth of each species examined herein. Tooth counts are for a single mandibular ramus

Sample	No. of teeth	Cusp shape	Shaft length	Ref.
Hypostominae: Hypostomini				
Hypostomus pyrineusi	8	Spoon	Short	Armbruster 2003
Hypostominae: Ancistrini				
Panaque albomaculatus	4	Spoon	Long	Schaefer & Stewart 1993
Panaque cf. *bathyphilus*	6	Spoon	Short	NKL unpublished data
Panaque gnomus	7	Spoon	Short	Schaefer and Stewart 1993
Panque nocturnus	6	Spoon	Short	Schaefer and Stewart 1993
Loricariinae				
Lamontichthys filamentosus	60	Spade	Long	Paixão & Toleda-Piza, 2009
Spatuloricaria puganensis	4	Spade	Long	NKL unpublished data

consist largely of amorphic detritus (N. K. Lujan, pers. obs.), and their dentition and jaw morphology (Figs 3 and 4) appear to be designed for scraping biofilms and lack features associated with an ability to gouge into wood. The mandible of *L. filamentosus* differs from those of other loricariids that we examined by having a long tooth row (Fig. 2, Table 2), and up to 10 times as many teeth, each of which is very small and weak compared with the teeth of wood-eaters (Figs 3 and 4, Table 3). The relatively large difference between $\delta^{15}N$ signatures of biofilm and *L. filamentosus* muscle tissue also suggests that this species is either largely dependent upon an intermediate consumer or that it selectively consumes relatively protein-rich or ^{15}N-enriched components of the biofilm matrix (Kelly & Martinez del Rio, 2010).

The most ^{15}N-enriched of the loricariid species examined was *S. puganensis* (Fig. 2), which has teeth that are sturdy and few in number, like those of wood-eating species, but are more elongate and acuate than even the teeth of *L. filamentosus* (Fig. 4). Although stomach contents data are lacking for *S. puganensis*, the genus *Spatuloricaria* has been reported by several authors (Saul 1975; Vanni *et al*. 2002; Melo, Machado & Pinto-Silva 2004) to be at least partially insectivorous. This conclusion based on stomach contents data suggests that an intermediate trophic level is likely contributing to the elevated $\delta^{15}N$ signature of *S. puganensis*; however, the slightly greater assimilation of more ^{15}N-enriched seston resources, suggested by the greater ^{13}C enrichment of *S. puganensis* relative to other loricariids, may also be a factor. Regardless, the long, sharp and sturdy teeth of *S. puganensis* (Fig. 4), plus its elongate mandibles that are morphologically distinct from those of all other loricariids (PC4 axis, Fig. 3), suggest that it may be specialized for probing and prying insect larvae from crevices. Marrero & Winemiller (1993) observed that clay nodules, which are abundant in many tropical rivers, were filled with holes occupied by mayfly (Ephemeroptera: Polymitarcidae), caddisfly (Trichoptera: Hydropsychidae) and true fly (Diptera: Chironomidae) larvae, and they hypothesized that the distinctive tubular snouts of several species of electric fish in both the New World (Gymnotiformes: Apteronotidae, Rhamphichthyidae) and Old World (Osteoglossiformes: Mormyridae) are likely convergent adaptations for the extraction and consumption of such crevice-dwelling insects. Although *S. puganensis* lacks a tubular snout, its elongate teeth that are centrally clustered on elongate mandibles may have a similar function.

Jaw morphologies and dietary niches of wood-eating, surface-grazing and macroinvertebrate-probing loricariids largely parallel feeding guilds previously recognized among coral reef fishes, inviting comparison between these diverse fish assemblages. Both coral reefs and coarse woody debris dams are defined by relatively stable and highly three-dimensional structures that are internally nonliving, but support surficial layers of complex and heterogeneous assemblages of heterotrophs and autotrophs. Food webs of both habitats are also strongly dependent upon detritus (Winemiller 1990; Depczynski & Bellwood 2003; Wilson *et al*. 2003). The surface gouging jaw morphology and foraging mode observed here among wood-eating loricariids in the genera *Hypostomus* and *Panaque* warrant comparison with surface excavating, coral-livorous parrotfishes (Labridae: Scarinae), fishes that also have highly specialized, durophagous jaws (Bellwood & Choat 1990) and intestinal physiologies specialized for the digestion of detritus (Crossman, Choat & Clements 2005). In a detailed anatomical and behavioural analysis of the jaws and feeding of 24 parrotfishes from the Great Barrier Reef, Bellwood & Choat (1990) recognized two distinct functional feeding groups: strong-jawed excavators and weaker-jawed scrapers. These groups clearly ingest different portions of the reef matrix (Choat, Clements & Robbins 2002), and there may be a selective advantage gained by parrotfishes gouging deeply into the reef, as they can access endolithic algae and heterotrophs, which can account for up to 50% of reef productivity (Tribollet *et al*. 2006).

