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A fish community of the São Francisco River headwaters riffles, southeastern Brazil

Lilian Casatti* and Ricardo M. C. Castro*

The ichthyofauna and main biotic and abiotic parameters of a 60 m long riffles stretch of the upper course of the São Francisco river, southeastern Brazil, were studied. A subaquatic collection and observation methodology, associating skin diving with mountain-climbing equipment, was devised. One hundred hours of diurnal and 48 hours of nocturnal underwater collections and observations were carried out and 21 fish species were collected. Among these, three were considered as accessory, four as accidental and 14 as truly residents in the study site, having therefore their spatial distributions, activity periods and feeding habits studied. The results were: *Astyanax rivularis*, *Bryconamericus stramineus* and *Bryconamericus* sp. are diurnal nektonic omnivorous species which collected items dragged by the current; *Apareiodon* cf. *ibitiensis*, *Parodon hilarii* and *Microlepidogaster* sp. are diurnal benthic algae grazers; the adult individuals of *Harttia* sp. and of *Hypostomus garmani* are nocturnal benthic algae grazers; *Characidium fasciatum* and *Ch. zebra* are diurnal benthic sit-and-wait predators of insect larvae; *Cetopsorhamdia iheringi*, *Imparfinis minutus* and *Trichomycterus* sp. are predominantly nocturnal benthic substrate speculators for insect larvae; and *Rhamdia quelen* is a crepuscular and nocturnal benthic insectivore-piscivore.

No presente trabalho foi estudada a ictiofauna de um trecho de corredeiras do curso superior do rio São Francisco, sudeste do Brasil. A característica marcante do ambiente estudado é a forte correnteza, limitando a utilização de métodos habituais de coleta de peixes e tornando problemática a manutenção da posição espacial de um mergulhador/observador. Em vista disso, foi idealizada uma metodologia de coleta e observação subaquáticas associando mergulho livre com equipamento e técnicas de alpinismo. Foram feitas 100 horas de observação diurna e 48 noturnas. Das 21 espécies de peixes encontradas três foram consideradas como acessórias, quatro como acidentais e 14 como residentes no trecho estudado. Para as últimas os períodos de atividades, as distribuições espaciais e as biologias alimentares foram estudados, com os seguintes resultados: *Astyanax rivularis*, *Bryconamericus stramineus* e *Bryconamericus* sp. são espécies diurnas, nectônicas e onívoras, praticando principalmente a cata de itens arrastados pela corrente; *Apareiodon* cf. *ibitiensis*, *Parodon hilarii* e *Microlepidogaster* sp. são espécies diurnas, bentônicas e algívoras, praticando o pastejo de algas perifíticas; os adultos de *Harttia* sp. e de *Hypostomus garmani* são noturnos, bentônicos e algívoros, sendo pastadores de algas perifíticas; *Characidium fasciatum* e *Ch. zebra* são diurnas, bentônicas e larvófagas, utilizando a tática alimentar de espreita; *Cetopsorhamdia iheringi*, *Imparfinis minutus* e *Trichomycterus* sp. são espécies predominantemente noturnas, bentônicas e larvófagas, praticando a especulação do substrato e *Rhamdia quelen* é crepuscular-noturna, bentônica e insetívora-piscívora.

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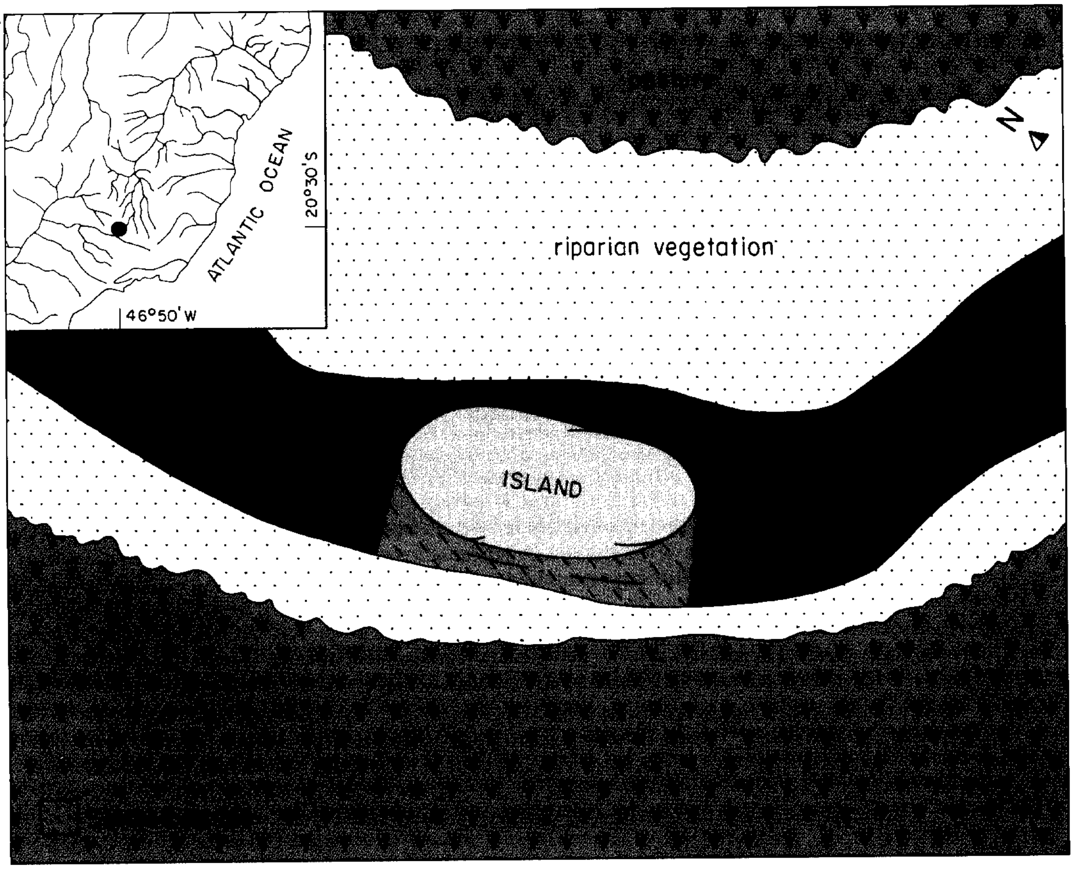


Fig. 1. Study site, showing the local vegetation distribution and its approximate position in the São Francisco river basin.

