Ecology of fishes of Quebrada Negra, Costa Rica, a first order neotropical lowland stream

Ecología de los peces de Quebrada Negra, Costa Rica, río neotropical de primer orden de tierras bajas

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Abstract: The fish communities at the Quebrada Negra, a tropical, first order lowland stream situated within the Piedras Blancas National Park, Costa Rica were studied with respect to the patterns of species abundance, distribution and co-occurrence. Field assessment was carried out in the dry season from February to April 2004 and during the rainy season from July to September 2004. As a characteristic rainforest stream in Costa Rica, Quebrada Negra undergoes seasonal changes in water flow, and this seasonality affects food availability, reproduction and fish movement. Species composition in a series of four defined choriotopes (cascades, riffles, sites with moderate velocities and pools) along a 1.4 km segment of the Quebrada Negra were sampled by electrofishing using a backpack electroshocker. In addition, direct observations on microhabitat choice were made by snorkelling. A sample of fish was analysed for food composition of the diet. In the course of the survey, 23 species were encountered representing 10 families. Eight species are considered to be endemic to Costa Rica. The most common species were the characid *Astyanax aeneus* (over 40% of all specimens) and the small poecilids *Brachyrhaphis rhabdophora* and *Poeciliopsis paucimaculata*. Further abundant constituents of the fish fauna were the bottom-dwelling gobiid *Sicydium salvini*, the two cichlids *Archocentrus sajica* and *Tomocichla sieboldii*, the three-barbeled catfish *Rhamdia guatemalensis* (Heptapteridae), the characid *Brycon behreae* and *Piabucina boruca* (Lebisianidae). These common species show distinct differences with regard to habitat choice: Pools are the most densely populated areas and are dominated by *Astyanax* and the two small poeciliids. *Sicydium* was most abundant in riffle sections with higher current velocity. Sampling sites in the cascades were dominated by *Brachyrhaphis*. Microhabitat choice, detected by direct observations, showed a clear spatial segregation. The characids *Astyanax* and the less frequent *Brycon* are open-water species whereas fishes of the families Poeciliidae and Cichlidae were commonly found along the shoreline. Species also differed in their vertical position in the water column. *Piabucina boruca* occupied surface regions, *Sicydium* preferred the bottom. The three co-occurring Poeciliidae showed a certain vertical segregation: *Brachyrhaphis rhabdophora* was more often encountered on the surface and in midwater regions, while *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata* preferred midwater and low regions. Fish abundances for most of the species were higher in the dry season, although numbers of *A. aeneus* and *S. salvini* increased markedly from the dry to the rainy season. *P. paucimaculata* and *P. retropinna* were rarely found in samples of the rainy season. Some species like *B. behreae* were present only in the rainy season. *A. aeneus* was the most common species in both seasons. Examinations of stomach and intestine contents showed that aquatic and terrestrial insects constituted the major portion of the diet of *A. aeneus*. *S. salvini* is an algal grazer and consumed detritus. The diets of *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata* consisted only of detritus and mud. *Brachyrhaphis* consumed mostly ants and tiny dipterans. The gut of *Piabucina boruca* was packed with terrestrial insects. *Tomocichla sieboldii* and *Archocentrus sajica* had a mixed diet of algae and aquatic insects.

Key words: fish, habitat choice, seasonality, biodiversity, underwater observations, food partitioning, Central America.

Resumen: Se realizó un estudio sobre las comunidades de peces en Quebrada Negra, un río de primer orden de agua tropical de tierras bajas, ubicado en el Parque Nacional Piedras Blancas, Costa Rica. El objetivo fue comprender los mecanismos y factores que determinan los patrones de abundancia de especies, distribución y coocurrencia . Al igual que otros ríos tropicales, el Quebrada Negra atraviesa cada año cambios estacionales debidos a las lluvias. Se ha demostrado que los cambios estacionales modifican la abuncancia de alimentos, las interacciones entre especies, la reproducción, los movimientos de los peces y la estabilidad de la comunidad, por esa razón el estudio se realizó durante la temporada seca (febrero a abril de 2004) y en la temporada de lluvias (julio a septiembre de 2004). Para determinar las composición específica, se tomaron muestras en 4 coriotopos a lo largo de un segmento de 1.4 km del Quebrada Negra: remansos, cascadas, rápidos y sitios de velocidades moderadas. Se utilizó un dispositivo de electroshock portátil para capturar con vida a los peces. Algunos peces fueron disecados para examinar el contenido del estómago y los intestinos. Además se realizaron observaciones con esnorkel en los sitios que lo permitían. A lo largo del estudio se encontraron un total de 23 especies correspondientes a diez familias. Ocho de las especies estudiadas son endémicas de Costa Rica. Las especies más comunes fueron el carácido *Astyanax aeneus* (más del 40% de los especímenes pertenecían a esta especie),

