

Fish communities in central Amazonian white- and blackwater floodplains

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Received 25 June 1998

Accepted 24 May 1999

Key words: Amazonia, fisheries, abundance, floodplain, igapó, várzea, inundated forest, community structure

Synopsis

In Amazonian floodplains, the flood cycle of the river is becoming the dominant seasonal factor, and fish communities are found to fluctuate greatly over the year. During inundation, fish migrate into floodplain forests to feed on fruits and seeds, in an area more than 300 000 km² in size. To document patterns of species diversity, distribution, abundance and temporal dynamics and in order to describe the ecological importance of the inundated forest, floodplain fish were captured using variously sized gill nets in white and black water areas inside and outside the floodplain forests during low, rising, high and falling water level in 1990 and 1991. Dominance varies to some extent in white water between floodplain forest (0.06) and open water (0.11) while it is unchanged in black water (0.04). Black water fish communities were more diverse. Most abundant among white water fish were *Liposarcus pardalis*, *Pygocentrus nattereri*, and *Pellona flavipinnis*, for example, or *Plagioscion squamosissimus*, *Serrasalmus rhombeus*, and *Serrasalmus manuelei* in black water. Among the most abundant white water fish, *Colossoma macropomum*, *Mylossoma duriventre* and *Osteoglossum bicirrhosum* occurred almost exclusively in inundated forests. Of the black water species there were a large number of species which were captured only in inundated forest, such as *Geophagus* cf. *altifrons*, *Hoplias malabaricus*, *Osteoglossum bicirrhosum* and *Uaru amphiacanthoides*. Catches varied with sample site, water level and direction of water level change. The average CPUE in white and black water was 190 and 41 g fish m⁻² and day, respectively, with maximum yields at low water and minimum yields at high water. Comparing rising and falling water levels, a significantly higher quantity of fishes was captured at falling water level. In black water, fish catches from the floodplain forest exceeded the open water catch by 183 to 550%, depending on season. Differences in respect of white water are smaller (106–281%). Fish communities in the area under investigation seem to be stochastically assembled, with significant differences between white and black water only. Many fishes move into the floodplain forest not only to feed but probably also for other reasons – to seek shelter, for example.

Introduction

Amazonian rivers can be classified in terms of their water quality. Three different types can be distinguished: whitewater rivers are muddy in color due to

their high sediment content, blackwater rivers have dark transparent water because of the large amounts of dissolved humic substances, while clearwater rivers drain areas where there is little erosion (Sioli 1950, Furch & Junk 1997).

The Amazon and its tributaries have a catchment area of 7.9 million km² and inundate at peak flood approximately 0.3 million km² annually. The seasonal distribution of rainfall produces great fluctuations in the water level of rivers. The mean flood amplitude in the Amazon at Manaus is about ten meters. Within the floodplain area, floodplain forests may be inundated anywhere from three to eleven months a year, depending on local floodplain topography and the intensity of the annual floods. There are estimates of 70 000 km² of floodplain forest in the Brazilian Amazon, equivalent to about 0.9% of the total area (Pires 1972). Mertes et al. (1995) estimate that downstream floodplain forests comprise 37% of wetland vegetation. In contrast, in upstream and middle reaches, more than 70% of wetland vegetation is floodplain forest, thus demonstrating the importance of these areas. The Amazonian forest is being progressively deforested. Bayley (1989) reports that 50% of the forest near Manaus has already been cleared. The deforestation rate is higher further downstream, where large areas have been cleared for cattle and buffalo ranching as well as for agriculture.

Most of the tree and bush species fruit during the high-water period (Ziburski 1990, Colonnello 1991). Ripe fruit falls into the water and stays afloat for differing periods of time, thus aiding hydrochoric seed distribution. For many fish species, the floodplain forest is a key source of food. It is well known that not only *Colossoma macropomum* (tambaqui), one of the most popular fish in the area, but also many other fish species feed almost entirely on fruits and seeds during the high-water period (Honda 1974, Gottsberger 1978, Smith 1979, Goulding 1980, 1983, 1989, Saint-Paul 1982, Ziburski 1990).