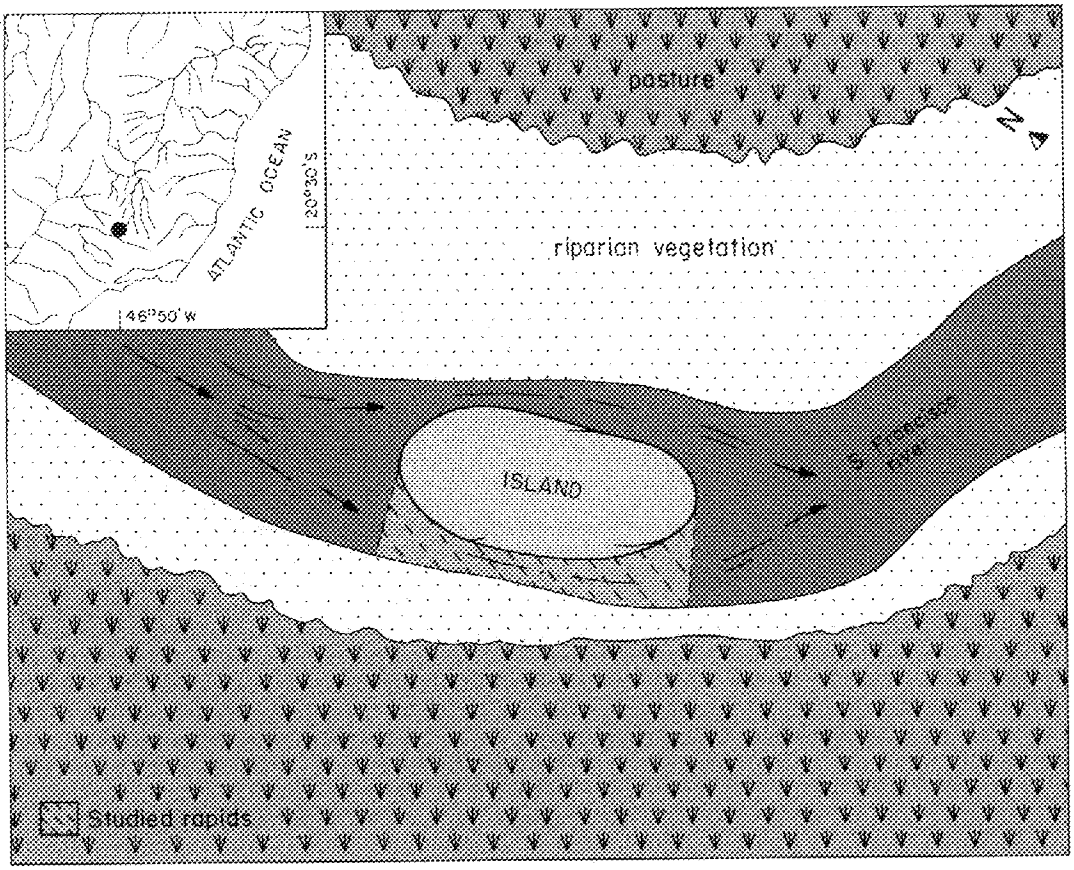
Introduction

The Neotropical fish fauna contains the largest number of species in the world, although the knowledge about the systematics and ecology of its fish communities is relatively incomplete and geographically restricted (see Bölhke et al., 1978; Lowe-McConnell, 1975, 1987). This condition is specially true for certain environments, such as headwater rapids and riffles, where the strong water currents seriously limit the application of traditional fish collection methods, as well as the application of the relatively recent underwater collecting and observation techniques. Although information about some freshwater fish communities in Brazil has been obtained efficiently using collecting and observation techniques during skin diving (see, for example, Sazima, 1986; Sabino & Castro, 1990; Buck & Sazima, 1995), none of the communities studied inhabited a large riffles area in the headwaters of a major river system, characterized by relatively strong water currents and high discharges.

We studied the ichthyofauna of a 60 m long riffles stretch in the upper course of the São Francisco river, State of Minas Gerais, southeastern Brazil, near the Parque Nacional da Serra da Canastra, recording the spatial distributions, activity periods, diets, and feeding behaviours of its fish species.

Study site

The field work was carried out in an approximately 60 m stretch of the São Francisco river upper course (20°30'S 46°50'W), State of Minas Gerais, southeastern Brazil (Fig. 1). The São Fran-



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The field work was carried out in an approximately 60 m stretch of the São Francisco river upper course (20°30'S 46°50'W), State of Minas Gerais, southeastern Brazil (Fig. 1). The São Francisco river, an independent Atlantic drainage with a total length of 3,200 km, is the most important water course giving access to the eastern Brazil interior. The São Francisco river basin ichthyofauna comprises approximately 18 families, 109 genera and 140 to 150 species, and is characterized by a high degree of endemism (Britski et al., 1986; Menezes, 1996).

At the study site the climate is subhumid subwarm tropical, with the mean annual temperatures ranging from 18 ° to 20 °C and mean annual rainfall up to 1,630 mm. December and January are the wettest months, with a rain average of over 100 mm, and the driest months are from May to August, with less than 40 mm (Nimer, 1989). The region is geomorphologically located in the 'Unidade Patamares da Canastra' and the original vegetation, now reduced to 5 % of its original area, comprises savannah-like 'cerrado' herbaceous formations, which are interposed by riparian vegetation (RADAMBRASIL, 1983).

Three portions of the riffles were distinguished on the basis of their predominant substrates and currents: a) upper stretch – with a predominance of sandy, gravelly substrate and slow current (0.3 m · s^{-1}), maximum width of 13 m and maximum depth of 0.5 m; b) middle stretch – with rocky substrate, fast current (2.3 m · s^{-1}), maximum width of 4 m and maximum depth of 0.5 m; c) lower stretch – with rocky, gravelly substrate, medium current (1.7 m · s^{-1}), maximum width of 7 m and maximum depth of 1.2 m.

Material and methods

Nine study trips were made from January 1994 to May 1995, each lasting five days. During these periods, we collected information on air and water temperatures; average current speed, measured by the method of dislocation of a floating object; current speed in different points of the riffles, measured by a Pitot tube (cf. Brower & Zar, 1984); horizontal water transparency measured with a Secchi disk while skin diving; dissolved oxygen concentration (cf. Wetzel & Likens, 1991) and pH. We collected most of the fishes during skin diving, using two small thin black fabric dip nets. The use of gill nets (13 × 1.4 m nylon nets, with 2.5 cm stretched mesh) was only possible in the upper stretch of the riffles where the current was weaker. Voucher specimens were deposited in the fish collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP 50734 to 50754).

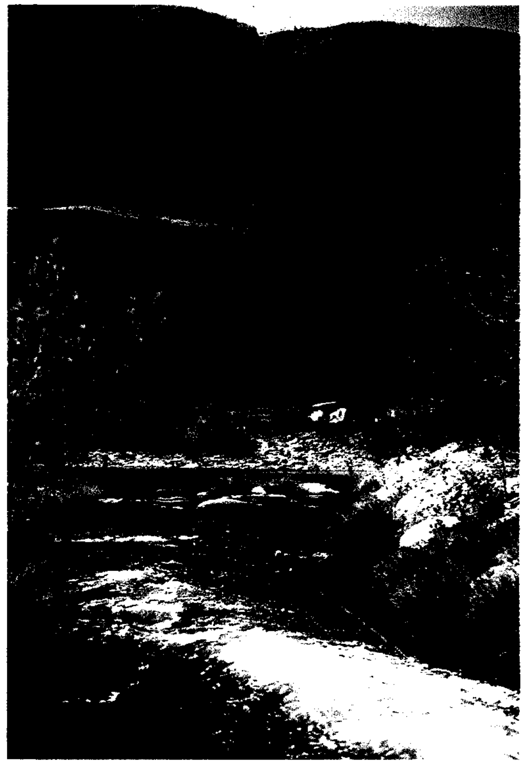

Fig. 2. General view of the work site and of the subaquatic fish collection and observation technique, combining skin diving with climbing equipment (photograph by R. M. C. Castro).

We used basic skin diving and mountain-climbing equipment (a carabiner, a harness, a blocker and a rope) for observations and underwater collection (Fig. 2). The technique consisted of tying one end of the rope to a fixed point (in our case to a tree) and passing the other one through the blocker, which was tied to a harness by the carabiner; the harness, in turn, was worn by the diver. The blocker, the main component of the system, contained a locking system that, once in place, allowed it to move only in the direction of the rope attachment point, allowing the diver to keep his hands free without being dragged by the current. Using this equipment, we collected data on spatial distribution, activity period and general behaviour of each fish species during a 100 diurnal and 48 nocturnal skin diving observation hours, using the 'ad libitum' and 'focal cisco river, an independent Atlantic drainage with a total length of 3,200 km, is the most important water course giving access to the eastern Brazil interior. The São Francisco river basin ichthyofauna comprises approximately 18 families, 109 genera and 140 to 150 species, and is characterized by a high degree of endemism (Britski et al., 1986; Menezes, 1996).

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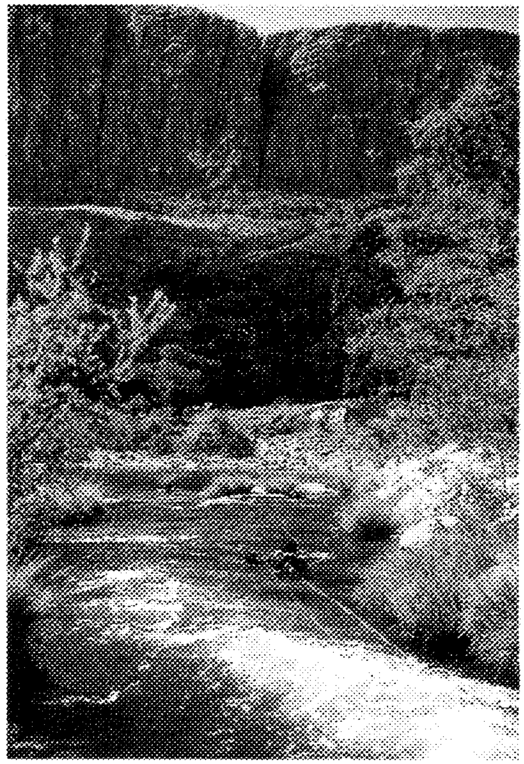

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We analyzed the stomach contents of the resident species (i.e., those present in more than 50 % of the collections, cf. Dajoz, 1978). The digestives tubes were removed and the ratio digestive tube lengths/SL were calculated (DTL/SL index); the stomachs were then removed, and their contents analysed (cf. Knöppel, 1970). Frequency of occurrence (Hyslop, 1980) and percent composition (Hynes, 1950) of food items were calculated for each item, as well as index of feeding overlap for *Apareiodon* cf. *ibitiensis* and *Parodon hilarii*, following Zaret & Rand (1971). The food items were grouped in broad taxonomic or ecological categories according to their origins (cf. Sabino & Castro, 1990); algae, aquatic insects, microcrustaceans, fishes and organic matter were considered as autochthonous, while vascular plants, terrestrial insects and arachnids were considered allochthonous. Like Power (1983) and Buck & Sazima (1995), we use periphyton to refer to microfloral growth on various aquatic substrates. The categories used for classification of the fish species by food preferences follows Angermeier & Karr (1983) and Castro & Casatti (1997), whereas the classification of fish feeding behaviours follows Curio (1976), Keenleyside (1979), Sazima (1986) and Grant & Noakes (1987).

