Relationship between morphology and diets of six neotropical loricariids

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Most loricariids are algivorous and detritivorous and play an important role in both the grazer and detritus food chains of neotropical waters. Relationships between morphological variation and diet were analysed in six syntopic species (*Rhinelepis aspera, Hypostomus regani, H. ternetzi, H. margaritifer, H. microstomus* and *Megalancistrus aculeatus*) fished commercially in a 10 km² area of the Upper Paraná River upstream from the Itaipu Reservoir. Species feeding on fine grained detritus use suction to obtain food, and possess a well-developed respiratory membrane, long gill rakers, rudimentary labial and pharyngeal teeth, a thin stomach wall, and a long intestine. Species feeding on coarser material (e.g. periphyton), ingest food by scraping the substratum. Their morphological characteristics are large, strong, spatulate teeth, short gill rakers, a well-developed stomach, and a shorter intestine. The first species group is composed by *R. aspera* while the latter by *M. aculeatus* and *H. microstomus*. The others species had an intermediary position.   © 2001 The Fisheries Society of the British Isles

Key words: detritivorous; diet; feeding strategies; illiophagy; Loricariidae; tropical fish.

INTRODUCTION

In the tropics, the aquatic detritus food chain includes a great variety of specialized fishes (Lowe McConnell, 1987), which constitute an important link in the bioenergetics of ecosystems. The best known detritivorous families are the Prochilodontidae, Curimatidae, and Loricariidae of South America, and some Cichlidae and Cyprinidae of Africa and Asia. The Loricariidae (the sucker mouth armoured catfishes) comprise *c.* 600 species distributed in the neotropics (Lowe McConnell, 1987), and are one of the largest and most specialized groups among the siluriforms (Gosline, 1947). They possess special adaptations involving morphology, feeding behaviour and digestive processes for feeding on detritus (Gerking, 1994).

Several studies have shown relationships between shape and feeding ecology, encompassing fish assemblages or groups of related fish (Liem, 1974; Motta, 1988; Winemiller, 1992; Norton, 1995; Winemiller *et al*., 1995; Adite & Winemiller, 1997; Bouton *et al*., 1998; Hugueny & Pouilly, 1999). Functional morphology of loricariids was examined by Angelescu & Gneri (1949), Power (1983, 1984), Py-Daniel (1984), Buck (1994), Buck & Sazima (1995), Fugi (1993) and Fugi *et al*. (1996). General observations on the feeding habits of

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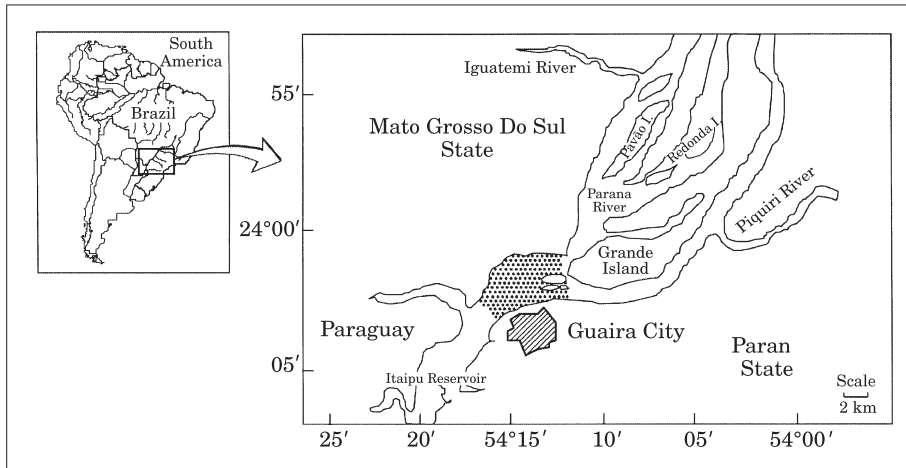
Fig. 1. Map indicating the sampling stations in the transition area between Itaipu Reservoir and Paraná River.

Hypostomus are found in literature dealing with community ecology (Uieda, 1984; Arcifa & Meschiatti, 1993; Meschiatti, 1995; Hahn *et al.*, 1997). According to these studies, loricariids feed mainly on sediment, detritus, periphyton and invertebrates scraped from the surface of the substratum. The aim of this research was to analyse the trophic morphology and its relationship with the diet of six sympatric loricariid catfishes.

MATERIALS AND METHODS

The investigation was conducted on a stretch of the Paraná River *c.* 7 km upstream from the former Sete Quedas waterfalls inundated by the Itaipu Reservoir, Guaíra PR Brazil. The collection site was within the transition area between the Itaipu Reservoir and upstream Paraná River, in which the substratum is rocky (Fig. 1).