A number of studies have dealt with aspects of this forest–fish relationship, mainly in the Central Amazon: Gottsberger (1978) and Goulding (1980, 1985, 1988) related the fruiting of some tree species to ichthyochorous propagation; Piedade (1984) and Kubitzki (1985) attested ichthyochory for *Astrocaryum jauari* and *Gentium venosum*; Honda (1974), Saint-Paul (1982), and Roubach & Saint-Paul (1994) analyzed nutrition on the basis of stomach contents, and Ziburski (1990) investigated the flotation capacity of some fruits and seeds. Goulding (1996) estimates 132 000 to 610 000 t fish year⁻¹ in white water, based only on the fruit production of floodplain forests. Estimating the total annual production of the floodplain forest to be at 16 to 53 million tons of fruit, this corresponds to a monetary value of fish production from the floodplains

in the range of US\$ 320 to 530 million (Waldhoff et al. 1996). Araujo-Lima et al. (1988) analyzed the economic value of the Amazonian flooded forest as a source of carbon for local fisheries. For the tambaqui, *Colossoma macropomum*, alone they calculate a revenue from the flooded forest of at least US\$ 8.4 million.

Although data are already available on the feeding behavior of Amazonian fish species, comparative data on seasonal composition and abundance of fishes in Amazonian white and black water floodplain forests are still limited. Such studies are often hampered by taxonomic uncertainties and by the logistical difficulties associated with collecting repeated samples at several localities, a prerequisite for adequate description of spatial and temporal variability (Rodríguez & Lewis 1990, 1994). The objective here was therefore to study seasonal changes in community structure, abundance and biomass of fishes from a white and a black water area in Central Amazonia.

Materials and methodology

Sampling

A comparative study lasting two years (1990 and 1991) examined the relevance of floodplain forests for fishes from a white (Lago do Inácio, Rio Manacapurú) and a black water area (Lago do Prato, Anavilhanas) (Figure 1). Lago do Inácio is a várzea lake (local name for white water floodplain) located close to the city of Manacapurú in the floodplain on the left bank of the Rio Solimões, approximately 80 km upriver from its confluence with the Rio Negro. Being connected to the Rio Solimões by a channel, the lake's surface area varies from 5 to 9 km² and its maximum depth from 4 to 10 m in accordance with the annual water level fluctuations. Although the greater part of the lake is open water, some areas are covered by aquatic macrophytes, while the southeastern shore is fringed with floodplain forest. Only during high water, when the entire várzea floods, does white water flow into the system from all sides.

Lago do Prato, the black water sample site, is located about 75 km upstream from Manaus on the Rio Negro within the Anavilhanas Archipelago. The islands are built from alluvial silt, transported out of the Guiana Shield by the Rio Branco. They form lake-like waterbodies that are found in the centers of many of the islands. They are filled and drained with the river channel water-level fluctuations through an inlet and outlet.