Table 1. Fish species collected in the São Francisco river headwater riffles, southeastern Brazil. * accessory species; ** accidental species; all others are resident species.

Characidae
  Subfamily Tetragonopterinae
    Astyanax rivularis (Lütken, 1874)
    Bryconamericus stramineus Eigenmann, 1908
    Bryconamericus sp.
  Subfamily Characidiinae
    Characidium fasciatum Travassos, 1956
    Characidium zebra Eigenmann, 1909
Anostomidae
    Leporellus vittatus (Valenciennes, 1849) *
Prochilodontidae
    Prochilodus costatus Valenciennes, 1849 **
Parodontidae
    Apareiodon cf. *ibitiensis* Campos, 1944
    Apareiodon cf. *piracicabae* (Eigenmann, 1907) *
    Parodon hilarii Reinhardt, 1866
Pimelodidae
    Cetopsorhamdia iheringi Schubart & Gomes, 1959
    Imparfinis minutus (Lütken, 1875)
    Rhamdia quelen (Quoy & Gairmard, 1824)
Trichomycteridae
    Trichomycterus brasiliensis Reinhardt, 1873 *
    Trichomycterus sp.
Loricariidae
  Subfamily Neoplecostominae
    Neoplecostomus franciscoensis Langeani, 1990 **
  Subfamily Hypoptopomatinae
    Microlepidogaster sp.
  Subfamily Loricariinae
    Harttia sp.
  Subfamily Hypostominae
    Hypostomus garmani (Regan, 1904)
    Hypostomus aff. *commersonii* Valenciennes, 1840 **
Cichlidae
    Geophagus brasiliensis (Quoy & Gaimard, 1824) **

Results

Environment. During the study period the air temperature varied from 10 to 31.5 °C; the water temperature 12.4-23 °C; the subaquatic horizontal transparency 1.6-9.6 m; the discharge from 1.8-3.2 $m^3 \cdot s^{-1}$ (dry and rainy seasons, respectively) and the dissolved oxygen concentration 8.9-21.7 $mg \cdot l^{-1}$. The organisms most frequently found attached to rock surfaces were filamentous algae (*Spirogyra* and *Oscillatoria*), whereas on the sand-gravel substrate diatom algae, ephemeropteran nymphs and dipteran and trichopteran larvae were the organisms most frequently found. There was almost no litter on the bottom and, using a 45 µm mesh zooplanic net held for five minutes against the current on two occasions, we collected only a few Rotifera and no drifting insects and plants fragments of terrestrial origin.

Ichthyofauna. We collected 405 fish specimens, belonging to eight families, 16 genera and 21 species (Table 1; Figures 3 and 4). Among the collected species, 50 % were siluriforms, 45 % characiforms and 5 % perciforms. Of all collected specimens, 384 (94.4 %) were collected with dip nets and 21 (5.6 %) with gill nets.

Astyanax rivularis, Bryconamericus stramineus, Bryconamericus sp., *Characidium fasciatum, Ch. zebra, Apareiodon* cf. *ibitiensis, Parodon hilarii, Cetopsorhamdia iheringi, Imparfinis minutus, Rhamdia quelen, Trichomycterus* sp., *Microlepidogaster* sp., *Harttia* sp. and *Hypostomus garmani* were considered residents (present in more than 50 % of the collections); *Leporellus vittatus, Apareiodon* cf. *piracicabae* and *Tricomycterus brasiliensis* accessory (present in 25 to 50 % of the collections) and *Prochilodus costatus, Neoplecostomus franciscoensis, Hypostomus* aff. *commersonii* and *Geophagus brasiliensis* accidental (present in fewer than 25 % of the collections).

Spatial distribution and activity period. The current speed apparently influenced the fish distribution within the riffles more than any other abiotic factor. The use of a Pitot tube during normal river flow conditions (between the dry and rainy seasons peaks), allowed the measurement of current speeds (v) in different points of the riffles (which varied from approximately zero to 1.6 $m \cdot s^{-1}$) and to correlate it with the spatial distributions of the resident fish species, as can be seen in Figure 5.

Astyanax rivularis, B. stramineus and *Bryconamericus* sp. are nektonic and diurnal species. During the day they occupied the marginal portions of the upper and lower stretches of the riffles, actively swimming in the water column, most of the time downstream from rocks ($v =$ 0.2-0.4 $m \cdot s^{-1}$) in the cases of *A. rivularis* and *Bryconamericus* sp., and just under the mid channel water surface ($v = 0.8\ m \cdot s^{-1}$), in *B. stramineus*. At night, the individuals of *A. rivularis* and *Bryconamericus* sp. remained motionless among the submerged roots of grasses (Poaceae) or sheltered in holes in the banks of the riffles ($v \sim 0\ m \cdot s^{-1}$), whilst the individuals of *B. stramineus* remained in deep main channel pools, upriver and downriver from the study site.

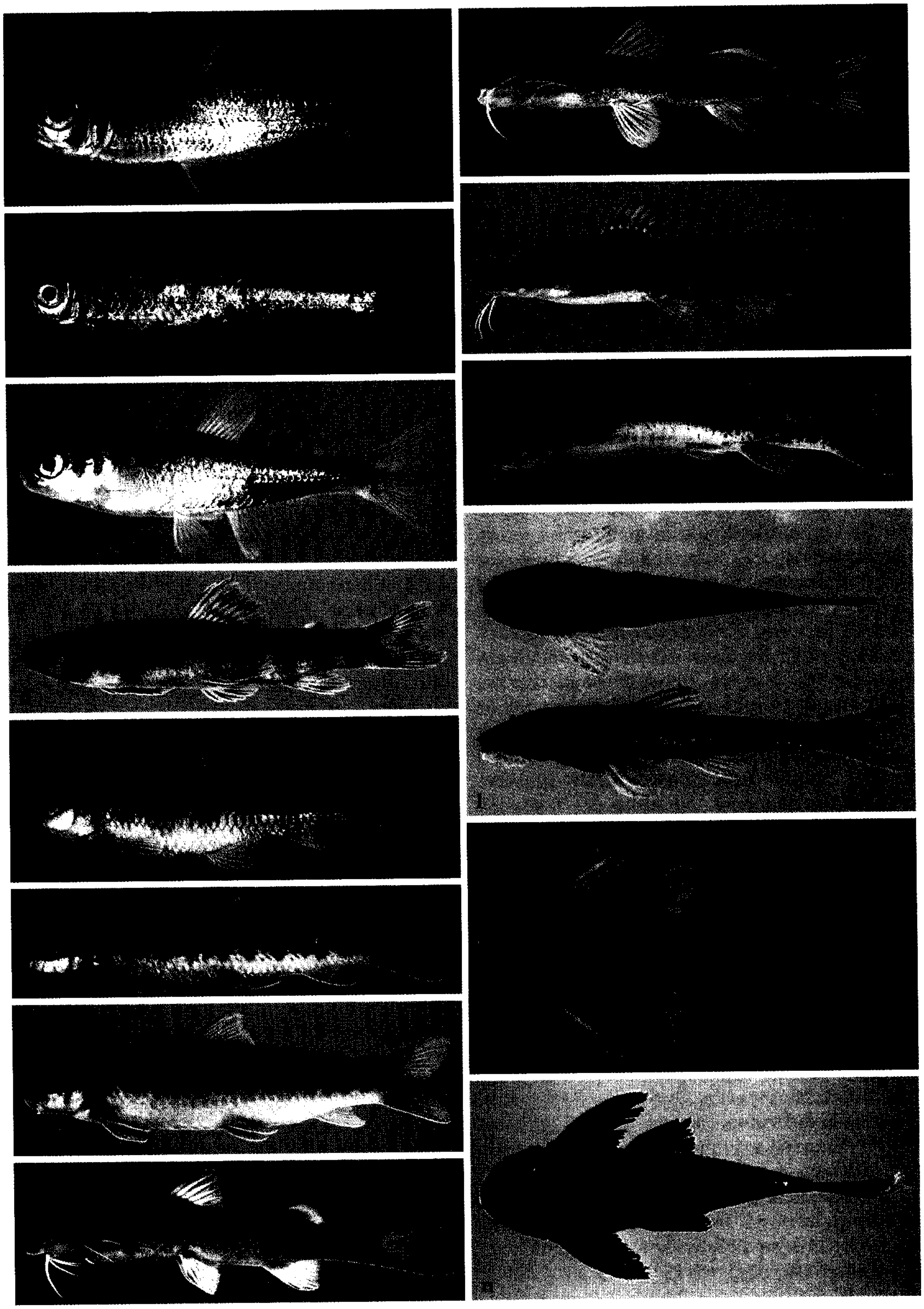
Characidium fasciatum and *Ch. zebra* are benthic and diurnal. During the day individuals of these species occupied the upper and lower stretches of the riffles, where they swam alone, among the bottom rocks. At night they remained motionless among the bottom rocks ($v = 0.2\ m \cdot s^{-1}$).