Morphological, biometric, and diet information of six species of Loricariidae, *Rhinelepis aspera* (Agassiz, 1829), *Hypostomus regani* (Von Iheringer, 1905), *H. ternetzi* (Boulenger, 1895), *H. margaritifer* (Regan, 1905), *H. microstomus* (Weber, 1908) and *Megalancistrus aculeatus* (Perugia, 1891), was obtained from specimens captured monthly by cast and gill nets during August 1996 and April 1997. Ten specimens of different sizes of each species were used for the morphological study of the digestive tract, except for intestine length measures. Specimens were measured, fixed in 10% formaldehyde, and sent to the laboratory. They were dissected, described, and sketched with the aid of a microscope and camera lucida. Teeth on the right maxilla were counted and their width measured from the junction base to the crown using a stereoscopic microscope with ocular micrometer. The length of the uncoiled intestine, was measured from stomach insertion to anus.

Estimation of diet was achieved by analysis of stomach contents. For individuals with empty stomachs, contents were examined from the anterior 5% of the intestine. Stomach contents of each species were analysed under the microscope and described according to occurrence and volumetric methods (Hyslop, 1980). Due to difficulty in separating some food items, volume was estimated from percentage values attributed to each item in relation to total volume of the stomach contents. Items were identified to the lowest possible taxonomic level using identification keys developed by Bourrelly (1972, 1981, 1985) and Pennack (1989). The term detritus was used to describe the amalgam of fine organic material in different stages of decomposition.

TABLE I. Number of teeth in the upper and lower hemimaxillaries, and width of teeth for the six studied species

	Upper maxillary teeth N (average)	Lower maxillary teeth N (average)	Width of teeth Average (s.d.)
R. aspera	45–70 (52)	40–62 (47)	0·15 ($\pm$ 0·003)
H. regani	60–104 (86)	58–114 (82)	0·27 ($\pm$ 0·02)
H. ternetzi	50–105 (77)	49–109 (85)	0·23 ($\pm$ 0·02)
H. margaritifer	25–32 (30)	27–30 (28)	0·42 ($\pm$ 0·14)
H. microstomus	09–16 (11)	11–16 (13)	0·48 ($\pm$ 0·07)
M. aculeatus	08–12 (10)	09–13 (11)	0·97 ($\pm$ 0·08)

Analysis of covariance (ANCOVA) was applied to test differences in intestine length among species. This method was used to remove the effect of fish length (L_S, co-variable; Huitema, 1980). Adjusted averages for intestine length were evaluated according to their significance by a Tukey *post hoc* comparison test of averages. Since the relationship between intestine length (L_i) and standard length of fish (L_S) was not linear, intestine length was natural log transformed.

The relative importance of food items was evaluated using the index of food importance (I) as follows:

$$I = 100 \ OV . (\Sigma \ OV)^{-1}$$

Where $O = \%$ occurrence and $V = \%$ volume.

Mantel's test of matrix comparison was used to test the hypothesis that food similarity may be correlated with morphological similarity (Douglas & Matthew, 1992; Fortin & Gurevitch, 1993). The food similarity matrix was calculated using scores of two DCA (detrended correspondence analysis) axes applied to the I data. The morphological similarity matrix was created based on qualitative data of each morphological characteristic (shape of mouth and jaws, number and width of teeth, pharyngeal teeth, structure of gill rakers, presence and development of stomach, and length and width of intestine) using Jaccard's coefficient.

RESULTS

MORPHOLOGY OF THE DIGESTIVE TRACT

Position and shape of the mouth

For all six species, the position of the mouth is ventral and the lips form a sucker. The upper lip is less developed than the lower and possesses a pair of barbels. Both upper and lower lips are fleshy, funnel-like, have adhesive papillae throughout, and can be used to adhere to the substratum. The roof of the mouth has crest-like folds and the mouth cavity is dorso-ventrally flattened (Fig. 2).

Rhinelepis aspera has a larger mouth and respiratory membranes than those of the other species. All the species of *Hypostomus*, except *H. microstomus,* have laterally elliptical lips. *H. microstomus* and *Megalancistrus aculeatus* have longitudinally elliptical lips (Fig. 2).