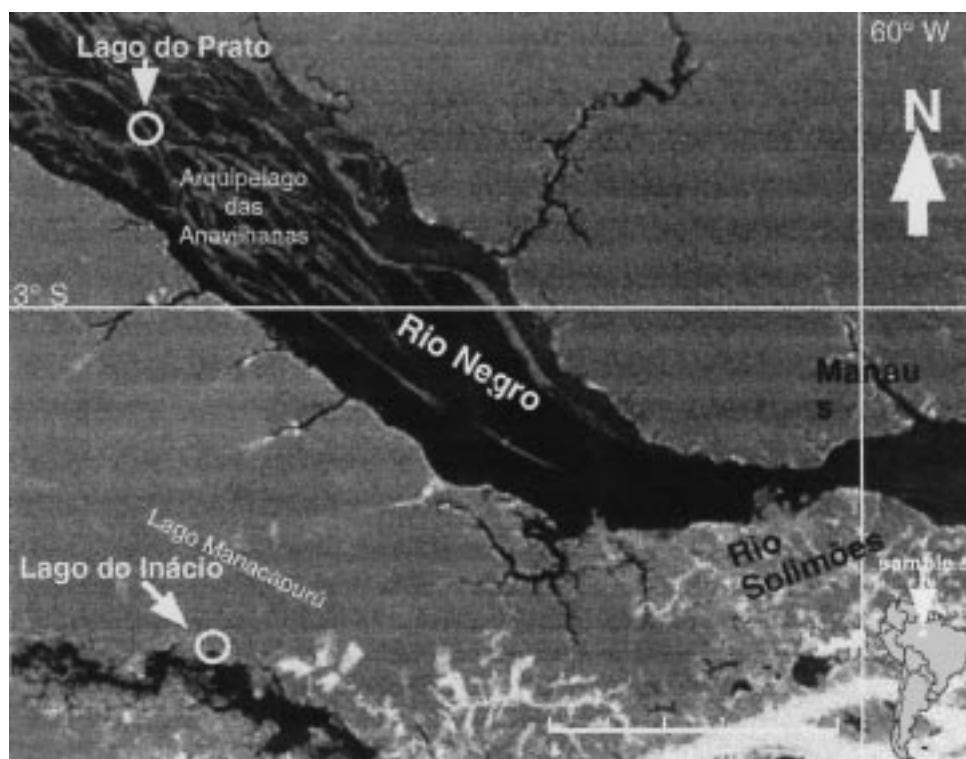


Figure 1. Study area with sampling sites in white water (Lago do Inácio) and black water (Lago do Prato).

Its surface area is similar to Lago do Inácio, but it is deeper on account of the minimal sediment load of the Rio Negro. Most of the shores are fringed with floodplain forest.

Fishes were captured by 13 variously sized gill nets (12–200 mm mesh size) at low, rising, high and falling water level (later considered as seasons) inside and outside the floodplain forests (later considered as habitats, e.g. white- or black water floodplain forest vs. open water) for two 24-hour cycles (later considered as time, e.g. day-/night-time catches) in both 1990 and 1991. Because of the lower water depth in the floodplain forests compared to open water, net size was reduced. The total area of gill net used inside and outside the floodplain forest was 777 m² and 1444 m², respectively. After the first day of sampling, fishing areas were changed in order to avoid fishes becoming accustomed to the gear.

‘Water level’ relates to the Rio Negro estuary at Manaus, as given by the Manaus Harbor Authorities. The difference between high- and low-water level was 11.2 m in 1990 and 12.1 m in 1991. Approaching both

sampling sites, water level inside the inundated forests at low water was so low that gill nets were set along the border to the open water. However, in 1991 the water depth of the Lago do Inácio was so extremely low in November that gillnet fishing was impossible, even close to the floodplain forest.

Captured fish were removed every six hours at 24:00 and 6:00 h (night-time catch) as well as at 12:00 and 18:00 h (day-time catch). Torn parts of the net were replaced. Each individual fish caught was recorded for species, mesh size, weight, and standard length.

Statistical analysis

Sørensen’s index (CC) (Sørensen 1948) was used to compare species composition at white- and blackwater study sites. This index considers the number of species common to two sites, and the computed similarity can be between 0% and 100%. Dominance structure in a community was described according to the logarithmic classification of Engelmann (1978).

Diversity indices are used to characterize species abundance relationships in communities. Diversity relates to the total number of species and how the abundance data are distributed among species. It was characterized using the following two indices: Species diversity (H'), a widely used index in community ecology, was calculated using the Shannon index (Pielou 1969). H' measures the average degree of uncertainty in predicting to what species an individual chosen at random from a collection of S species and N individuals will belong. H' is maximum when all S species are represented by the same number N of individual. The Simpson-index (γ), which varies between 0 and 1 denotes the probability that two individuals drawn at random from a community will belong to the same species (Simpson 1949). If the probability is high that both individual belong to the same species, then the diversity of the community sample is low. While the Simpson index is mainly influenced by the dominance of the most frequent species, in the Shannon index it is the mean frequent species. A species-effort curve was derived for all catches from the white- and the black water areas respectively by plotting the cumulative species number against the number of samples taken.

The 'catch per unit of effort' (CPUE) was calculated as total weight in kg captured per day and m^2 of gill net set. CPUE was used as an approximate index of catch by weight. For the analysis of diurnal variations, day-time (12:00 and 18:00 h) and night-time (24:00 and 6:00 h) samples were pooled.