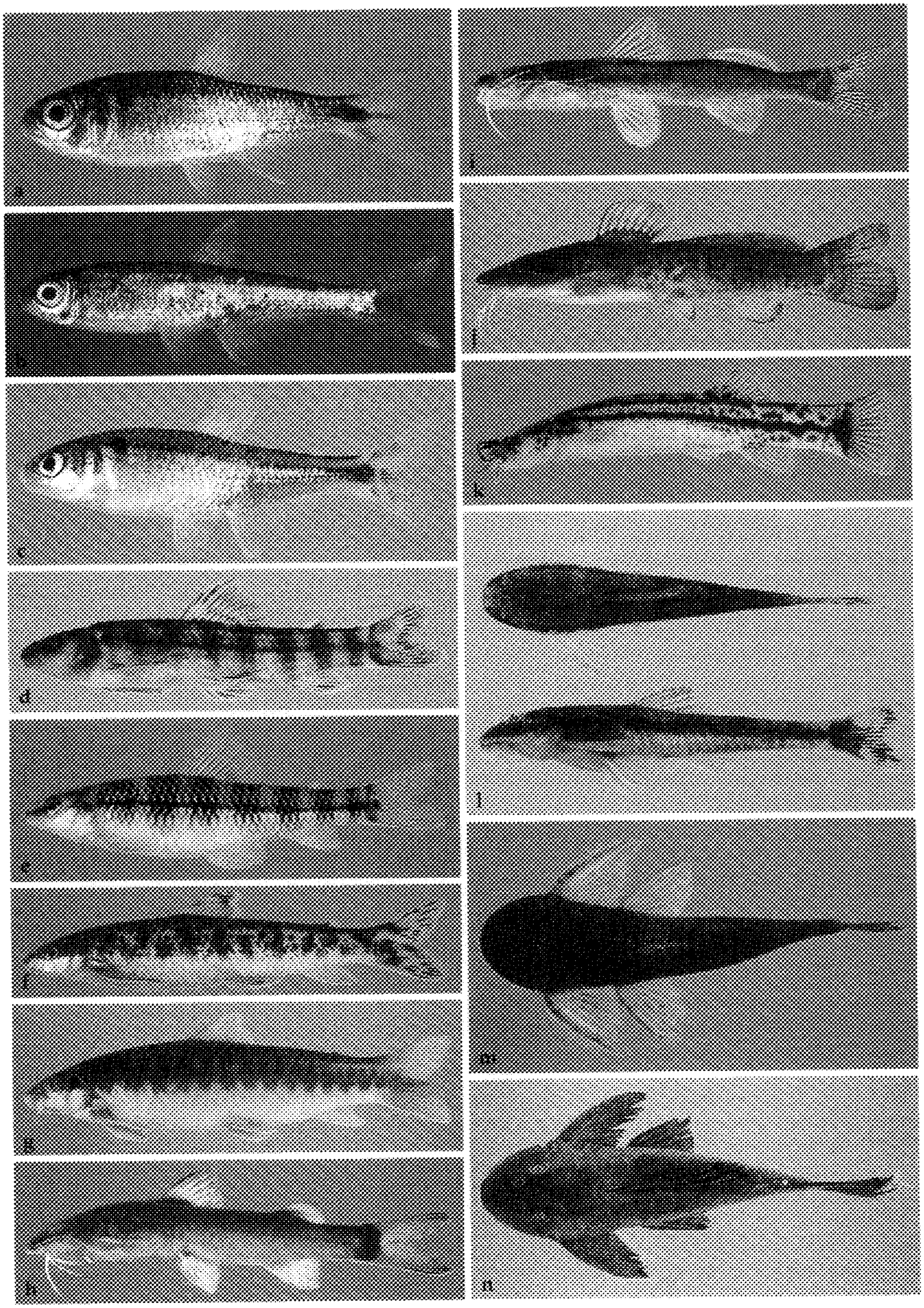
Apareiodon cf. *ibitiensis* and *P. hilarii* are benthic and diurnal species. During the day groups of six to 25 individuals of *Apareiodon* cf. *ibitiensis* (Fig. 6) occupied mainly the lower stretch of the riffles, where they swam almost continuously, most of the time orientated upstream, over the bottom rocks ($v = 1.1\ m \cdot s^{-1}$). Soon after sunset, they were observed motionless, among the larger bottom rocks. Apparently there is a size-related spatial distribution segregation in which the smallest-sized fishes (SL ca. 35.0 mm) explored the banks ($v \sim 0\ m \cdot s^{-1}$), usually near to groups of *A. rivularis* and *Bryconamericus* sp. Slightly larger young individuals (SL ca. 60.0 mm) were organized in small schools and showed the same general behaviour presented by adult individuals (ca. 98 mm SL), although restricted to the areas of weaker current. During the day, the solitary individuals of *P. hilarii* swam actively, upstream orientated, near the bottom of the riffles middle stretch ($v = 1.6\ m \cdot s^{-1}$). At night they remained motionless among the bottom rocks, cryptically colored in relation to the substrate.

Cetopsorhamdia iheringi was active mainly at night, although observed active by day on several occasions. The individuals of *I. minutus* and *R. quelen* were active exclusively at night, starting their activity at sunset. *Trichomycterus* sp. is an exclusively diurnal species. Whenever they were active, the individuals of these species moved along the small spaces among the bottom rocks (Fig. 7). When inactive, they remained sheltered among the bottom rocks ($v = 0.2\ m \cdot s^{-1}$).

The individuals of *Microlepidogaster* sp. were active by day and remained movably attached to the submerged marginal vegetation (twigs, branches, leaves and roots) by their oral disks and pelvic fins, mainly in the riffles upper stretch. At night, the individuals remained motionless among the bottom rocks. Differences in the activity periods and spatial distributions were observed among young and adult individuals of *Harttia* sp. and *H. garmani*. Juveniles (SL ca. 23 mm) were active during the day, movably attached to the rocks near the margins ($v = 0.3\ m \cdot s^{-1}$) by their oral disks, as opposed to the adults, which began their activity at nightfall, and attached themselves to larger rocks, in places with stronger current ($v = 1.1\text{-}1.6\ m \cdot s^{-1}$).

Diet and feeding behaviour. Considering the riffles fish community diet as a whole, 79 % of the items found were autochthonous and 21 % allochthonous (Fig. 8). Among the autochthonous ones, the most representative items were dipteran and trichopteran larvae and ephemeropteran nymphs, together with filamentous green algae (mainly *Spirogyra*), blue-green algae (cyanobacteria – mainly *Lyngbya* and *Oscillatoria*) and diatoms (mainly *Navicula* and *Pinnularia*). No significant seasonal differences in diet were observed. Based on the food items predominant in the diet, we organized the fish species into the following