Teeth

The maxillary teeth are arranged to form a rake-like structure. Among species, major differences exist with regard to number, width and shape (Table I; Figs 2 and 3). *Rhinelepis aspera* has narrow teeth, threadlike, small and
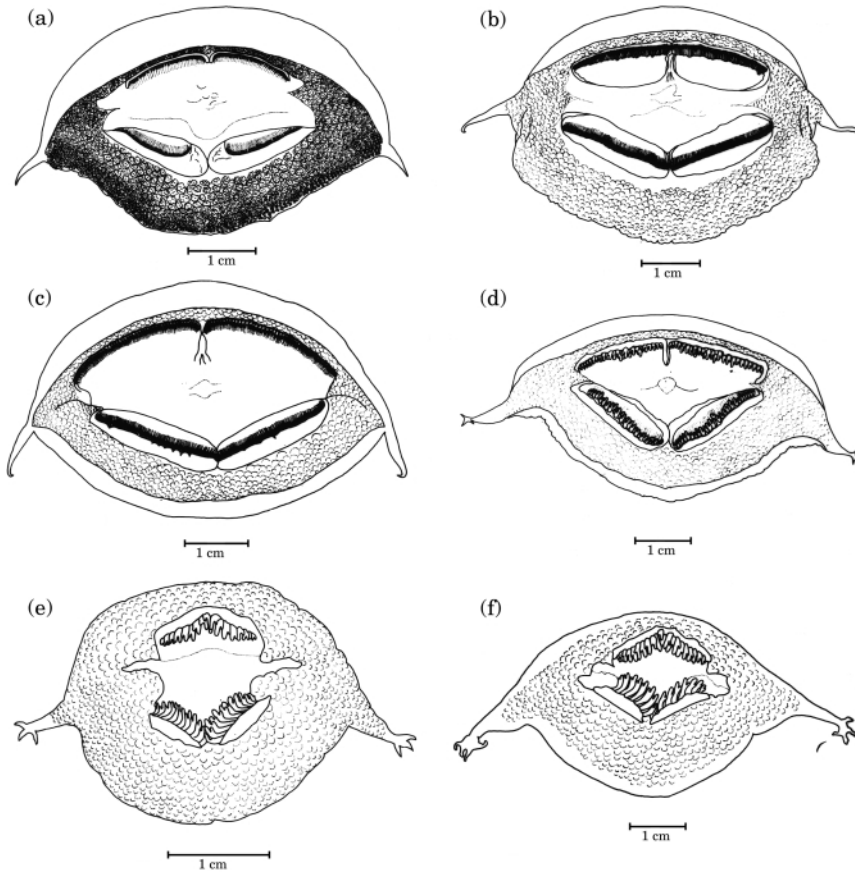
FIG. 2. Position and form of mouth (ventral view) for six loricariids. (a) *R. aspera*; (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus*.

TABLE II. Probabilities for *post hoc* Tukey comparison of intestine lengths

	R. aspera	H. regani	H. margaritifer	H. microstomus
R. aspera (n=30)				
H. regani (n=39)	<0·0001			
H. margaritifer (n=15)	<0·0001	0·081		
H. microstomus (n=26)	<0·0001	<0·0001	<0·0001	
M. aculeatus (n=32)	<0·0001	<0·0001	<0·0001	<0·0001

unicuspid [Figs 2(a) and 3(a)]. In the remaining species, teeth have a bicuspid crown with the median lobe longer than the lateral one. Tooth crowns are curved and trowel-like. Among *Hypostomus*, the teeth of *H. regani* and *H. ternetzi* are thinner than those of the others [Fig. 3(b), (c)]. In the remaining *Hypostomus* teeth are larger and stronger, and in *M. aculeatus* they are large and strong. In both of them, tooth lobes are more arched and shorter [Fig. 3(d)–(f)].
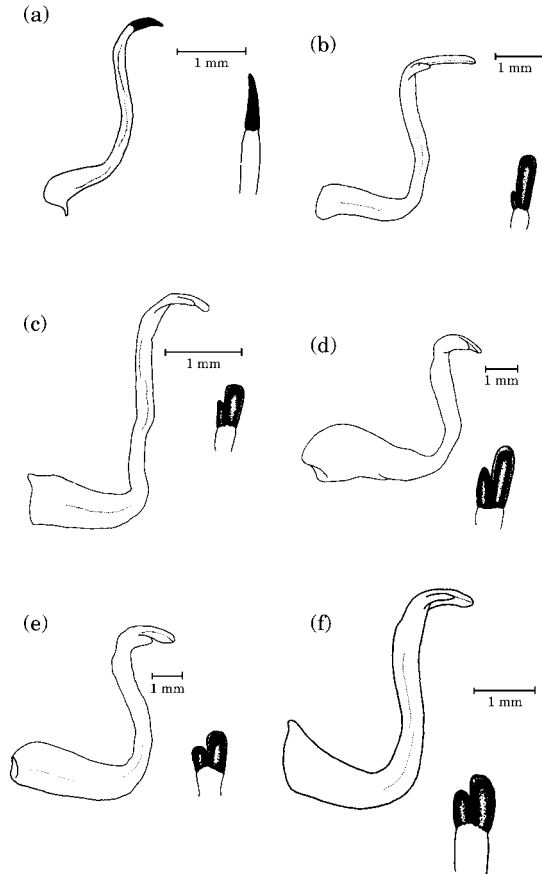
FIG. 3. Shape of implanted teeth in the maxillary and mandibular arches of six loricariids. (a) *R. aspera*; (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus.*

In *H. microstomus* and *M. aculeatus*, the jaws are angled acutely and form a diamond [Fig. 2(e), (f)]. *Hypostomus margaritifer* has a mouth shape inter-mediate between the last two pairs of species and the others, which have dental plates of semi-lunar shape [Fig. 2(a)–(d)].

Pharyngeal teeth

Pharyngeal teeth are located on the last branchial arch close to the opening of the oesophagus. *Rhinelepis aspera* has rudimentary tooth plates with smooth crown teeth arranged in two arched rows on the roof of the pharynx [Fig. 4(a)]. The other species also have teeth on tooth plates, but these are located on the floor and roof of the pharynx [Fig. 4(b)–(f)]. Numerous isolated cone-shaped teeth are present (Fig. 4). In all species of *Hypostomus* and *M. aculeatus*, the upper plates are better developed than the lower, with variations in shape and size among species.