The principal component analysis (PCA) was used to detect ecological similarities between the specific sample units of blackwater and whitewater localities, respectively (Tabachnick & Fidell 1989). This method breaks down a resemblance matrix (in our case study, a correlation matrix based on the biomass data of the fish species investigated) into a set of orthogonal components (or axes). Each axis corresponds to an eigenvalue of the matrix and accounted for a specific variance of the data set. The first few axes on which the sample units are positioned represent the largest percentage of the total variation that can be explained.

Given the fact that the data were collected over wide environmental gradients, one might expect that the linear PCA model is poorly able to represent the true SU relationships. However, the calculated distribution of the sample units in species hyperspace are neither 'arched' nor 'spiraled', so use of a detrended or non-linear ordination method did not seem necessary.

Results

Site-specific fish species

During two years' collecting, a total of 238 species from 28 families were captured, 148 from white and 172 from black water. Between 73 and 113 species were captured per excursion in white water, whereas for blackwater species the number varied between 83 and 109. A total of 88 species were captured in both black and white waters. A complete species list is provided in Table 1. At both sampling sites, the number of species were always higher in inundated forest than in open water (Table 2).

The Callichthyidae and Electrophoridae occurred in white water only, while Cetopsidae and Ctenoluciidae were confined to black water. The Sørensen coefficient of community similarity between white- and black-water sites was 54%. Although the number of species is only 10% higher in Anavilhanas, the comparison of the two species-effort curves (Figure 2) suggests that species richness is not approximated in either curve. The more asymptotic relationship in black water suggests that the number of species susceptible to capture by gill nets is higher.

Species dominance was grouped using the logarithmic classification according to Engelmann (1978). As can be shown by grouping species abundance into dominance classes, most species are sporadic, while there is an extremely low number (5 to 9) of eudominant, dominant and subdominant species sensu Engelmann (1978) (Table 2). Total species number is considerably higher in both white- and blackwater floodplain forest compared to the samples in open water. The number of subrecent and sporadic species is surprisingly high at both sites. The dominance index for white water was 0.08 and for black water 0.03. Dominance varied in white water between floodplain forest and open water (0.06 and 0.11, respectively) while it was unchanged in black water (0.04).

The species diversity in communities, taking both total number of species and evenness into consideration, was calculated using the Shannon index H' . For white water the diversity index was 2.9 and for black water 3.8. However, there are strong seasonal differences at both sites. In white water, the diversity was highest at rising water and lowest at low water. In black water, the situation was somewhat different, in that diversity was more stable throughout the year, peaking during low water.

Table 1. Occurrence of fish species sampled in the black and white water, grouped by families.