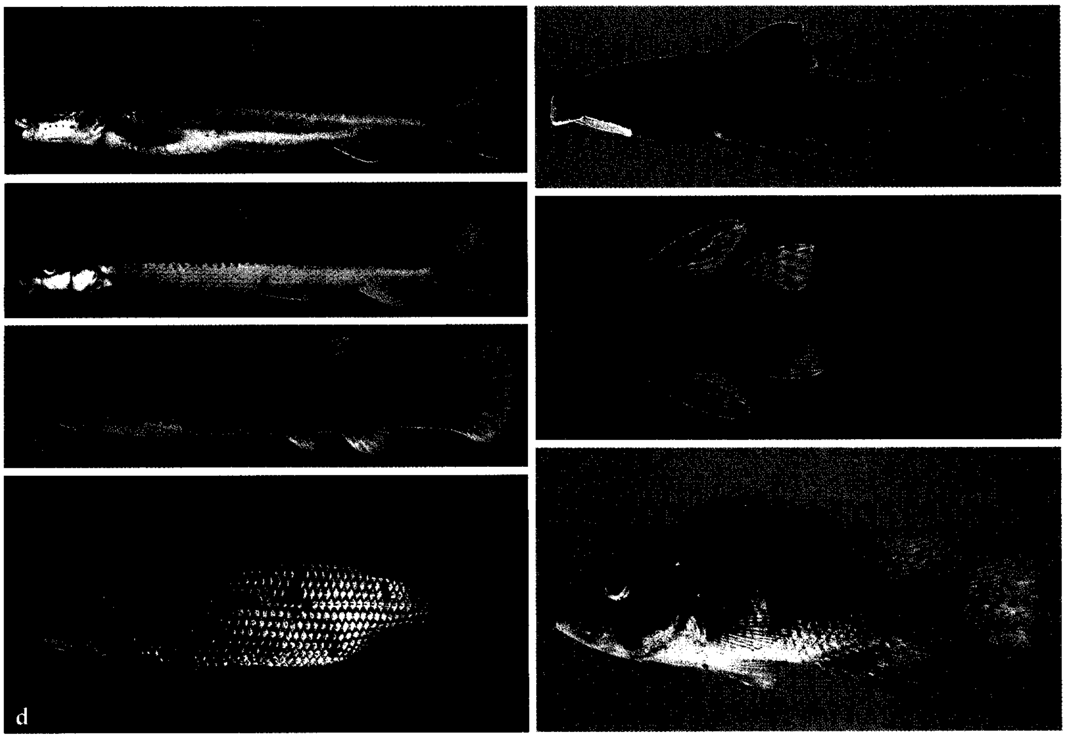


Fig. 4. Representative specimens of the riffles accessory species: **a,** *Leporellus vittatus*, MZUSP 50739, 199.0 mm SL; **b,** *Apareiodon* cf. *piracicabae*, MZUSP 50742, 107.5 mm SL; **c,** *Trichomycterus brasiliensis*, MZUSP 50748, 71.5 mm SL; and accidental species: **d,** *Prochilodus costatus*, MZUSP 50740, 315.5 mm SL; **e,** *Neoplecostomus franciscoensis*, MZUSP 50749, 106.0 mm SL; **f,** *Hypostomus* aff. *commersoni*, MZUSP 50753, 66.2 mm SL; **g,** *Geophagus brasiliensis*, MZUSP 50754, 58.6 mm SL (photographs by R. M. C. Castro).

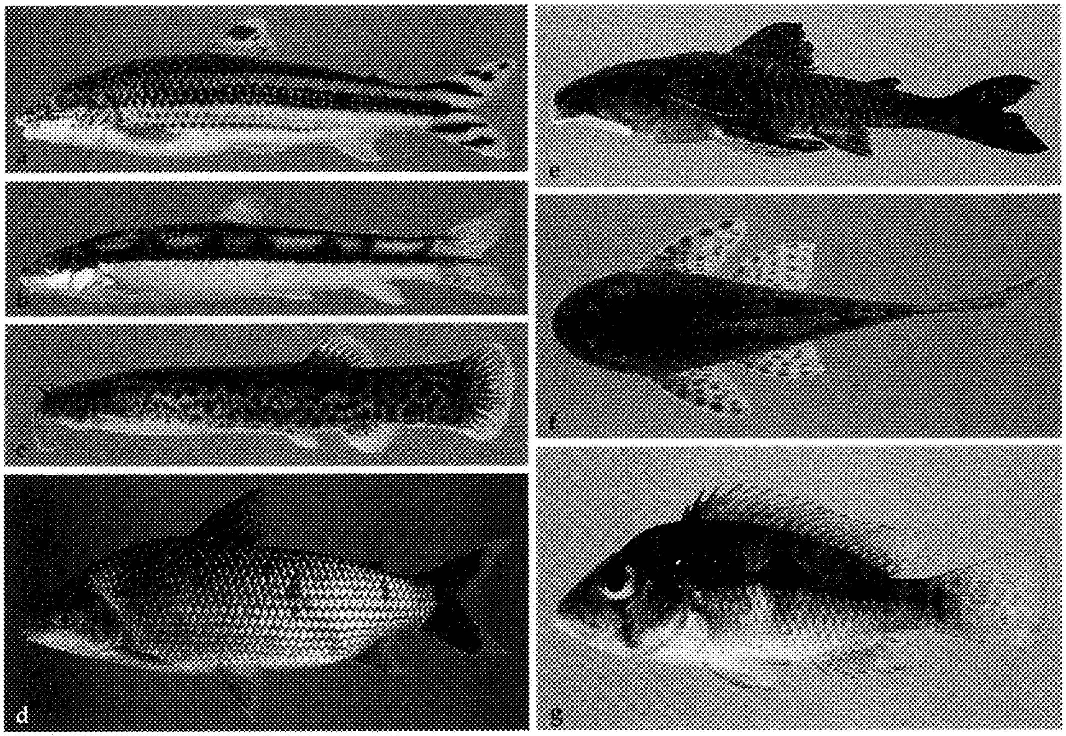
feeding categories. In Table 2 the resident species are organized according to their feeding categories and the number of examined specimens, standard length ranges and DTL/SL ratios are listed for each species.

a) omnivores: *A. rivularis, B. stramineus* and *Bryconamericus* sp.

These represented 21 % of the resident species, with approximately 55 % of the three species's food items found to be autochthonous: algae (diatoms, filamentous Cyanophyta, *Spyrogyra*), dipteran larvae (Chironomidae, Ceratopogonidae, Simulidae), ephemeropteran nymphs (Baetidae, Leptophlebiidae), and trichopteran larvae; and 45 % allochthonous: vascular plants fragments and terrestrial insects (Formicidae, Diptera, Coleoptera).

Astyanax rivularis and *Bryconamericus* sp. collected food items carried by the current (drift feeding, cf. Grant & Noakes, 1987) (Fig. 9) and sometimes trimmed the submerged roots of

◁ **Fig. 3.** Representative specimens of the riffles resident species: **a,** *Astyanax rivularis*, MZUSP 50734, 42.0 mm SL; **b,** *Bryconamericus stramineus*, MZUSP 50735, 47.2 mm SL; **c,** *Bryconamericus* sp., MZUSP 50736, 38.5 mm SL; **d,** *Characidium fasciatum*, MZUSP 50737, 43.0 mm SL; **e,** *Ch. zebra*, MZUSP 50738, 47.5 mm SL; **f,** *Apareiodon* cf. *ibitiensis*, MZUSP 50741, 97.9 mm SL; **g,** *Parodon hilarii*, MZUSP 50743, 130.7 mm SL; **h,** *Cetopsorhamdia iheringi*, MZUSP 50744, 73.6 mm SL; **i,** *Imparfinis minutus*, MZUSP 50745, 56.5 mm SL; **j,** *Rhamdia quelen*, MZUSP 50746, 178.1 mm SL; **k,** *Trichomycterus* sp., MZUSP 50747, 47.5 mm SL; **l,** *Microlepidogaster* sp., MZUSP 50750, 30.0 and 33.5 mm SL; **m,** *Harttia* sp., MZUSP 50751, 103.9 mm SL; **n,** *Hypostomus garmani*, MZUSP 50752, 123.5 mm SL (photographs by R. M. C. Castro).



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These represented 21 % of the resident species, with approximately 55 % of the three species's food items found to be autochthonous: algae (diatoms, filamentous Cyanophyta, *Spyrogyra*), dipteran larvae (Chironomidae, Ceratopogonidae, Simulidae), ephemeropteran nymphs (Baetidae, Leptophlebiidae), and trichopteran larvae; and 45 % allochthonous: vascular plants fragments and terrestrial insects (Formicidae, Diptera, Coleoptera).

Astyanax rivularis and *Bryconamericus* sp. collected food items carried by the current (drift feeding, cf. Grant & Noakes, 1987) (Fig. 9) and sometimes trimmed the submerged roots of

◁ **Fig. 3.** Representative specimens of the riffles resident species: **a**, *Astyanax rivularis*, MZUSP 50734, 42.0 mm SL; **b**, *Bryconamericus stramineus*, MZUSP 50735, 47.2 mm SL; **c**, *Bryconamericus* sp., MZUSP 50736, 38.5 mm SL; **d**, *Characidium fasciatum*, MZUSP 50737, 43.0 mm SL; **e**, *Ch. zebra*, MZUSP 50738, 47.5 mm SL; **f**, *Apareiodon* cf. *ibitiensis*, MZUSP 50741, 97.9 mm SL; **g**, *Parodon hilarii*, MZUSP 50743, 130.7 mm SL; **h**, *Cetopsorhamdia iheringi*, MZUSP 50744, 73.6 mm SL; **i**, *Imparfinis minutus*, MZUSP 50745, 56.5 mm SL; **j**, *Rhamdia quelen*, MZUSP 50746, 178.1 mm SL; **k**, *Trichomycterus* sp., MZUSP 50747, 47.5 mm SL; **l**, *Microlepidogaster* sp., MZUSP 50750, 30.0 and 33.5 mm SL; **m**, *Harttia* sp., MZUSP 50751, 103.9 mm SL; **n**, *Hypostomus garmani*, MZUSP 50752, 123.5 mm SL (photographs by R. M. C. Castro).