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y los pequeños poecilidos *Brachyrhaphis rhabdophora* y *Poeciliopsis paucimaculta*. Otras especies abundantes encontradas cerca del fondo del río fuerón los peces gobidos *Sicydium salvini*, dos ciclidos *Archocentrus sajica* y *Tomocichla sieboldii*, el pez gato *Rhamdia guatemalensis* (Heptapteridae), el carácido *Brycon behreae* y *Piabucina boruca* (Lebisianidae). Las especies anteriormente mencionadas muestran diferencias con respecto al hábitat de su elección. Las pozas tienen la mayor densidad de población y son áreas dominadas por *Astyanax* y los dos poecilidos. En áreas con mayores corrientes de agua el más popular fue *Sicydium* y en áreas de cascadas el más abundate fue *Brachyrhaphis*. La elección del microhábitat, detectada por observaciones directas, mostro una clara segregación espacial. Los carácidos *Astyanax* y los menos comunes *Brycon* son especies de aguas abiertas en comparación con los peces de familias como Poeciliidae y Cichlidae que prefieren los bordes del río. Las especies también difieren en la posición vertical de la columna de agua. *Piabucina boruca* ocupa las regiones superficiales mientras *Sicydium* prefiere el fondo. Los tres Poeciliidae co-ocurrentes muestran cierta segregación vertical. *Brachyrhaphis rhabdophora* se encuentra comunmente en la superficie y en las regiones medias mientras que *Poeciliopsis retropinna* y *Poeciliopsis paucimaculata* prefieren las regiones medias o bajas. La abundancia de peces para la mayoría de las especies fue mayor durante la temporada seca, aunque cierto porcentaje de *A. aeneus* y *S. salvini* incrementaron notoriamente de la temporada seca a la temporada de lluvias. Algunas especies como *B. behreae* estuvieron presentes solamente en la temporada de lluvias. *A. aeneus* fue la más común de las especies en ambas temporadas. Análisis del contenido estomacal e intestinal de las especies muestra que los insectos acuáticos y terrestres son la principal dieta de *A. aeneus*. En cuanto a *S. salvini* se encontró que es un especie que basa su alimentación en algas y detritus. Las dietas de *Poeciliopsis retropinna* y *Poeciliopsis paucimaculata* consiste en detritus y lodo. *Brachyrhaphis* basa su dieta en hormigas y pequeños dípteros. Los contenidos del estómago de *Piabucina boruca* mostraron insectos terrestres. Finalmente *Tomocichla sieboldii* y *Archocentrus sajica* presentaban una dieta variada de alga e insectos acuáticos.

Palabras clave: Peces, selección de hábitat, estacionalidad, biodiversidad, observaciones bajo el agua, partición de la comida, América Central.

Introduction

The fish fauna of the Neotropical region is one of the most diverse in the world, estimated to include approximately 8.000 species (SCHAEFER 1998). In comparison to the temperate zone, tropical rivers are characterised by a higher number of species (WINEMILLER & JEPSEN 1998). In Costa Rica, three of the four Central American ichthyological provinces overlap, accounting for its considerable diversity. Since 1963, 25 new species of Costa Rican freshwater fish have been described (BUSSING 1998).

Streams within the Rio Esquinas catchment in Costa Rica (Piedras Blancas National Park) were analysed with regard to abiotic parameters such as morphology, hydrology, hydrochemistry and canopy cover by the riparian vegetation (see TSCHELAUT et al. 2008). This paper concentrates on the analysis of the fish community of Quebrada Negra, a first order stream, with respect to factors determining habitat selection, food composition and temporal segregation within the fish community.

Materials and Methods

Field sampling was conducted twice, once in the dry season from February to April 2004 and once during the rainy season from July to September 2004, along a 1.4 km segment of Quebrada Negra. Stream reaches were divided into habitat units or choriotopes classified by their physical structure, current velocity, depth and substrate. In the dry season three different choriotope types (riffles, pools and cascades) were distinguished. In the rainy season an additional 4th type, the transition zone between pools and riffles with moderate current velocity was distinguished.

A backpack electroshocker was used to stun fish temporarily for capture. Anode diameter was 30 cm. To estimate the size of fish populations the removal method (DELURY 1951) was used. Block nets of 20×2 m, 7 mm mesh were set at the upper and lower ends of the sites to prevent the escape of the fish. Two to three passes were made from the lower to the upper end of a site. For each pass the amount of effort (shocking time) was equal. Fishes were identified using the keys in BUSSING (1998).

Forty-four collections were made, 17 in the dry season and 27 in the rainy season. At each station, water current velocity was recorded with an Ottflügel, Type C2, in 40% water depth above the stream bottom. The extent of each site was noted. Water width was recorded up to four times, water depth three to nine times. Sediment size was estimated visually and the percentage of the following five categories at each sampling site was noted: < 2 mm, 2-6.3 mm, 6.3-20 mm, 20-63 mm, > 63 mm. The distance of each site from the waterfall, situated near the source, was recorded and noted in a map.

A sample of fish was preserved in 4% formalin and later dissected to examine stomach and intestine contents. Food items were categorised under microscopical inspection into sediment, detritus, algae, terrestrial invertebrates, aquatic invertebrates and fishes.

Snorkelling observations on microhabitat choice of fish were made. Positions of fish were recorded for 10 to 20 minute periods. Additional behaviour notes were

Table 1: Numbers of fish caught by electrofishing, mean total length [mm], proportion [%] of total quantity and presence (+) or absence (-) of each species in the dry (DS) and rainy season (RS) based on 44 samples.

species	family	specimen	mean TL [cm]	DS	RS
Astyanax aeneus (Günther, 1860)	Characidae	565	7.5	+	+
Bryconamericus terrabensis (Meek, 1914)		14	10.1	+	+
Brycon behreae (Hildebrand, 1938)		40	13.6	-	+
Hyphessobrycon savagei (Bussing, 1967)		1	5.9	-	+
Brachyrhaphis rhabdophora (Regan, 1908)	Poeciliidae	252	3.1	+	+
Poecilia gillii (Kner & Steindachner, 1863)		16	4.4	+	-
Poeciliopsis paucimaculata (Bussing 1967)		133	4.0	+	+
Poeciliopsis retropinna (Regan, 1908)		45	4.8	+	+
Amphilophus lyonsi (Gosse, 1966)	Cichlidae	9	6.9	+	+
Archocentrus sajica (Bussing 1974)		49	6.9	+	+
Parachromis loisellei (Bussing 1990)		1	8.9	-	+
Tomocichla sieboldii (Kner & Steindachner, 1863)		43	8.7	+	+
Imparfinis lineatus (Bussing 1970)	Heptapteridae	5	8.4	+	+
Pimelodella chagresi (Steindachner, 1876)		4	8.1	+	+
Rhamdia guatemalensis (Günther, 1864)		28	12.3	+	+
Eleotris picta (Kner & Steindachner, 1863)	Eleotridae	2	14.0	+	+
Gobiomorus maculatus (Günther, 1859)		3	16.0	+	+
Awaous banana (Günther, 1861)	Gobiidae	8	6.4	-	+
Sicydium salvini (Grant, 1884)		100	3.9	+	+
Piabucina boruca (Bussing, 1967)	Lebiasinidae	37	11.1	+	+
Trichomycterus striatus (Meek & Hildebrand, 1913)	Trichomycteridae	16	6.5	+	+
Gobiesox potamius (Briggs, 1955)	Gobiesocidae	1	3.6	-	+
Agonostomus monticola (Bancroft, 1836)	Mugilidae	1	22.0	-	+

taken. Seven underwater observations were made in the dry season, nine during the rainy season.