| species | black | white | species | black | white | species | black | white |
|---|-------|-------|------------------------------------|-------|-------|--------------------------------------|-------|-------|
| Ageneiosidae | | | <i>Hoplarchus psittacus</i> | + | | Loricariidae | | |
| <i>Ageneiosus brevifilis</i> | + | + | <i>Mesonauta insignis</i> | + | + | <i>Acarichthys heckelii</i> | | + |
| <i>Ageneiosus cf. guianensis</i> | + | | <i>Pterophyllum scalare</i> | + | | <i>Ancistrus</i> sp. | + | + |
| <i>Ageneiosus dentatus</i> | + | + | <i>Satanoperca acuticeps</i> | + | + | <i>Dekeyseria amazonica</i> | | + |
| <i>Ageneiosus dentatus</i> 2 | + | + | <i>Satanoperca jurupari</i> | | + | <i>Dekeyseria scaphirhyncha</i> | + | + |
| <i>Ageneiosus</i> sp. | | + | <i>Satanoperca liliith</i> | + | | <i>Furcodontichthys novaesi</i> | + | |
| <i>Ageneiosus ucayalensis</i> | + | | <i>Satanoperca</i> sp. | | + | <i>Hypostomus carinatus</i> | + | |
| <i>Ageneiosus vittatus</i> | + | + | <i>Symphiodon acquifasciatus</i> | | + | <i>Hypostomus cf. horridus</i> | | + |
| <i>Tympanopleura</i> sp. | + | | <i>Uaru amphiacanthoides</i> | + | + | <i>Hypostomus emarginatus</i> | | + |
| Anostomidae | | | Clupeidae | | | Loricariidae | | |
| <i>Anostomoides laticeps</i> | + | | <i>Ilisha amazonica</i> | + | | <i>Gliptoperichthys gibbiceps</i> | + | + |
| <i>Anostomus gracilis</i> | + | | <i>Pellona castelnaeana</i> | + | + | <i>Hypostomus hoplonites</i> | | + |
| <i>Anostomus</i> sp. (cf. <i>trimaculatus</i>) | + | | <i>Pellona flavipinnis</i> | + | + | <i>Hypostomus</i> sp. | | + |
| <i>Laemolita proximus</i> | + | + | <i>Pristigaster cayenna</i> | + | | <i>Hypostomus</i> sp. 1 | | + |
| <i>Laemolita laeniata</i> | + | | Ctenoluciidae | | | <i>Hypostomus</i> sp. 2 | | + |
| <i>Leporinus agassizi</i> | + | | <i>Boulengerella maculata</i> | + | | <i>Liposarcus pardalis</i> | | + |
| <i>Leporinus cf. cylindriciformis</i> | | + | <i>Boulengerella ocellata</i> | + | | <i>Loricariichthys acutus</i> | + | + |
| <i>Leporinus fasciatus</i> | + | | <i>Boulengerella</i> sp. | + | | <i>Loricariichthys maculatus</i> | | + |
| <i>Leporinus friderici</i> | + | + | Curimatidae | | | <i>Loricariichthys platymetopon</i> | | + |
| <i>Leporinus</i> sp. | | + | <i>Curimata cf. inornata</i> | + | + | <i>Loricariichthys</i> sp. | | + |
| <i>Leporinus falcipinnis</i> | + | | <i>Curimata cf. planirostris</i> | + | | <i>Peckoltia cf. vittata</i> | | + |
| <i>Leporinus trifasciatus</i> | | + | <i>Curimata inornata</i> | + | | <i>Pseudoloricaria laeviscula</i> | + | |
| <i>Rhytioidus argenteofuscus</i> | | + | <i>Curimata kneri</i> | + | | <i>Pseudoloricaria punctata</i> | + | |
| <i>Rhytioidus microlepis</i> | | + | <i>Curimata ocellata</i> | + | | <i>Pseudorhinelepis genibarbis</i> | | + |
| <i>Schizodon fasciatus</i> | + | + | <i>Curimata vittata</i> | + | + | <i>Reganella depressa</i> | + | |
| Auchenipteridae | | | <i>Curimatella alburna</i> | | + | Osteoglossidae | | |
| <i>Auchenipterichthys thoracatum</i> | + | | <i>Curimatella meyeri</i> | + | | <i>Osteoglossum bicirrhosum</i> | + | + |