Poaceae (browsing, cf. Sazima, 1986) or algae attached to rocks (grazing, cf. Keenleyside, 1979) (Fig. 10). When collecting items carried by the current, the fishes swam upstream orientated, either in the middle of the water column, or at the margins or downstream from rocks (current speed of 0.4 $m \cdot s^{-1}$). *Bryconamericus stramineus* captured food solely by collecting items from the water surface (surface picking, cf. Sazima, 1986).

b) larvivores: *Ch. fasciatum, Ch. zebra, C. iheringi, I. minutus* and *Trichomycterus* sp.

These five species represented 36 % of the resident species, with approximately 85 % of the food items found to be autochthonous: ephemeropteran nymphs (Baetidae, Tricorythidae, Leptophlebiidae), trichopteran larvae (Hydropsychidae, Hydroptilidae, Phylopotamidae), and dipteran larvae (Chironomidae, Ceratopogonidae, Simuliidae, Empididae); and 15 % allochthonous: vascular plants fragments, Acarina and terrestrial insects (Formicidae, Diptera, Coleoptera).

Characidium fasciatum and *Ch. zebra* performed sit-and-wait predation (cf. Sazima, 1986), in which the fishes remained among the rocks and used their paired fins to rest on the bottom; they visually inspected the nearby substrate areas and, whenever a prey was detected, they swam towards it very fast, thrusted against the substrate, and grabbed it with their mouths.

Cetopsorhamdia iheringi, I. minutus and *Trichomycterus* sp. hunted their prey by excavating the substrate, using their mouths and barbels to turn over the sand-gravel substrate, while actively swimming among the bottom rocks (hunting by speculation, cf. Curio, 1976; grubbers excavating while moving, cf. Sazima, 1986).

c) algivores: *Apareiodon* cf. *ibitiensis, P. hilarii, Microlepidogaster* sp., *Harttia* sp. and *H. garmani*

These five species represented 36 % of the resident species. For the group as a whole, all the items were autochthonous: green algae (*Spirogyra*), blue-green algae (*Lyngbya, Oscillatoria*), diatoms (*Navicula, Pinnularia*), and organic matter (highly digested algae remains). The allochthonous items (vascular plants fragments) were present in only three of the 31 analyzed individuals of *Apareiodon* cf. *ibitiensis*.

The individuals of *Apareiodon* cf. *ibitiensis* and *P. hilarii* fed in a similar way on algae attached to rocks (grazing, cf. Keenleyside, 1979). We found 99 % feeding overlap between the diet of these species. They remained most of the time upstream orientated, holding their positions over the rock surfaces with the help of their well developed and horizontally orientated paired fins, scraping algae off the rocks with their pedicellate mobile and spatulate upper jaw teeth (Figs. 6 and 11). Whenever an individual of *Apareiodon* cf. *ibitiensis* approached the feeding site of an individual of *P. hilarii*, the latter quickly approached the invader, touched the rear part of its body with its snout and forced it away.

The three species of loricariid are algae grazers (cf. Keenleyside, 1979), using their ventral suctorial mouths to attach themselves to solid surfaces, and their comb-like teeth to feed on attached organic material. *Microlepidogaster* sp. scraped algae off the submerged branches, leaves and roots of the marginal vegetation, whereas the individuals of *Harttia* sp. and *H. garmani* fed on periphytic rock-attached algae.

d) insectivore-piscivore: *R. quelen*

This species represented 7 % of the resident species. We found a tetra characin (*A. rivularis*) and terrestrial insect remains in the only specimen collected. When feeding, the individuals of *R. quelen* apparently used their barbels to search for prey on bottom, although without turning over the substrate. We were unable to see any individual of this species actively eating.

Anecdotal observations about non-resident fish species. The few *Leporellus vittatus* individuals seen were swimming rapidly in the deeper and faster flowing areas of the riffles, using their well developed pectoral fins to stay for brief amounts of time on algae-covered rock surfaces, in a manner somewhat similar to the parodontids. The only *Prochilodus costatus* observed and collected was hiding in a large rock crevice, completely immobile, at night. Only three *Apareiodon* cf. *piracicabae* were seen, apparently inactive among the bottom rocks, at night. Of the two observed *Trichomycterus brasiliensis*, one was immobile among the roots of submerged marginal vegetation, at night; the other was actively swimming among bottom rocks by day. The two individuals of *Neoplecostomus franciscoensis* and *Hypostomus* aff. *commersonii* were attached to a large rock, grazing on periphytic algae, at night. The only three *Geophagus brasiliensis* (all juveniles) found were immobile among bottom rocks, in an area of relatively slow flowing riffles by day.

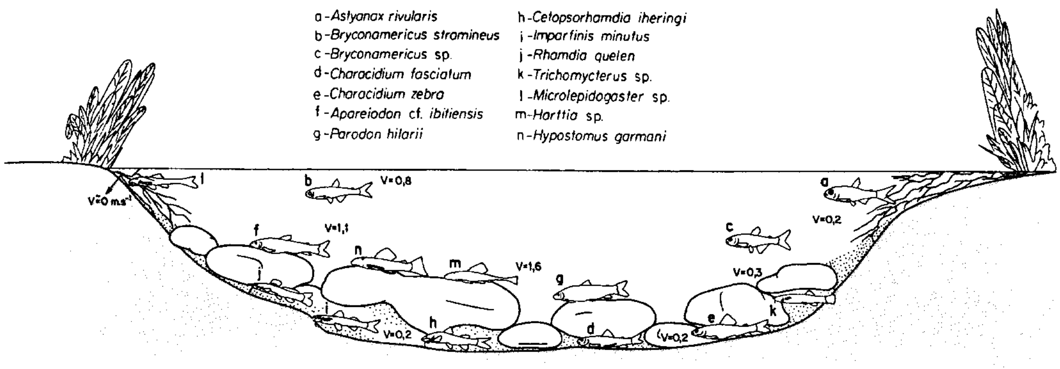


Fig. 5. Generalized diagram showing the studied São Francisco river riffles current speeds (m · s^{-1}), measured at their lower stretch, and the observed spatial distributions of the resident fish species, during their active periods.

Discussion

Environment and spatial distribution of the resident species. In rivers with a significant current, in the contact region between the water flow and its rocky bed there is a layer of slow-flowing or still water even in places with a strong current, resulting from the friction between the bottom and the water flow. Also due to this friction there are pockets, of variable size and shape, of slow-flowing water just downstream from medium to large sized rocks (Hynes, 1970; Schäfer, 1984). Although our study site presented strong current and high discharge, we found the types of lentic water pockets and areas described above. These areas were utilized, for a variable amount of time, as feeding or shelter sites by all the 14 resident species, a fact that stresses the paramount importance of the water current and substrate composition in shaping the structure of the fish community (cf. Hynes, 1970).

The most widespread current related behavioural adaptation observed in the studied riffles was the preferential living in lentic water areas or layers, such as the water layers adjacent to the bottom (pimelodids, trichomycterids) and the river banks (tetragonopterines), the free spaces among the bottom sand and gravel grains (trichomycterids) and rocks (pimelodids, trichomycterids; young loricariids by day; characidiines and parodontids by night), and the pockets of relatively slow-flowing water just downstream from medium to large size rocks (tetragonopterines). The most easily observed current related morphological adaptations (see Fig. 3) are features that favor manoeuvering or position maintenance in strong current. These includes the presence of greatly expanded and horizontally orientated paired fins (characidiines, parodontids and loricariids), suctorial oral discs (loricariids) and a pronouncedly fusiform (characidiines, parodontids) or depressed body (loricariids) (see Hynes, 1970; Vogel, 1981, for morphological and behavioral adaptations enabling fish to live in fast flowing water).

Table 2. Number of examined specimens (N), range of standart length (SL in mm) and ratio digestive tube length/standart length (DTL/SL) of the São Francisco river headwater riffles resident species, organized by feeding categories.