The variation in species abundances was analysed using a detrended correspondence analysis (DCA) and calculated with the software package CANOCO. DCA is a multivariate technique derived from reciprocal averaging: it maximises the correlation between species scores and sample scores along an assumed gradient (HILL & GAUCH 1980) and was used to examine associations between distribution patterns and abiotic factors.

Results

Faunal Composition

Fish collections by electro-shocking at 44 sampling sites at Quebrada yielded a total catch of 1.343 specimens. Twenty-three species were recorded, representing ten families (Table 1). Seventeen species were recorded during the dry season and 22 species during the rainy season. Ten species were rare (< 10 individuals recorded). A minimum of two and a maximum of twelve species were found at any sampling site.

The most common species was the characid *Astyanax aeneus*, followed by the two poeciliids *Brachyrhaphis rhabdophora* and *Poeciliopsis paucimaculata* (see Table 1). Other common species are the gobiid *Sicydium salvini*, the cichlids *Archocentrus sajica* and *Tomocichla sieboldii*, the poecilid *Poeciliopsis retropinna*, *Rhamdia guatemalensis* (Heptapteridae) and *Piabucina boruca* (Lebiasinidae).

The following eight species are considered to be endemic to Costa Rica: *Archocentrus sajica*, *Brachyrhaphis rhabdophora*, *Bryconamericus terrabensis*, *Gobiesox potamius*, *Hyphessobrycon savagei*, *Imparfinis lineatus*, *Piabucina boruca* and *Poeciliopsis paucimaculata*.

Habitat choice

Table 2 and Figure 1 provide information on the structure of the fish assemblages in the four choriotope types. Most of the common species occur at all the choriotopes although in varying densities and percentage composition of the community. In pools, *Astyanax aeneus* is clearly the dominant species. Nearly half of all individuals belonged to that species (Table 1). All the other characids appear to prefer pool locations. The same holds true for the three-barbeled catfish. Densities of the two common cichlids *Archocentrus sajica* and *Tomocichla sieboldii* were also clearly higher in pools than in the other choriotope types. *Piabucina boruca* showed a preference for pool sections and was absent in riffle sections. The two poeciliids *Brachyrhaphis rhabdophora* and *Poeciliopsis paucimaculata* are common in all choriotope

Table 2: Proportion [%] and density [individuals per 10 m^2] of each species in the four choriotopes sampled (pools, cascades, sites with moderate velocities and riffles)

Species	Pools		Cascades		sites w. mod.vel.		riffles	
	[%]	density	[%]	density	[%]	density	[%]	density
Astyanax aeneus	48.3	8.06	25.4	0.79	25.7	1.55	10.1	0.71
Bryconamericus terrabensis	1.3	0.22						
Brycon behreae	3.5	0.59			1.9	0.12	0.6	0.04
Hyphessobrycon savagei	0.1	< 0.10						
Brachyrhaphis rhabdophora	15.6	2.64	54.9	1.72	14.3	0.86	23.4	1.55
Poecilia gillii	1.8	0.30						
Poeciliopsis paucimaculata	8.1	1.36			14.3	0.86	19.6	1.46
Poeciliopsis retropinna	3.9	0.66			3.8	0.23		
Amphilophus lyonsi	0.7	0.11			1.0	< 0.10	0.6	< 0.10
Archocentrus sajica	4.5	0.75			1.0	< 0.10	0.6	< 0.10
Parachromis loisellei	0.1	< 0.10						
Tomocichla sieboldii	3.3	0.54	4.2	0.13	2.9	0.17	1.9	0.13
Imparfinis lineatus	0.1	< 0.10	1.4	< 0.10			1.9	0.13
Pimelodella chagresi	0.4	< 0.10						
Rhamdia guatemalensis	2.3	0.38	1.4	< 0.10	1.9	0.12	0.6	< 0.10
Eleotris picta	0.2	< 0.10						
Gobiomorus maculatus	0.2	< 0.10					0.6	0.04
Awaous banana	0.6	0.10			1.9	0.12		
Sicydium salvini	1.4	0.24	8.5	0.26	25.7	1.55	32.9	2.30
Piabucina boruca	3.1	0.51	4.2	0.13	1.9	0.12		
Gobieesox potamius	0.1	< 0.10						
Trichomycterus striatus			1.4	< 0.10	3.8	0.23	7.0	0.49
Agonostomus monticola	0.1	< 0.10						