| <i>Auchenipterus nuchalis</i> | + | + | <i>Cyphocharax abramoides</i> | + | + | Pimelodidae | | |
| <i>Auchenipterus</i> sp. | + | + | <i>Cyphocharax microcephalus</i> | + | + | <i>Brachyplatystoma filamentosum</i> | + | + |
| <i>Centromochlus heckelii</i> | + | + | <i>Potamorhina altamazonica</i> | + | + | <i>Calophysus macropterus</i> | + | + |
| <i>Parauchenipterus galeatus</i> | + | + | <i>Potamorhina latior</i> | + | + | <i>Leiarius marmoratus</i> | | + |
| <i>Parauchenipterus</i> sp. | | + | <i>Potamorhina pristigaster</i> | | + | <i>Phractocephalus hemiliopterus</i> | + | |
| <i>Pseudopapilio</i> sp. | + | | <i>Psectrogaster amazonica</i> | | + | <i>Pimelodella</i> sp. | + | |
| <i>Tatia</i> sp. | + | | <i>Psectrogaster rutiloides</i> | + | + | <i>Pimelodina flavipinnis</i> | + | + |
| Callichthyidae | | | Cynodontidae | | | <i>Pimelodus altissimus</i> | | + |
| <i>Cataphractus</i> sp. | + | | <i>Cynodon gibbus</i> | + | + | <i>Pimelodus blochi</i> | + | + |
| <i>Hoplosternum littorale</i> | + | | <i>Hydrolycus</i> sp. | + | | <i>Pimelodus</i> sp. | + | + |
| Cetopsidae | | | <i>Hydrolycus scomberoides</i> | + | + | <i>Pinirampus pirinampu</i> | + | + |
| <i>Cetopsis cocuiniens</i> | + | | <i>Rhaphiodon vulpinus</i> | + | + | <i>Platymetichthys notatus</i> | + | + |
| <i>Hemicetopsis</i> sp. | + | | Doradidae | | | <i>Pseudoplatystoma fasciatum</i> | + | + |
| Chilodidae | | | <i>Anadoras gryphus</i> | | + | <i>Pseudoplatystoma tigrinum</i> | + | + |
| <i>Caenotropus labyrinthicus</i> | + | | <i>Astrodoras asterifrons</i> | + | | <i>Pseudopimelodus</i> sp. | + | |
| Characidae | | | <i>Centrodoras</i> sp. | + | | <i>Sorubim lima</i> | + | + |
| <i>Acestrorhynchus falcirostris</i> | + | + | <i>Centrodoras</i> sp. 2 | | | Potamotrygonidae | | |
| <i>Acestrorhynchus guianensis</i> | + | + | <i>Doras</i> sp. | + | | <i>Potamotrygon motoro</i> | + | |
| <i>Acestrorhynchus microlepis</i> | + | + | <i>Megalodoras uranoscopus</i> | | + | <i>Potamotrygon</i> sp. | + | + |
| <i>Acestrorhynchus</i> sp. | | + | <i>Opsodoras cf. trimaculatus</i> | + | | Prochilodontidae | | |
| <i>Agoniatos anchovia</i> | + | | <i>Opsodoras</i> sp. | + | + | <i>Prochilodus nigricans</i> | | + |
| <i>Astyanax</i> sp. | | + | <i>Opsodoras</i> sp. 2 | | + | <i>Semaprochilodus insignis</i> | + | + |
| <i>Brycon cephalus</i> | + | + | <i>Opsodoras</i> sp. 3 | + | | <i>Semaprochilodus taeniurus</i> | + | + |
| <i>Brycon melanopterus</i> | + | + | <i>Opsodoras</i> sp. 4 | | + | Ramphichthyidae | | |
| <i>Brycon pesu</i> | + | | <i>Opsodoras</i> sp. 5 | + | | <i>Ramphichthys marmoratus</i> | | + |
| <i>Brycon</i> sp. | + | | <i>Opsodoras ternetzi</i> | + | | <i>Steatogenys elegans</i> | + | |
| <i>Bryconops gracilis</i> | + | | <i>Opsodoras trimaculatus</i> | + | | Sciaenidae | | |
| <i>Chalceus erythrurus</i> | | + | <i>Physopoxis lyra</i> | + | | <i>Pachypops grunniens</i> | + | |
| <i>Chalceus macrolepidotus</i> | + | | <i>Platydoras costatus</i> | + | | <i>Pachypops trifilis</i> | + | |
| <i>Charax gibbosus</i> | + | | <i>Pseudodoras niger</i> | + | + | <i>Plagioscion montei</i> | + | + |