Fishes that scrape surfaces using numerous small, weak and elongate teeth aligned in transverse rows are abundant on coral reefs (Depczynski & Bellwood 2003) and include various taxa in the diverse families Acanthuridae, Blenniidae and Pomacanthidae (Motta 1988; Konow *et al*. 2008). Most of these reef fishes, like most loricariids, were once commonly perceived to be algivores; however, more detailed dietary analyses have revealed many to be highly dependent on detritus scraped from the epilithic algal complex (Depczynski & Bellwood 2003; Wilson *et al*. 2003). Specialized browsers that selectively probe crevices with elongate mandibles and medially clustered teeth, like the foraging mode hypothesized for *S. puganensis*, are also common on coral reefs. Indeed, species of the family Chaetodontidae display a wide range of jaw lengths, some of which (e.g. *Chaetodon trifasciatus*) are relatively abbreviated and comparable to *S. puganensis*, whereas others are extremely elongate and tube-snouted (e.g. *Forciper* spp.) in a manner similar to tube-snouted electric fishes of tropical inland waters (Marrero & Winemiller 1993).

The morphological and isotopic diversity of fishes ingesting and assimilating coarse woody detritus in the Marañon River of northern Peru suggest that even relatively refractory allochthonous detritus may be an important basal resource for metazoan food webs in Neotropical rivers. Loricariids appeared to be the most abundant members of the fish assemblage associated with coarse woody debris at our field site, composing approximately 70% of all individuals collected via electroshocking (237 of 337 individual fishes; N. K. Lujan, unpublished data). Although the biogeographic distributions of wood-eating loricariids remain coarsely described, their diversity and abundance appear to be greatest in mid- to large-size piedmont rivers (Schaefer & Stewart 1993; Armbruster 2003; Lujan, Hidalgo & Stewart 2010), where loricariids are also known to play an important role in nutrient cycling by selectively consuming and retaining phosphorus (Hood, Vanni & Flecker 2005; Knoll *et al*. 2009). These patterns and processes contrast with those in temperate rivers where shredders are primarily arthropods and are most abundant in headwaters, and where even detritivorous fishes are more stoichiometrically balanced (Peterson & Cummins 1974; Anderson & Sedell 1979; Vannote *et al*. 1980; Schindler & Eby 1997). Studies of macroinvertebrate-dominated Neo-

tropical streams outside of the Amazon Basin have tended to support the River Continuum Concept (Greathouse & Pringle 2006; Tomanova *et al*. 2007). However, our results and others from the central Amazon Basin (Wantzen & Wagner, 2006; Chara *et al*. 2007) indicate that this model may not describe patterns and dynamics in tropical continental rivers. To refine models of longitudinal river dynamics for application to these rivers, improved understanding of fish detritivory and shredding is needed. Rapidly expanding threats to the natural function of Neotropical rivers from deforestation (Anderson & Maldonado-Ocampo 2011), hydroelectric projects (Killeen 2007) and overfishing (Garcia *et al*. 2009) add urgency to this research.

Acknowledgements

We gratefully acknowledge Jonathan W. Armbruster and Alex S. Flecker for enthusiastic discussions of wood-eating loricariids and for financial and logistical support of the PER06 expedition on which samples for this study were collected; Krista A. Capps for field assistance and water physicochemical data; Darwin Osorio, Donald Taphorn and David C. Werneke for logistical support and assistance in collecting specimens; Hernan Ortega and Blanca Rengifo of the Natural History Museum of San Marcos University for permits and logistical support of fieldwork; Tom Maddox of the University of Georgia Stable Isotope Lab and Jason Curtis of the University of Florida Light Isotope Lab for conducting stable isotope analyses Jason German for illustrations and layout in Fig. 4; K. Hoagland and the Botanical Society of America for permission to reproduce images (d1) and (d2) in Fig. 4; and Magdalena Moskal-del Hoya and Elsevier for permission to reproduce image (d3) in Fig. 4. This study is a product of the Planetary Biodiversity Inventory: All Catfish Species (NSF DEB-0315963). Additional funding came from Archie Carr Center for Sea Turtle Research, an American Society of Ichthyologists and Herpetologists Raney Award (to DPG), NSF grant IOB-0519579 (D.H. Evans, PI), R.D. Miles of the University of Florida, and the estate of George and Carolyn Kelso via the International Sportfish Fund.

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Received 18 December 2010; accepted 31 May 2011
Handling Editor: Peter Wainwright