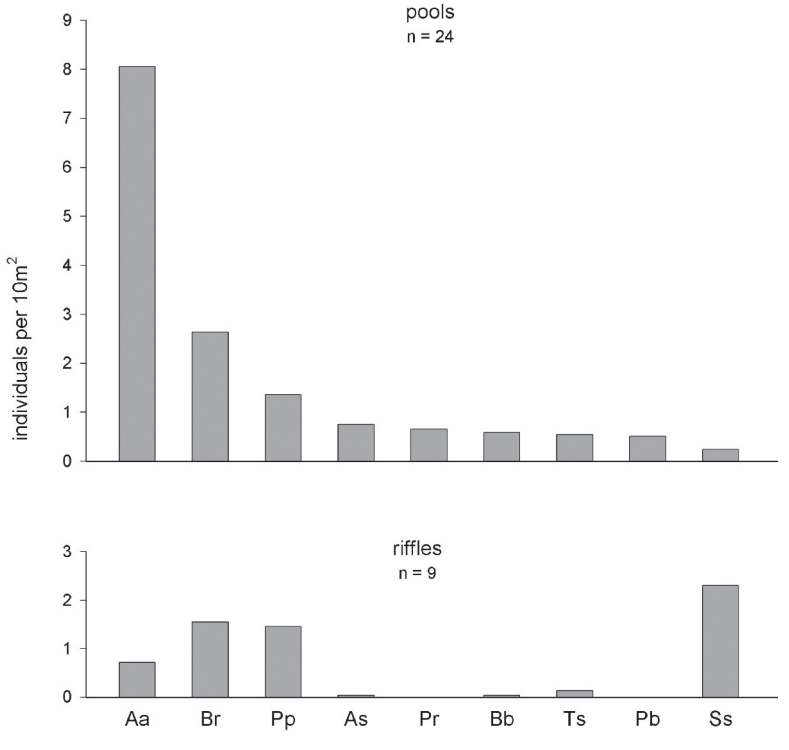

Fig. 1: The densities of seven species in pools and riffles. Only species with a density > 0.5 individuals per 10 m^2 in at least one of the choriotopes are shown (see Table 2). Aa = *Astyanax aeneus*, Pb = *Piabucina boruca*, Pr = *Poeciliopsis retropinna*, Br = *Brachyrhaphis rhabdophora*, As = *Archocentrus sajica*, Ts = *Tomocichla sieboldii*, Pp = *Poeciliopsis paucimaculata*, Ss = *Sicydium salvini*, n = sample size.

types. Sampling sites in the cascades were dominated by *B. rhabdophora*, with a share of more than 50 percent of all specimens caught. *B. rhabdophora* was also found frequently in the other three choriotopes. In riffle locations with higher current velocities, *Sicydium salvini* was the most frequent species followed by the three eurytopic species *A. aeneus*, *B. rhabdophora* and *P. paucimaculata*.

Microhabitat choice by visual observation

Spatial segregation is an important mechanism of niche partitioning. Fishes in the Quebrada Negra differed both in their choriotope preference and in their microhabitat position as observed by direct underwater observation. Visual observations by snorkelling provided some information on position choice in a cross-section of the stream. A generalised summary of these observations is provided in Figure 2.

The characids *Astyanax* and the less frequent *Brycon* are open-water species. These two characids preferred sites in the middle of the stream, whereas fishes of the families Poeciliidae and Cichlidae were found almost exclusively near the shore. The poecilids, which form dense populations, show an interesting form of niche overlap, because three species of similar size and body form co-occur and exhibit a similar microhabitat distribution. Like most other tropical fishes, the species also differed in their vertical position in the water column.

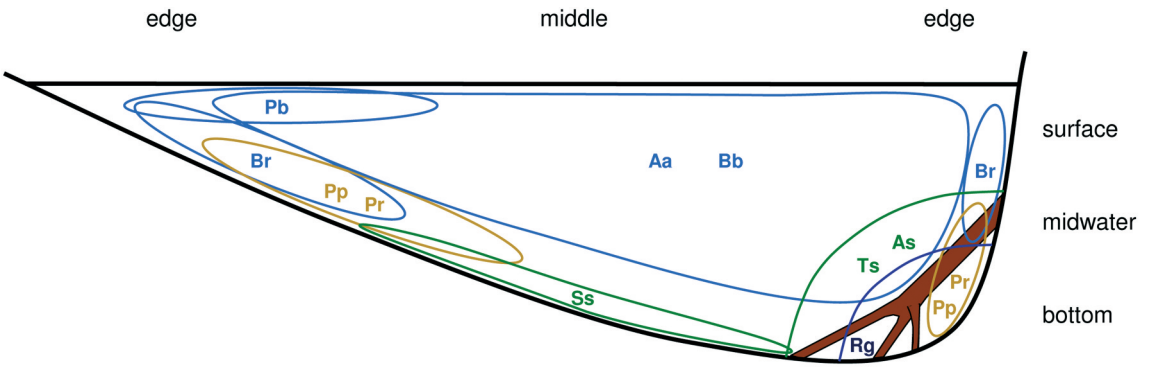

Fig. 2: Microhabitat choice of detected fish during underwater observations in pools along the study site. Br = *Brachyrhaphis rhabdophora*, Pr = *Poeciliopsis retropinna*, Pp = *Poeciliopsis paucimaculata*, Pb = *Piabucina boruca*, Bb = *Brycon behreae*, Aa = *Astyanax aeneus*, Ss = *Sicydium salvini*, As = *Archocentrus sajica*, Ts = *Tomocichla sieboldii*, Rg = *Rhamdia guatemalensis*; Fishes mainly feed on: light blue = terrestrial insects:, dark blue = aquatic insects, brown = detritius, green = algae.

Some species occupied surface regions (e.g. *Piabucina boruca*), while others preferred midwater regions or the bottom (e.g. *Sicydium salvini*).

The three co-occurring Poeciliidae, which were mostly observed in the edge zones, showed a certain vertical segregation: *Brachyrhaphis rhabdophora* was more often encountered at the surface and in midwater strata while *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata* preferred midwater and low strata.

Seasonal segregation

Densities in the dry and rainy season were compared. Except for *Astyanax aeneus*, *Sicydium salvini* and *Brycon behreae*, densities were higher in the dry season (Fig. 3). *A. aeneus* was the most common species in both seasons. *B. behreae* was only present during the rainy season. Whereas the numbers of *S. salvini* increased markedly from the dry to the rainy season, *Poeciliopsis paucimaculata* and *Poeciliopsis retropinna* were rarely found in samples from the rainy season.

Food partitioning

Although the food analysis of the Quebrada Negra fishes is preliminary due to small sample sizes, several species clearly exhibited fairly rigid selection for specific items. Aquatic and terrestrial insects constituted the major portion of the diet of *Astyanax aeneus* and *Bryconamericus terrabensis* (Table 3). *Sicydium salvini* is an algal grazer and consumed detritus. The diets of *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata* consisted solely of detritus and mud. *Brachyrhaphis* consumed mostly airborne material, ants and small dipterans. The gut of *Piabucina boruca* was packed with terrestrial insects, mostly ants. *Rhamdia guatemalensis* and *Imparfinis lineatus* consumed only aquatic insects. *Tomocichla sieboldii* and *Archocentrus sajica* had a mixed diet of algae and aquatic insects.