| <i>Ctenobrycon hauxwellianus</i> | | + | <i>Pterodoras granulatus</i> | + | + | <i>Plagioscion squamosissimus</i> | + | + |
| <i>Galeocharax</i> sp. | + | | <i>Trachydoras</i> sp. | + | | Serrasalminae | | |
| <i>Moenkhausia</i> sp. | + | + | Engraulidae | | | <i>Colossoma macropomum</i> | | + |
| <i>Poptella</i> sp. | + | | <i>Anchovia surinamensis</i> | + | + | <i>Metynnis cf. maculatus</i> | + | + |
| <i>Roeboides myersi</i> | + | + | <i>Lycengraulis batesi</i> | | + | <i>Metynnis hypsauchen</i> | + | |
| <i>Triporthus albus</i> | + | + | <i>Lycengraulis grossidens</i> | | + | <i>Metynnis</i> sp. | + | |
| <i>Triporthus angulatus</i> | + | + | <i>Lycengraulis</i> sp. | | + | <i>Metynnis</i> sp. 2 | + | |
| <i>Triporthus cultier</i> | | + | Erythrinidae | | | <i>Myleus cf. torquatus</i> | + | + |
| <i>Triporthus elongatus</i> | + | + | <i>Hoplerethrinus unitaeniatus</i> | | + | <i>Myleus rubripinnis</i> | + | + |
| Cichlidae | | | <i>Hoplias cf. malabicus</i> | | + | <i>Myleus schomburgki</i> | + | |
| <i>Acaronia nassa</i> | + | + | <i>Hoplias malabaricus</i> | + | + | <i>Myleus</i> sp. | + | |
| <i>Astronotus ocellatus</i> | + | + | Electrophoridae | | | <i>Myleus</i> sp. 1 | + | |
| <i>Biotodoma cupido</i> | + | | <i>Electrophorus electricus</i> | + | | <i>Myleus</i> sp. 2 | + | |
| <i>Chaetobranchopsis</i> sp. | | + | Hemiodidae | | | <i>Mylossoma aureum</i> | | + |
| <i>Chaetobranchius flavescens</i> | | + | <i>Anodus cf. elongatus</i> | + | | <i>Mylossoma duriventris</i> | + | + |
| <i>Cichla monoculus</i> | + | + | <i>Anodus elongatus</i> | + | + | <i>Piaractus brachipomus</i> | | + |
| <i>Cichla orinocensis</i> | + | | <i>Anodus melanopogon</i> | + | + | <i>Pygocentrus nattereri</i> | | + |
| <i>Cichla temensis</i> | + | + | <i>Anodus</i> sp. | + | + | <i>Serrasalmus altuvei</i> | + | |
| <i>Cichlasoma amazonarum</i> | | + | <i>Argonectes scapularis</i> | + | | <i>Serrasalmus calmoni</i> | | + |
| <i>Crenicichla cf. microcephala</i> | + | | <i>Hemiodus goeldi</i> | + | | <i>Serrasalmus cf. rhombus</i> | + | + |
| <i>Crenicichla cf. reticulata</i> | + | + | <i>Hemiodus immaculatus</i> | + | + | <i>Serrasalmus elongatus</i> | + | + |
| <i>Crenicichla cincta</i> | + | | <i>Hemiodus microlepis</i> | + | + | <i>Serrasalmus manueli</i> | + | |
| <i>Crenicichla johanna</i> | | + | <i>Hemiodus</i> sp. | + | + | <i>Serrasalmus rhombus</i> | + | + |
| <i>Crenicichla lugubris</i> | + | + | <i>Hemiodus unimaculatus</i> | + | + | <i>Serrasalmus serrulatus</i> | + | + |
| <i>Geophagus altifrons</i> | + | | <i>Micromischodus sugillatus</i> | + | | <i>Serrasalmus spilopleura</i> | | + |
| <i>Geophagus cf. altifrons</i> | + | | <i>Pterohemiodus</i> sp. | + | | <i>Serrasalmus striolatus</i> | + | |
| <i>Geophagus proximus</i> | + | + | Hypophthalmidae | | | Sternopygidae | | |
| <i>Geophagus</i> sp. | + | | <i>Hypophthalmus edentatus</i> | + | + | <i>Eigenmannia macrops</i> | + | |
| <i>Heros</i> sp. | + | + | <i>Hypophthalmus fimbriatus</i> | + | + | <i>Eigenmannia</i> sp. | | + |
| | | | <i>Hypophthalmus marginatus</i> | + | + | <i>Rabdolichops caviceps</i> | + | |
| | | | | | | <i>Sternopygus macrurus</i> | + | |