Feeding categories and species	N	SL	DTL/SL
Omnivores:			
Astyanax rivularis	34	32.0-88.0	1.2
Bryconamericus stramineus	21	36.5-49.5	0.8
Bryconamericus sp.	34	22.6-47.0	1.0
Larvivores:			
Characidium fasciatum	24	37.3-57.5	0.7
Characidium zebra	7	53.3-64.5	0.7
Cetopsorhamdia iheringi	15	34.5-86.0	0.8
Imparfinis minutus	28	41.2-73.0	0.5
Trichomycterus sp.	39	16.5-49.9	0.6
Algivores:			
Apareiodon cf. *ibitiensis*	31	47.5-104.0	1.4
Parodon hilarii	24	85.5-136.7	1.4
Microlepidogaster sp.	16	24.0-35.0	2.5
Harttia sp.	22	23.5-35.0	4.3
Hypostomus garmani	20	23.0-130.2	5.0
Insectivore-piscivore:			
Rhamdia quelen	1	176.0	1.1

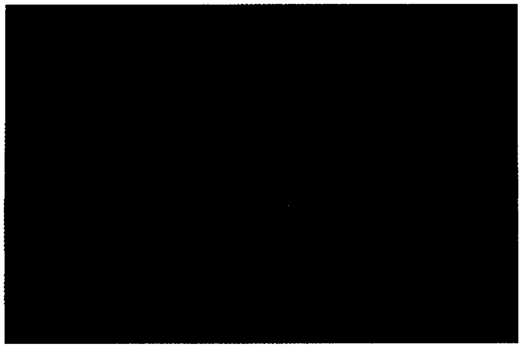


Fig. 6. Upstream orientated group of *Apareiodon* cf. *ibitiensis*, grazing on riffles lower stretch bottom rocks attached algae, by day (photograph by R. M. C. Castro).

Fig. 7. Adult of *Trichomycterus* sp., hiding by day among the bottom rocks of upper stretch of riffles (photograph by R. M. C. Castro).

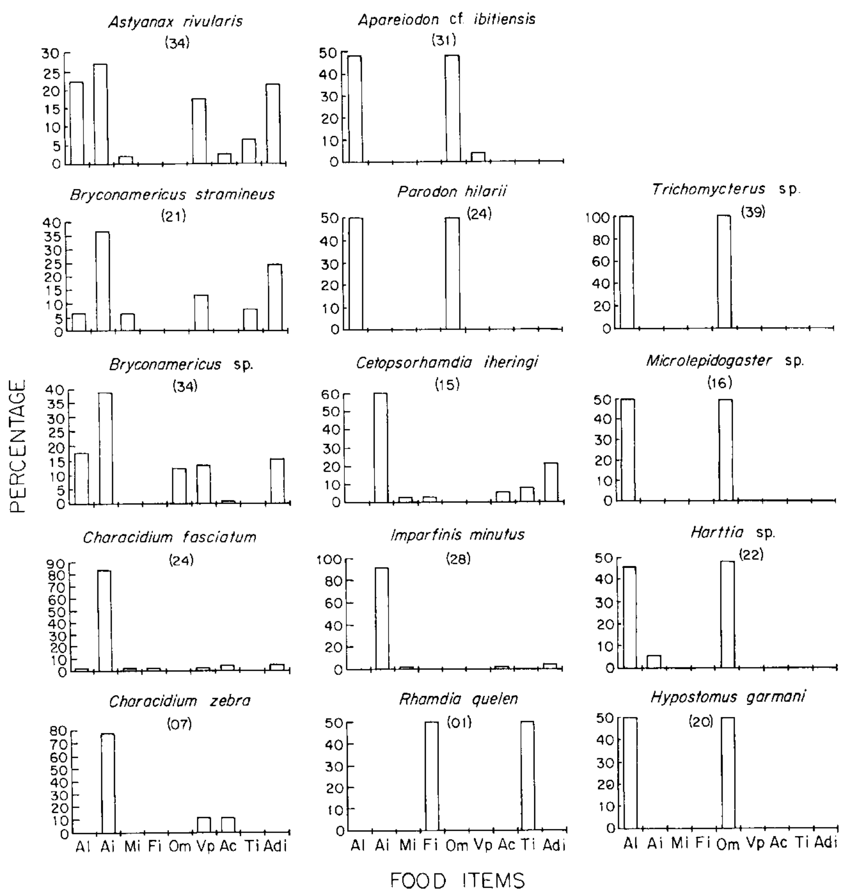
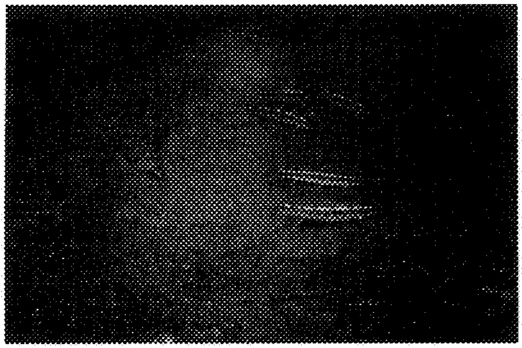


Fig. 8. Percent composition of the diets of the resident species, with the food items grouped in categories; autochthonous items: **Al,** algae (filamentous and diatoms); **Ai,** aquatic insects (mostly juveniles of Diptera, Ephemeroptera and Trichoptera); **Mi,** microcrustaceans; **Fi,** fishes and fishes scales; **Om,** organic matter; allochthonous: **Vp,** debris of vascular plants; **Ac,** Acarina; **Ti,** terrestrial insects (adults of Diptera, Orthoptera and Hymenoptera); **Adi,** fragments of adult insects.



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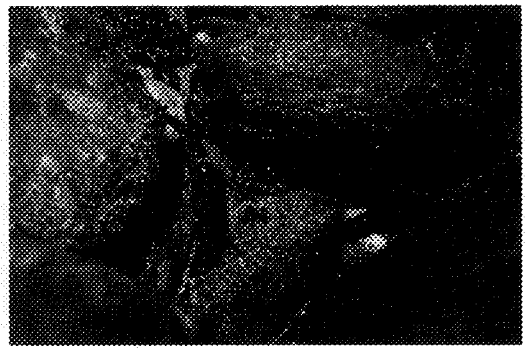

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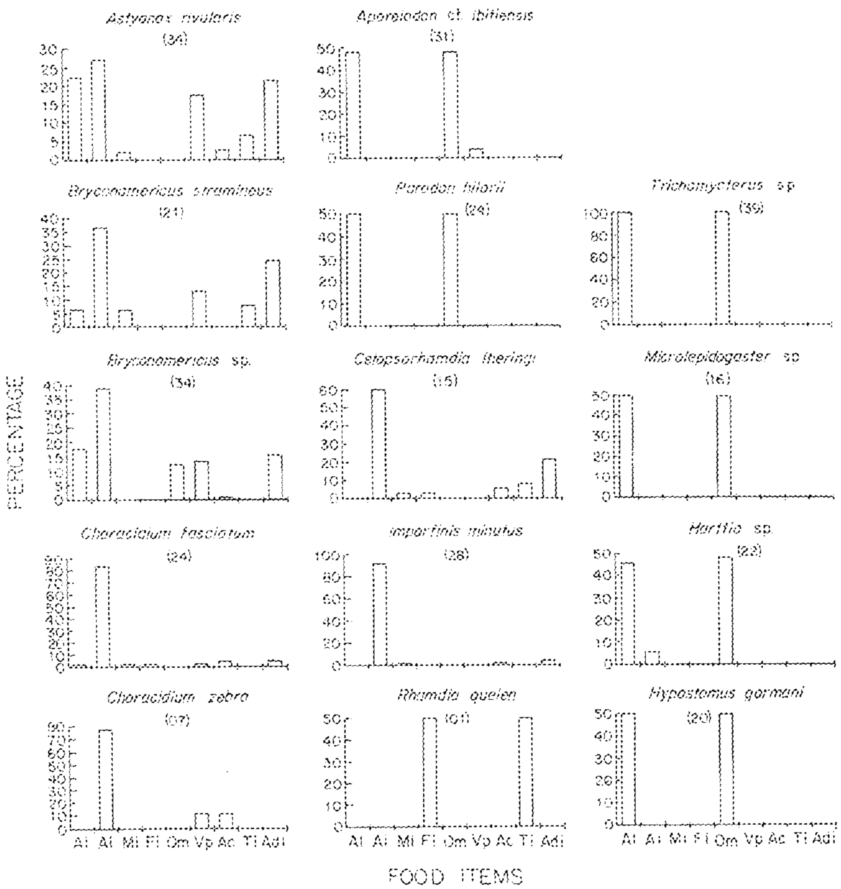

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Fig. 9. *Bryconamericus* sp. individual pursuing a current carried food particle, on the riffles lower stretch, by day (photograph by R. M. C. Castro).

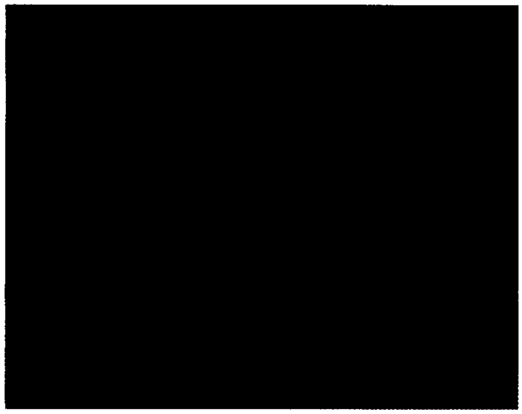

Fig. 10. *Bryconamericus* sp. individual grazing on riffles lower stretch bottom rocks attached algae, by day (photograph by R. M. C. Castro).