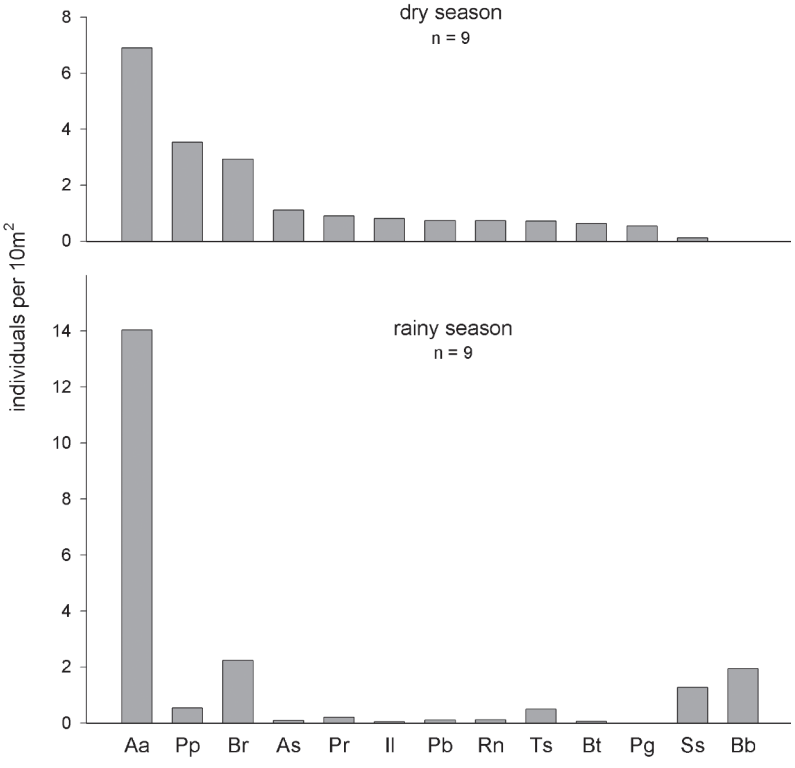

Fig. 3: Seasonal changes in density. Thirteen species in nine site of all choritope types which were sampled in both seasons are compared. Only species with a density > 0.5 individuals per $10m^2$ in any season are shown. Aa = *Astyanax aeneus*, Pp = *Poeciliopsis paucimaculata*, Br = *Brachyrhaphis rhabdophora*, As = *Archocentrus sajica*, Pr = *Poeciliopsis retropinna*, Il = *Imparfinis lineatus*, Pb = *Piabucina boruca*, Rg = *Rhamdia guatemalensis*, Ts = *Tomocichla sieboldii*, Bt = *Bryconamericus terrabensis*, Pg = *Poecilia gillii*, Ss = *Sicydium salvini*, Bb = *Brycon behreae*, n = sample size.

Table 3: Stomach and intestine contents of fish species of Quebrada Negra

- no food, □ additional food, ■ dominant food							
species	**n**	**size range [cm]**	**algae**	**sediment / detritus**	**terrestrial insects**	**aquatic insects**	**fish**
Astyanax aeneus	12	5.1 – 10.0	-	-	■	■	-
Bryconamericus terrabensis	4	10.0 – 12.0	-	-	■	■	-
Brachyrhaphis rhabdophora	14	2.5 – 4.2	-	-	■	□	-
Poecilia gillii	5	3.3 – 4.1	□	■	-	-	-
Poeciliopsis paucimaculata	21	2.8 – 6.2	□	■	-	-	-
Poeciliopsis retropinna	16	3.8 – 6.9	□	■	-	-	-
Tomocichla sieboldii	6	5.4 – 11.9	■	-	-	■	□
Imparfinis lineatus	2	7.7 – 7.8	-	-	-	■	-
Rhamdia guatemalensis	3	8.9 – 10.2	-	-	-	■	-
Sicydium salvini	5	5.9 – 7.5	■	■	-	-	-
Piabucina boruca	4	8.5 – 12.6	-	-	■	-	-