Gill rakers

In *R. aspera*, gill rakers are long and extend externally to the branchial filaments, covering the branchial arch entirely [Fig. 5(a)]. Rakers are numerous,
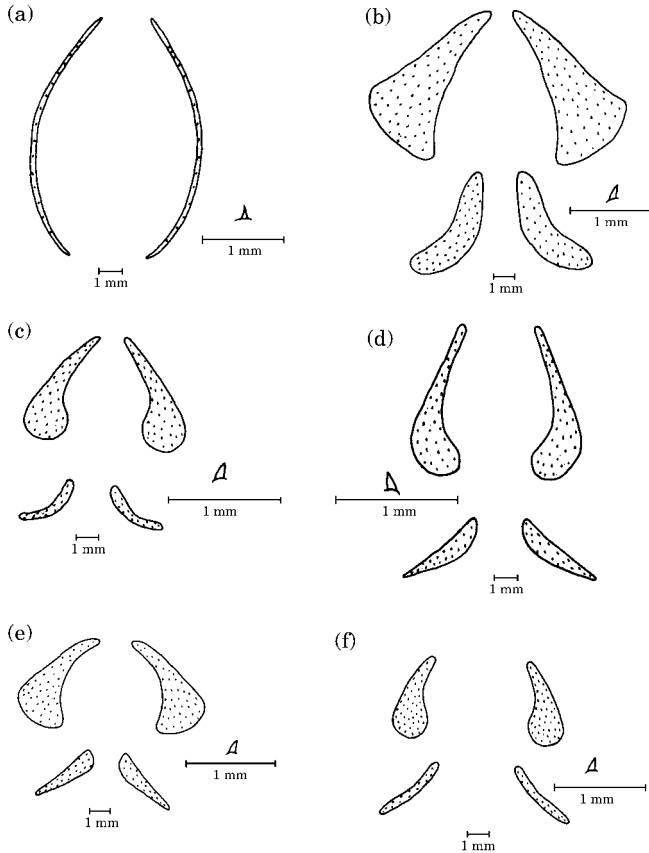
Fɪɢ. 4. Shape and distribution of pharyngeal teeth of six loricariids. (a) *R. aspera*; (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus*. Frontal view, showing upper and lower tooth plates. Note the absence of lower tooth plate in *R. aspera*.

thin and juxtaposed. Each raker resembles a feather in which various villi extend laterally from the filaments [Fig. 5(a)]. The other five species have numerous blade-like and juxtaposed rakers which cover only half of the branchial filaments. Gill rakers of these species have small filaments with small cone-shaped projections in the external face [Fig. 5(b)–(f)]. In all species, mucus was present in the branchial chamber, with adherent particles in most cases.

Stomach

With the exception of *R. aspera*, all species have a defined stomach. Separation between stomach and intestine is marked by the presence of a pyloric sphincter (Fig. 6). Stomachs of the four *Hypostomus* species are small, thin-walled, sac-like, and lie in the dorsal region of the abdominal cavity [Fig. 6(b)–(e)]. In *M. aculeatus*, the stomach is more muscular and proportionally bigger [Fig. 6(f)] with folds in the internal mucosa, and lies in the lateral region of the visceral cavity.
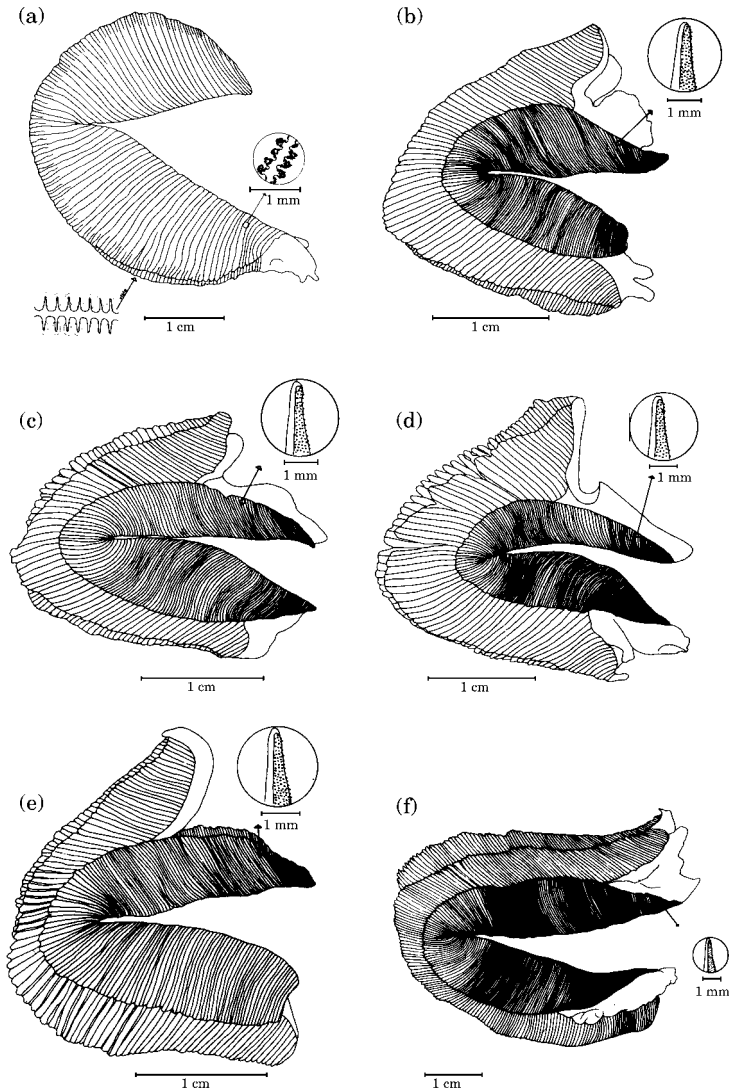
FIG. 5. Structure of branchial rakers of six loricariids. (a) *R. aspera*; (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus*.