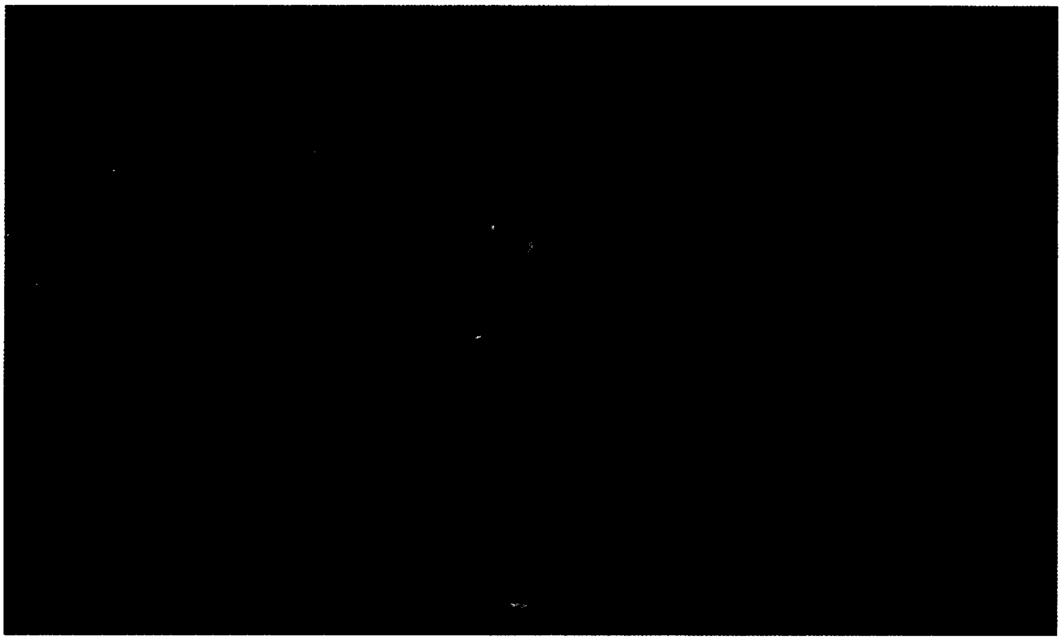

Fig. 11. Upstream orientated *Apareiodon* cf. *ibitiensis* specimen, using its expanded and horizontally orientated paired fins to hold its position over a rock surface while grazing on periphytic algae, on the riffles upper stretch, by day (photograph by R. M. C. Castro).

In riffles the current speed usually creates turbulence, promoting a rapid circulation of nutrients and dissolved gases that, together with the clear and transparent waters of most riffles allow a rapid and abundant algal periphytic growth (Hynes, 1970). According to Angermeier & Karr (1983), in Panama streams the number of invertebrates was 3.5 times larger in riffles than in pools as a consequence of the greater availability of edible algae in the riffles. A larger amount of aquatic invertebrates in riffles compared with pools was also observed by Henry et al. (1994) in the upper part of a stream in southeastern Brazil, and the authors attributed this to the large amount

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Thus, apparently there was a relatively large amount of autochthonous food available to the fishes at our study site: periphytic and bentic algae and aquatic juveniles insects. Although we did not quantify the available food, we believe that this hypothesis is supported by the fact that the algivorous and larvivorous species represented 72 % of all resident species.

Activity period. Generally speaking, characiforms as a whole are considered as diurnal while siluriforms are considered predominantly crepuscular/nocturnal (Fink & Fink, 1979; Lowe-McConnell, 1987). All the characiform species studied by us were diurnal; but among the siluriforms, two species, *Microlepidogaster* sp. and *Trichomycterus* sp., were diurnal; and some isolate *C. iheringi* individuals displayed diurnal activity. During an unpublished study performed by the second author and collaborators in southeastern Brazilian streams, *Microlepidogater francirochai* and one unidentified species of *Trichomycterus* were observed actively feeding by day.

Feeding. The coexistence of various fish species in one environment seems to be possible due to the differential use of spatial, temporal and food resources (see Weatherley, 1963, for general considerations and Zaret & Rand, 1971; Knöppel, 1970 and Sabino & Castro, 1990, for examples of resources partitioning in neotropical freshwater fish communities). Although we did not perform a general niche overlap analysis, the almost complete segregation of the studied species regarding activity periods and foraging and feeding microenvironments, suggests the possible occurrence of environmental resource partitioning by the fish species.

According to Lowe-McConnell (1975, 1987), in rivers upper stretches and in tropical streams generally, the fishes depend primarily on allochthonous food material, such as terrestrial insects and terrestrial plant fragments (see Zaret & Rand, 1971; Saul, 1975; Sabino & Castro, 1990 and Castro & Casatti, 1997, for examples from the neotropics). In our study the autochthonous food items (aquatic insects and periphytic algae) were by far the most important ones for the community as a whole. We observed that allochthonous food items were rapidly dragged away by the strong current, allowing only the nektonic drift-feeder species (tetragonopterines) to capture some of them. This was also verified by the presence of the highest percentage of allochthonous food items found in the tetragonopterines species diets (45 % for the tetragonopterines species, compared with a maximum of 15 % for the remaining species).

The DTL/SL values found for the herbivores species were the highest and the values for omnivores, larvivores and insectivore-piscivore species the lowest. The relatively low and very similar values found for omnivores, larvivores and insectivore-piscivore species seems to agree with Knöppel (1970)'s opinion, based on a study of amazonian fishes, that the alimentary canal morphology cannot be used exactly as a index to the feeding habits of fish species due to the irregularity in the length of the intestine and the general uniformity of the intestine coils in different fish families.

Compared to data about diet and feeding behaviour in the South American ichthyological literature, for the omnivorous species, our results generally agree with Teixeira (1989) and Castro & Casatti (1997), who also recorded that algae and terrestrial insects dominated diets in various *Astyanax* species.

For the larvivorous species, the habits of *Characidium* spp. agrees with findings of Costa (1987), Sabino & Castro (1990) and Castro & Casatti (1997). Sabino & Castro (1990) also observed that *Characidium* sp. (= *C. japuhibensis*) uses sit-and-wait predation and substrate speculation feeding strategies. The predominance of aquatic insect larvae and nymphs in the stomachs of *Cetopsorhamdia iheringi* was also reported by Schubart & Gomes (1959) for a stream in southeastern Brazil. As for *Rhamdela minuta* (= *I. minutus*), Sazima & Pombal (1986) record solitary, nocturnal habit and suggest a mainly tactile and chemosensorial orientation in specimens from southeastern Brazil; Sabino & Castro (1990) report insectivore habits (mostly aquatic insects) and the use of substrate speculation feeding strategies in *Rhamdella minuta* (= *I. piperatus*) in a southeastern Brazil coastal stream.

For the algivorous species, our findings about the parodontids feeding behavior and diets are extremely similar to the ones of Sazima (1980), in a study of two species of *Apareiodon*. The almost total diet overlap found between *Apareiodon* cf. *ibitiensis* and *P. hilarii*, is possibly competitively diminished to a significant degree by the fact that, although these two species apparently fed on the same items, they spent most of the time spatially segregated: the larger and robust *P. hilarii* foraged in the deeper and fast-flowing central riffles areas, whereas the smaller and slender *Apareiodon* cf. *ibitiensis* foraged mostly in the riffles shallows and relatively slow-flowing lateral rocky areas. In addition, the agonistic behaviour observed during sporadic encounters between *P. hilarii* and *Apareiodon* cf. *ibitiensis* can be considered as a territorial defense of food sites, similar to the one found by Buck & Sazima (1995) for two armored catfish algivore species in southeastern Brazil. Loricariidae eat algae almost exclusively (Power, 1983, 1984; Buck & Sazima, 1995) and this agrees with our findings.

General considerations. The water velocity and the substrate type apparently are the factors shaping the studied fish community structure. Their interplay generated areas rich in food (patches of rapidly growing periphytic algae and the aquatic insect larvae that directly or indirectly fed on them) and many shelters whose availability are probably the main environmental factors allowing, in an adaptive and evolutionary sense, the formation of a community adapted to fast waters. In addition, predators like birds, small mammals and caimans are probably hindered in their fishing activities by the strong current, and the riffles food resources are apparently shared by several species, for even though some species had similar feeding habits, there were marked differences in their spatial distributions and activity periods.

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