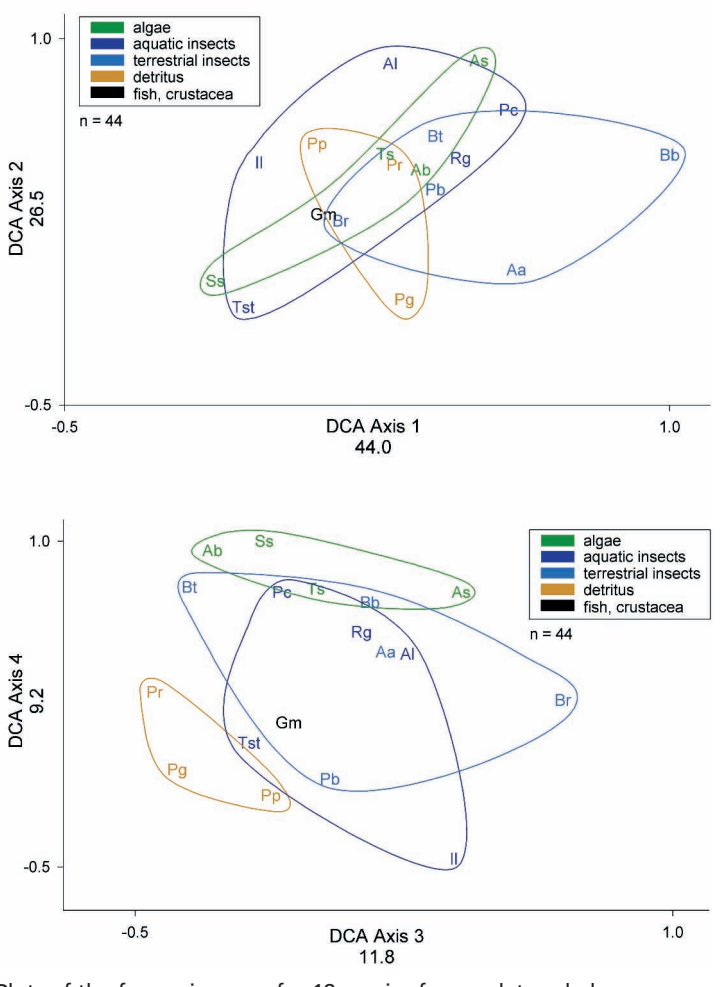

Fig. 4: Plots of the four axis scores for 18 species from a detrended correspondence analysis (DCA). Five abiotic variables were closely related to fish assemblage distribution. Depending on food preference of each species, fishes were assigned to trophic guilds. Ss = *Sicydium salvini*, Tst = *Trichomycterus striatus*, Il = *Imparfinis lineatus*, Pp = *Poeciliopsis paucimaculata*, Gm = *Gobiomorus maculatus*, Br = *Brachyrhaphis rhabdophora*, Al = *Amphilophus lyonsi*, Ts = *Tomocichla sieboldii*, As = *Archocentrus sajica*, Pr = *Poeciliopsis retropinna*, Pg = *Poecilia gillii*, Ab = *Awaous banana*, Bt = *Bryconamericus terrabensis*, Pb = *Piabucina boruca*, Rg = *Rhamdia guatemalensis*, Pc = *Pimelodella chagresi*, Aa = *Astyanax aeneus*, Bb = *Brycon behreae*, n = sample size

Key abiotic variables determining micro-habitat choice

The detrended correspondence analysis helps to describe associations between species' distribution patterns and key abiotic variables. The DCA indicated that 5 variables were closely related to fish assemblage distribution (Fig. 4). The first axis explains 44.0% of the variance, and is strongly correlated with mean depth and sediment size and negatively correlated with mean current velocity. The second axis is also significant according to these three parameters and explains 26.5% of the variance. This suggests that current velocity, depth and sediment particle size were the most important environmental variables structuring the fish assemblage. In Fig. 4, upper graph, species which prefer fast-flowing microhabitats are situated at the bottom left corner whereas in the top right corner species characteristic for pools are shown.

The third DCA axis is strongly correlated with distance from the source of the Quebrada Negra and negatively correlated with mean current velocity. This axis describes a longitudinal gradient running from downstream sections to upstream sites and explains 11.8% of the variance. The fourth axis is strongly correlated with season. Fishes which were common in the dry season are shown near the origin of axis 4.

Fishes were assigned to trophic guilds. Omnivorous species were not displayed as a particular group, but were assigned to one of five trophic guilds depending on the main part of the food composition. Detritivorous species were mostly found in the dry season in downstream reaches with moderate current velocity. Algivorous fish are more abundant in the rainy season. Species which feed on terrestrial insects were found in choriotopes of higher current velocity along the longitudinal gradient. Fish of the guild that feed on aquatic insects were found in all choriotope types and in both seasons.

Discussion

When compared with temperate rivers, tropical streams like Quebrada Negra are characterised by higher species numbers (WINEMILLER & JEPSEN 1998).

Due to the hydromorphological dynamics of the Quebrada Negra, habitat heterogeneity is high, providing numerous microhabitats. Differences in species assemblage composition within four different choriotopes reflect differences in abiotic factors.

Fish abundances varied between seasons. Seasonality plays an important role and has been shown to modify food availability (LOWE-MCCONNELL 1964, 1979, POWER 1984, PREJS & PREJS 1987, GOULDING et al. 1988), species interactions (WINEMILLER 1989), reproduction (BAYLEY 1988, BOUJARD 1992), fish movement (LOWE-MCCONNELL 1987, WINEMILLER & TAPHORN 1989) and community stability (RODRÍGUEZ & LEWIS 1994). In neotropical regions, the increase of diversity and richness during the wet season is associated with recruitment from adjacent areas or with the beginning of the reproductive cycle (LOWE-MCCONNELL 1987). Changing fish abundances can reflect fish movement, as has been documented for a variety of tropical river floodplains. The Quebrada Negra experiences a high seasonality in precipitation that produces seasonal patterns of river discharge. A variety of physicochemical attributes is associated with this hydrological seasonality.

Seasonality plays an important role in tropical river food webs. Flooding brings fishes into contact with a greater abundance and diversity of allochthonous food resources, especially within forested watersheds (GOULDING 1980; HENDERSON 1990). Omnivory can be considered an adaptive response to strong seasonal fluctuations in water level, which influence the availability of food resources (ANGERMEIER & KARR 1983, LOWE-MCCONNELL 1987, BAYLEY 1988, WINEMILLER 1990, GOULDING et al. 1988).

In the Quebrada Negra, the population sizes and densities of Poeciliidae decreased from the dry to the rainy season. This reflects a seasonality in food supply. The availability of algae and detritus was reduced after floods. Periphyton production decreased in the rainy season because of scouring and decreased light availability. Detrital sources may have increased in the dry period as a result of seasonal leaf fall (CHAPMAN & CHAPMAN 1990). In small tropical streams, flash floods scour substrates and reduce the availability of benthic food resources such as periphyton (PRINGLE & HAMAZAKI 1997). The degree of trophic diversification in tropical river fish assemblages is greater than that of fish assemblages in similar habitats of temperate regions (WINEMILLER 1991). Compared to temperate river fishes, tropical fishes show proportionally more herbivorous, detritivorous and omnivorous feeding behaviours (BOWEN 1983, WINEMILLER 1990, 1991, WOOTTON & OEMKE 1992). Detritus dominates the organic matter pool in most tropical rivers, and detritivorous fish comprise a significant portion of the ichthyobiomass (BAYLEY 1973, WINEMILLER 1995). Detritivory apparently plays a key role in detritus decomposition in common fish such as *P. paucimaculata*. Invertebrate feeders and piscivores also show greater niche specialisation in the tropics (ZARET & RAND 1971): reduced diet overlaps between species during the dry season were observed. The diversification of feeding niches means that fishes play significant roles in most food chains of aquatic food webs (WINEMILLER 1990).