Intestine

In all species, the intestine is characterized by a network of loops arranged in more or less horizontal planes within the ventral region of the abdominal cavity. Loops form spirals around a central axis formed by the principal hepatic lobule. In *R. aspera*, the initial stretch of its intestine has a small aperture that is linked directly to the oesophagus [Fig. 6(a)]. Its intestinal loops have a smaller diameter and less muscular walls than those of the other species [Fig. 7(a)]. Among the *Hypostomus* spp., intestine diameter is greater in *H. microstomus* and *H. margaritifer* [Fig. 7(d), (e)] and smaller in *H. regani* and *H. ternetzi*
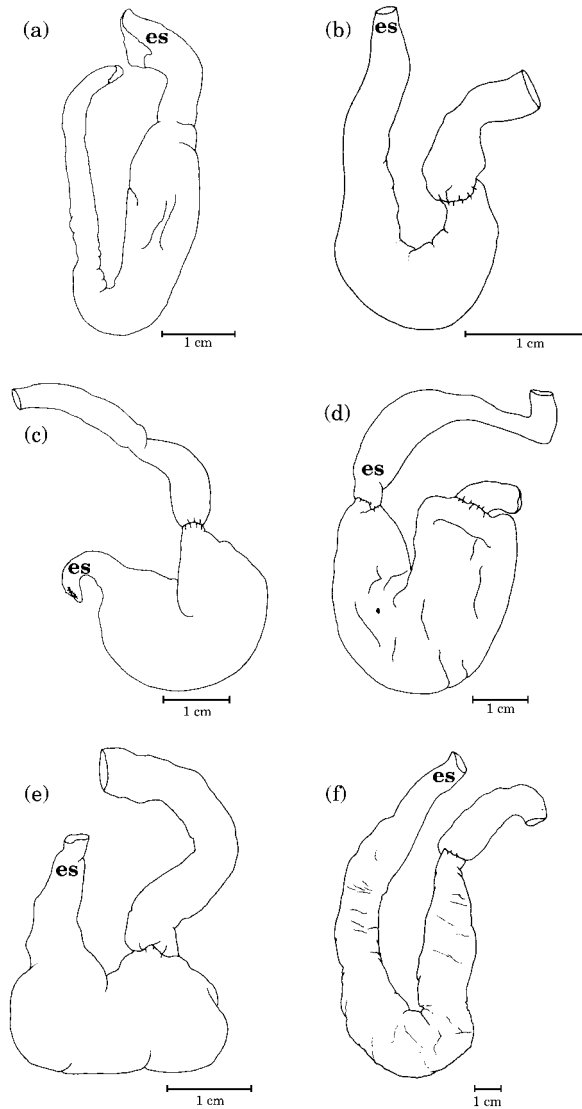
FIG. 6. Stomach shape and structure of six loricariids. (a) *R. aspera* (section of intestine); (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus*. es, oesophagus.

[Fig. 7(b), (c)]. *Megalancistrus aculeatus* is different from the rest in having a greater intestinal diameter and folds in the internal mucosa.