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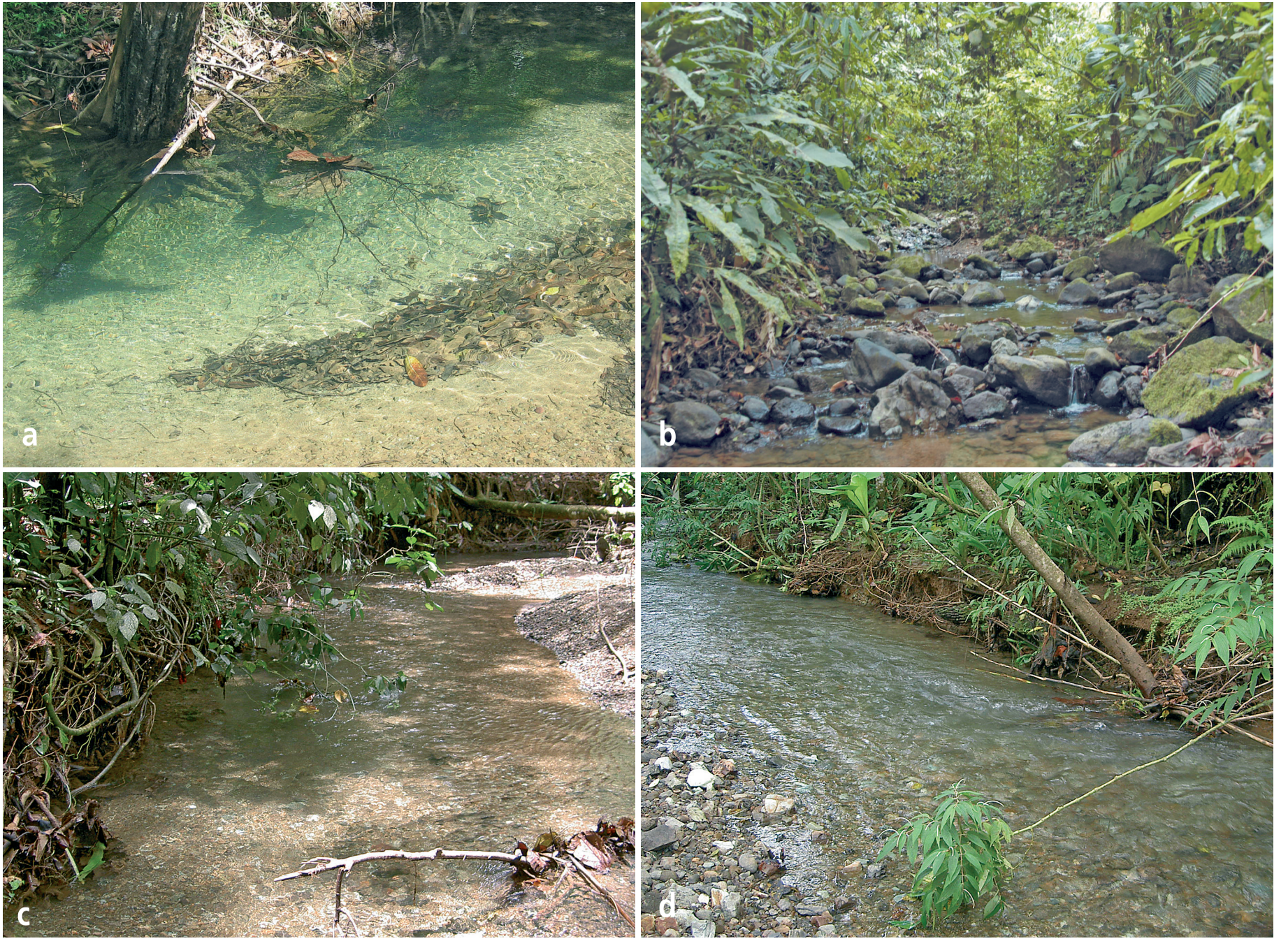

Plate 1: Four distinguished choriotope types. (**a**) pool, (**b**) cascade, (**c**) site with moderate velocity, (**d**) riffle