Analysis of covariance indicated that the slopes of the intestine length on standard length differed between species ($F=2.44$; $P=0.036$). The slope for *H. ternetzi* was lower than in the other species. As *H. ternetzi*, *H. regani* and *H. margaritifer* had similar intestine and standard lengths, the former species was excluded from the original data set, and the ANCOVA model was repeated. In this new analysis, the slopes were not significantly different ($F=1.656$; $P=0.164$). Given equal slopes a statistical comparison among species intestine length, controlling for fish standard length, was based on a comparison of the intercepts
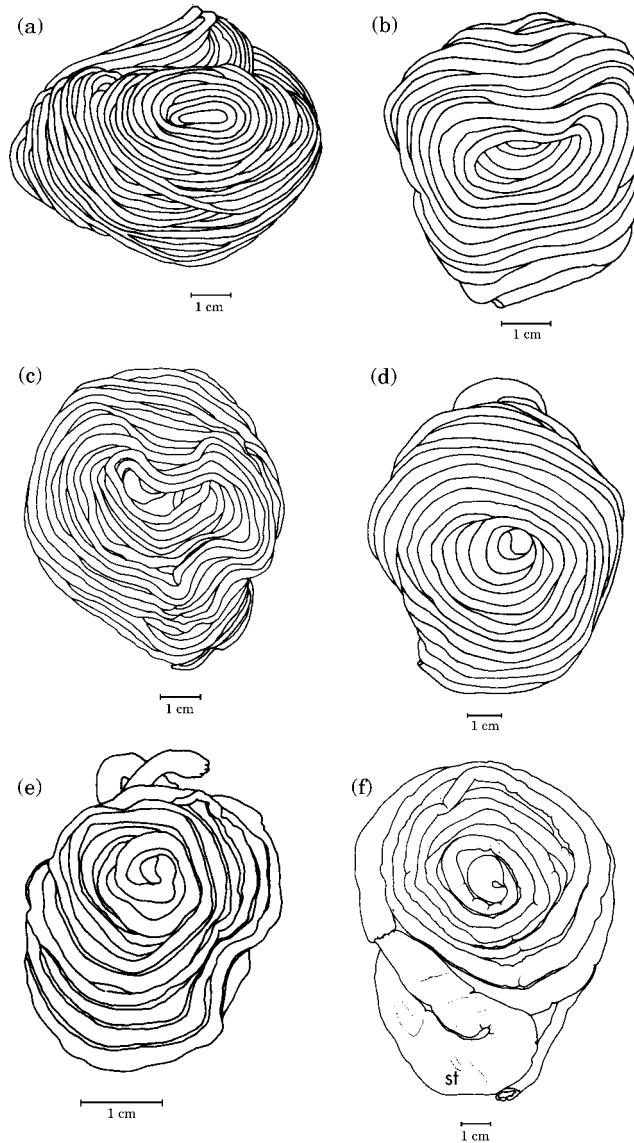
FIG. 7. Intestine shape and structure of six loricariids (ventral). (a) *R. aspera*; (b) *H. regani*; (c) *H. ternetzi*; (d) *H. margaritifer*; (e) *H. microstomus*; (f) *M. aculeatus*. st, stomach.

(Sokal & Rohlf, 1981). There were significant differences among species intestine lengths after controlling for species standard sizes ($F=843\cdot8$; $P<0\cdot001$). Also, according to the ANCOVA model, fish standard length explained a significant portion of the total sum of squares of intestine length ($F=675\cdot97$; $P<0\cdot0001$). This model, including both variables, explained 97 % of the total variation in intestine length.

A *post hoc* comparison test (Tukey) for unequal *n* indicated that only *H. regani* and *H. margaritifer* intestine lengths were not significantly different (Fig. 8; Table II). *Rhinelepis aspera* had the longest intestine length and *M. aculeatus* the
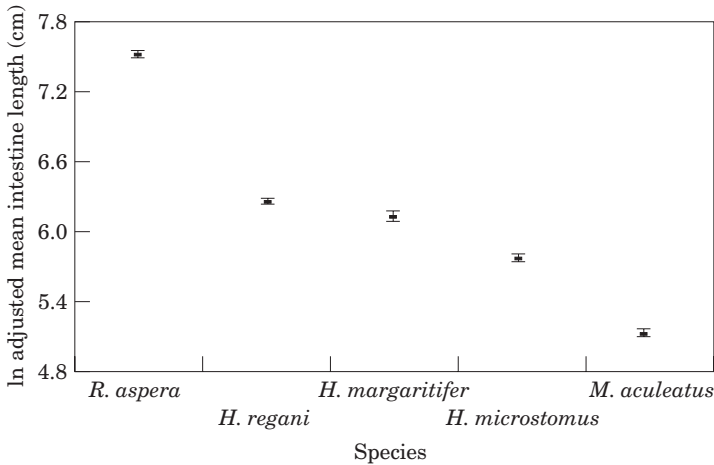
FIG. 8. Adjusted averages for intestine length for six loricariid species. Average and standard deviation of intestines measured (Tukey *post hoc* comparison test, $P<0.01$).

shortest. These adjusted means are the expected values (log-transformed) of intestine length for the mean standard length of all fishes analysed (ln 24·6 cm).

DIET

Loricariids consumed five principal items: sponges, organic detritus, bryophytes, bryozoans and sediment (Table III). The food spectrum of *R. aspera* is primarily organic detritus and small quantities of sediment; with few periphytic organisms. Although *H. regani* consumed great quantities of organic detritus as well, it ingested plant detritus, sediment, and periphytic organisms such as bryozoans, sponges and aquatic insect larvae. Bryozoans and organic detritus were the primary food of *H. ternetzi*, which also consumed more sediment, rotifers, chironomids, gastropods and harpacticoids than the other species. *Hypostomus margaritifer* ingested essentially plant material, primarily bryophytes and Rhodophyceae. Other periphytic organisms such as insect larvae, bryozoans and sponges contributed to the diet of *H. margaritifer*.

Sponges were principal food resource of *H. microstomus* and *M. aculeatus*, with chironomids, gastropods, Trichoptera and bryozoans also eaten. Diets of these fishes consisted of larger items, with fine organic detritus and sediments less important relative to diets of the other species.

Comparison between the similarity matrices of diet and morphology with the Mantel test showed that there was a significant relationship between trophic morphology and diets ($r= -0·503$; $P<0·05$).

DISCUSSION

Morphology of the head and digestive tract both constrains and facilitates food acquisition since these structures determine the manner in which fish take in and process food (Douglas & Matthews, 1992; Podoskina, 1993; Winemiller *et al.*, 1995). The well-developed oral valves and wide mouth cavity of *R. aspera* probably allow it to ingest fine sediments using suction. *Rhinelepis aspera*

probably does not scrape hard substrata, because it has small conical teeth. *Megalancistrus aculeatus*, *H. microstomus* and *H. margaritifer* have larger, stronger, spatulate teeth and a lozenge-shaped dental arch, that should allow them to scrape hard surfaces and ingest coarser food items. *Hypostomus regani* and *H. ternetzi* have lips and dental arches in a semi-lunar shape, and narrow teeth appropriate for scraping smaller particles from surfaces.

Pharyngeal teeth are used for grinding and tearing ingested food (Angelescu & Gneri, 1949; Lagler *et al.*, 1977). Pharyngeal teeth are less developed in loricariids than in other families, probably because loricariids feed mostly on fine particles. This is especially the case for *R. aspera*. These observations disagree with Angelescu & Gneri (1949), who reported pharyngeal teeth to be associated with the absence of a well-defined stomach. Among the *Hypostomus* species (except *H. regani*) and *M. aculeatus*, no clear differences were found with regard to pharyngeal teeth, whereas the thickness of the stomach wall varied greatly.

The six species of loricariids studied here had well-developed gill rakers when compared with other species of the same family with similar feeding habits, such as *Loricaria vetula* Valenciennes (= *Paraloricaria vetula*) and *Loricariichthys platymetopon* Isbrücker & Nijssen (Angelescu & Gneri, 1949; Fugi, 1993), yet they were similar to other loricariids such as *Loricaria anus* Valenciennes (= *Loricariichthys anus*), *Hypostomus plecostomus* L. and *H. hoplonites* Py-Daniel (Py-Daniel, 1984), that feed on small-sized particles by straining ingested food (Bowen, 1983; Verigina, 1990; Ahlgren, 1996). *Rhinelepis aspera* has a branchial apparatus that is modified and different from that of other species. Besides retention of particles, rakers seem to protect the branchial filaments since they are larger and arranged externally covering the branchial filaments. These functions have been suggested for other species (Lagler *et al.*, 1977). The sieve originates from adjacent spines in the external face of the rakers allowing the retention of very small particles. Mucus was observed on rakers of all species, suggesting that food selection occurs in the mouth-pharyngeal cavity and that the particles are transferred to the oesophagus together with mucus.

Although stomach morphology varied among species, gut morphology was similar among congeneric species. *Rhinelepis aspera* does not have a differentiated stomach, and the stomach is well-developed in *M. aculeatus*. The stomachs of *Hypostomus* species, with an intermediate degree of development, were always empty. Many authors have reported empty stomachs in the Loricariidae (Angelescu & Gneri, 1949; Py-Daniel, 1984; Fugi, 1993), with indication of two functions, digestion and respiration. In contrast with *Hypostomus* that uses the stomach for accessory respiration, *R. aspera* has a large U-shaped respiratory diverticulum (Armbruster, 1998*a*, *b*).

A long coiled intestine is characteristic of most species of the Loricariidae (Angelescu & Gneri, 1949; Power, 1983). The intestine is generally more developed in species with less developed stomachs (Verigina, 1990). This was the case for *R. aspera*, which had the highest average intestine length and no distinct stomach. *M. aculeatus* had the lowest average intestine length and the best developed stomach.

Intestine length is related directly to diet and food digestibility (Kapoor *et al.*, 1975; Bowen, 1983; Sturmbauer *et al.*, 1992; Lobón-Cerviá & Rincón, 1994). There was a direct relationship between the quantity of detritus in the diet and

TABLE III. Food items ingested by the six species of loricariids. Percentage of volume (V); occurrence (O); food index (I) (principal items shaded)