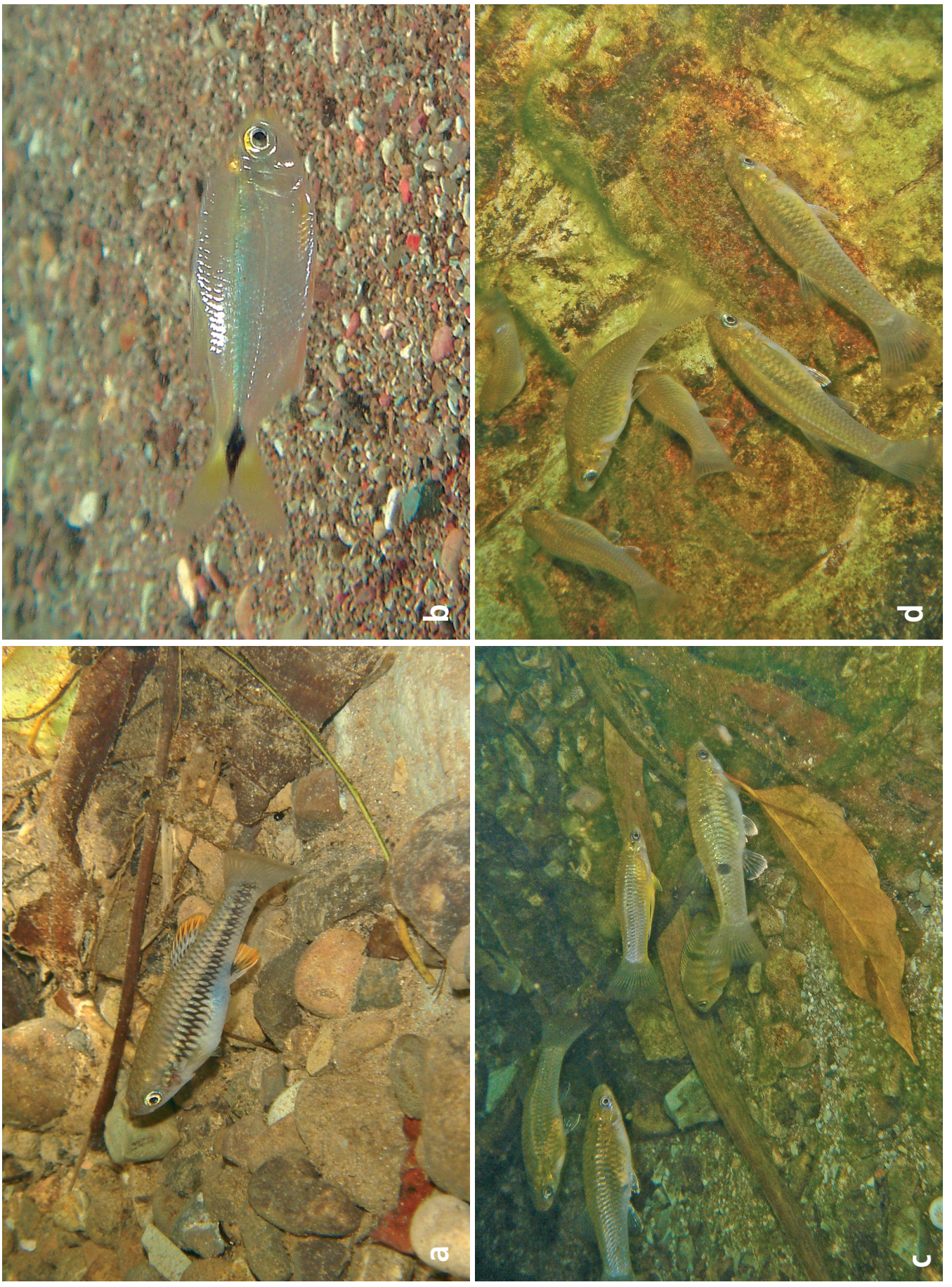

Plate 2: (**a**) *Brachyrhaphis rhabdophora*, (**b**) *Astyanax aeneus*, (**c**) *Poeciliopsis paucimaculata* (**d**) *Poeciliopsis retropinna*

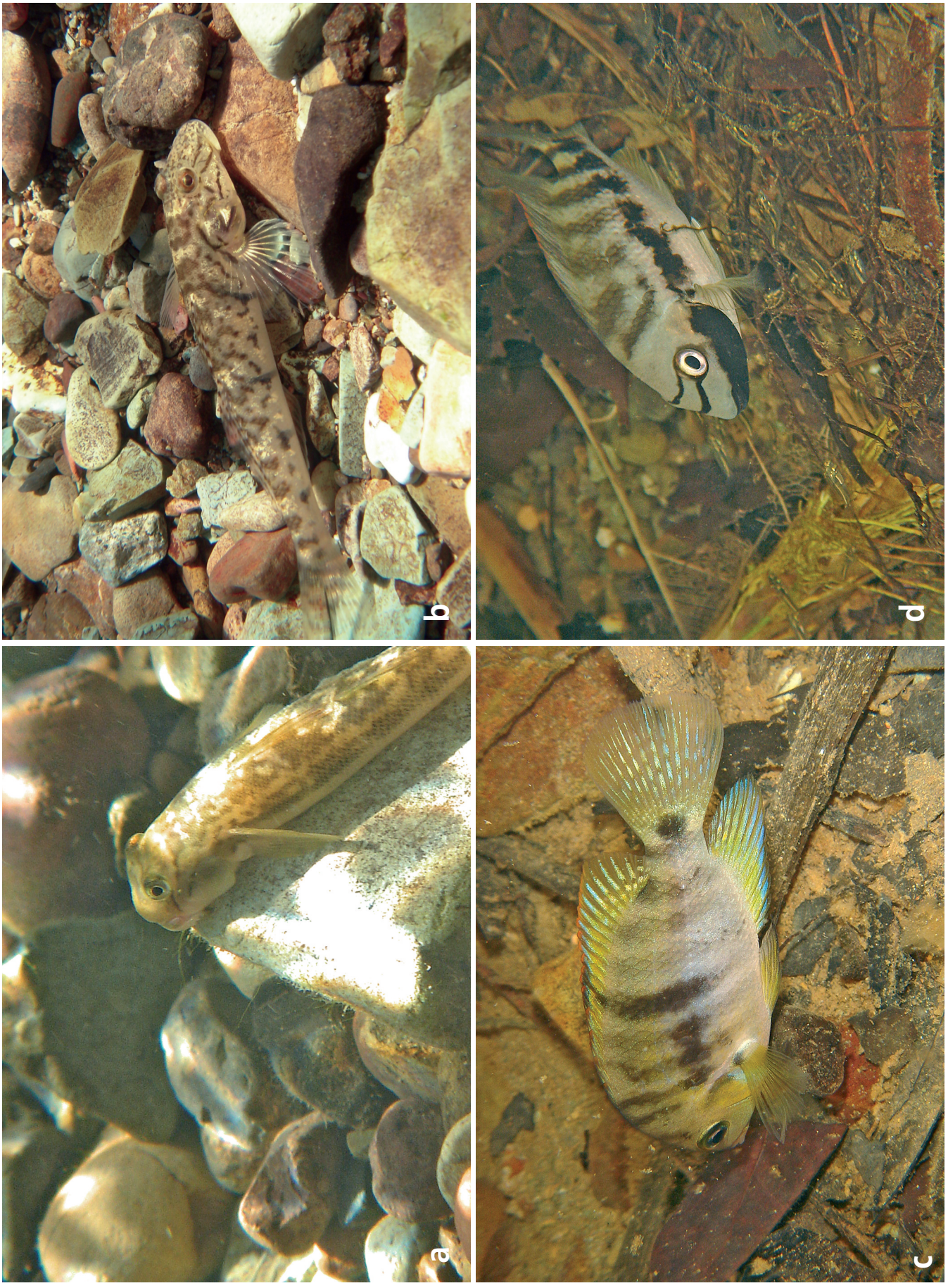

Plate 3: (**a**) *Sicydium salvini*, (**b**) *Awaous transandeanus*, (**c**) *Archocentrus sajica*, (**d**) *Tomocichla sieboldii*