Food items	R. aspera			H. regani			H. terneizi		
	V	O	I	V	O	I	V	O	I
Tecameba	—	2	—	—	2	—	—	1	—
Sponges	—	26	—	0·52	20	0·43	2·63	25	2·60
Rotifera	—	1	—	—	8	—	<0·01	18	<0·01
Bryozoa	—	2	—	0·79	4	0·13	42·27	25	41·84
Harpacticoida							—	2	—
Hydracarina							—	2	—
Gastropoda					1		<0·01	4	<0·01
Ephemeroptera					2				
Trichoptera				<0·01	10	—	—	4	—
Chironomidae				<0·01	18	<0·01	0·08	9	0·03
Organic detritus	96·01	26	96·03	71·45	25	72·81	23·27	25	23·03
Cyanophyta	—	26	—	0·01	15	0·01	—	10	—
Pennales	—	26	—	—	24	—	—	24	—
Rhodophyta				—	4	—	—	2	—
Chlorophyta	—	26	—	—	11	—	—	12	—
Bryophyta	0·07	1	<0·01	0·01	1	<0·01			
Potamogetonaceae	—	1	—						
Plant detritus	—	10	—	6·70	21	5·73	0·24	7	0·07
Sediment	3·92	26	3·97	20·50	25	20·89	31·51	26	32·43
No. of guts		26			25			26	
Class of standard length		12·0–35·2			14·5–31·8			13·9–35·7	

—, I and volume <0·0001.

TABLE III. Continued

Food items	H. margartifer			H. microstomus			M. aculeatus		
	V	O	I	V	O	I	V	O	I
Tecameba									
Sponges	0·07	12	0·05	60·42	25	71·89	59·36	24	70·22
Rotifera	—	6	—	—	4	—	—	9	—
Bryozoa	2·95	6	1·17	9·75	3	1·39	7·74	8	3·05
Harpacticoida									
Hydracarina									
Gastropoda				—	1	—	<0·01	3	—
Ephemeroptera									
Trichoptera	—	6	—	—	6	—	<0·01	7	<0·01
Chironomidae	—	6	—	—	11	—	—	11	—
Organic detritus	20·70	17	23·31	10·77	13	6·66	17·87	15	13·21
Cyanophyta	0·02	16	0·02	0·01	16	0·01	<0·01	24	<0·01
Pennales	0·01	18	0·01	<0·01	26	<0·01	0·06	25	0·08
Rhodophyta	9·35	14	8·67	0·06	5	0·01	0·68	1	0·03
Chlorophyta	<0·01	16	<0·01	—	9	—	<0·01	16	<0·01
Bryophyta	49·06	14	45·49	0·07	1	<0·01	<0·01	16	<0·01
Potamogetonaceae							3·70	2	0·36
Plant detritus	—	5	—	3·09	3	0·44			
Sediment	17·84	18	21·26	15·83	26	19·59	10·58	25	13·04
No. of guts		18			26			25	
Class of standard length		25·4–31·3			13·8–27·0			8·4–47·0	

—, I and volume <0·0001.

intestine length. *Rhinelepis aspera* and *H. microstomus* provided the extreme examples. The former had a diet composed mostly of detritus, whereas the latter showed a high incidence of animal prey, which are presumably easier to digest (Bowen, 1983; Junger *et al.*, 1989). However, it should be emphasized, that values for relative intestine length (especially in the case of *R. aspera*) were higher than those quoted in the literature for species with similar feeding habits (Py-Daniel, 1984; Leite *et al.*, 1988; Junger *et al.*, 1989; Kramer & Bryant, 1995). The shortest intestine was found in *M. aculeatus*, which has a well-developed stomach and conspicuous folds in the intestinal mucosa. Al-Hussaini (1949) and Verigina (1990) stated that variation in intestine length may be compensated for by variation in the mucosa layer, and may reflect different adaptations for similar ecological demands (Junger *et al.*, 1989).

The high percentage of organic detritus and low percentage of organisms and periphytic algae (<0·001%) in the diet of *R. aspera* suggest that this species feeds principally on fine particulate organic matter (mud). The morphology of its digestive tract provides further evidence of illiophagy: (1) teeth are less developed and make it difficult to ingest more rigid and more adherent food; (2) the well-developed oral valves facilitate orobranchial suction; (3) gill raker structure is adapted for the ingestion of finely particulate material; (4) thin delicate pharyngeal denticles; (5) the absence of a stomach, which is typical of species with microphagous feeding (Verigina, 1990); (6) a very long intestine. Verigina (1990) and Fugi (1993) found similar characteristics for species of Cyprinidae and other bottom-feeding fishes that consume large quantities of detritus.

Besides consuming detritus, the other loricariids fed on periphytic organisms such as algae, chironomids, gastropods, Ephemeroptera, bryozoans, sponges and bryophytes. Mouth shape facilitates close contact with substrata and teeth are spatulate for scraping the substrata (Uieda, 1995). Similar feeding strategies by other loricariids are reported by Power (1983, 1984) in the Frijoles River (Panama); Py-Daniel (1984) in the Solimes River (Amazon); and Buck & Sazima (1995) in a coastal stream in the southeastern region of Brazil. However, present results differ from those above due to the low volume of algae in the diets despite its high occurrence (except for *H. margaritifer*). This suggests that most species do not select this item, but ingest it incidentally while scraping the substratum (Gerking, 1994). According to Power (1983), mouths with sucking lips, as in the Loricariidae, make it difficult to ingest small organisms selectively.

In the present research, the correlation between morphological and diet similarity shows the importance of feeding specialization in the segregation of trophic niches among sympatric species.

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