Table 2. Dominance classes of fish sampled in white and black water, separated into inundated forest and lake [following Engelmann's (1978) recommendation for a logarithmic relation between the dominance classes].

| Dominance classes | White water | | | Black water | | |
|--------------------------|-------------|------------------|------|-------------|------------------|------|
| | Total | Inundated forest | Lake | Total | Inundated forest | Lake |
| eudominant (>32%) | 0 | 0 | 0 | 0 | 0 | 0 |
| dominant (10.0–31.9%) | 3 | 3 | 3 | 0 | 1 | 0 |
| subdominant (3.2–9.9%) | 2 | 2 | 3 | 9 | 7 | 9 |
| recedent (1–3.1%) | 15 | 20 | 12 | 16 | 15 | 22 |
| subrecedent (0.32–0.99%) | 19 | 24 | 14 | 35 | 32 | 14 |
| sporadic (<0.32%) | 109 | 81 | 87 | 112 | 95 | 65 |
| Total species number | 148 | 130 | 119 | 172 | 150 | 110 |

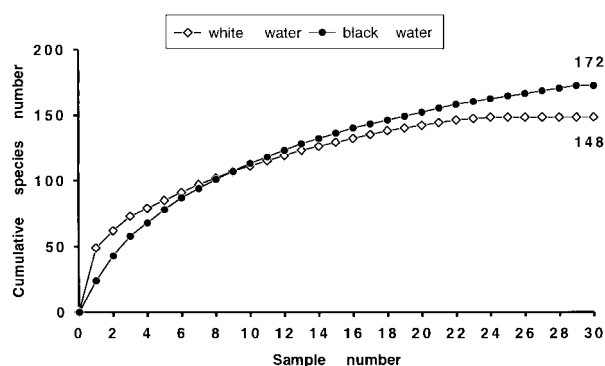


Figure 2. Species-effort curve for white- and blackwater sampling sites.

During the two years of collection, a total of 20 904 fish were sampled from white water and 5628 from black water. However, the quantity captured depended not only on the sample site and the water level, but also on the direction of the water level change. For fisheries purposes, data on biomass are of special importance. Therefore, biomass-based CPUE was calculated in temporal and local resolution and shown for the 50 most abundant species in Tables 3 and 4.

The most abundant whitewater species (Table 3) was the loricariid *Liposarcus pardalis* (20.31 kg) (formerly *Pterygoplichthys multiradiatus*), called acarí-bodo locally, an armoured catfish at most 35 cm in length and grazing mostly on algae and detritus. It uses its stomach as an auxiliary respiratory organ. It is followed by piranha-cajú *Pygocentrus nattereri* (9.67 kg), a predator of up to 25 cm standard length, while third place was taken by the freshwater clupeid *Pellona flavipinnis* (locally apapá-branco), a predator

of up to 50 cm length (4.30 kg). The most abundant blackwater fish (Table 4) was the sciaenid *Plagioscion squamosissimus* (locally pescada) (1.89 kg), a silvery, heavy-bodied fish that attains 48 cm standard length and which feeds on invertebrates and fishes. It is followed by two piranha species: *Serrasalmus rhombeus* (locally piranha preta), attaining 40 cm total length and *S. manuli*. Both feed on fishes, insects as well as fruits and seeds. There are three species which are common to the 20 most abundant at both sites: *P. squamosissimus*, *S. rhombeus* and the mouth-breeding osteoglossid *Osteoglossum bicirrhosum* (locally aruanã), a laterally compressed, surface-living predator reaching a length of 100 cm.

Taking a more detailed look, there were significant differences in occurrence when samples were distinguished according to local (inundated forest vs. lake) and temporal (day-time vs. night-time, season) differences (Table 3, 4). They were defined as more than 75% of the total biomass being caught at the respective location and/or time.

Seventeen percent of the total number of species contribute significantly to 75% of the biomass captured in the white water. It is clearly apparent that temporal and local differences were represented by different species numbers. Significant species were *L. pardalis* (site: forest, lake, time: day, night, rising, falling, low), *P. flavipinnis* (time: high, falling) and *P. nattereri* (site: forest, lake; time: day, night, rising, high, low). The number of species which represent the catch in terms of biomass also varies considerably. The higher this number, the more homogeneous the species distribution is at the specific location. Comparing forest vs. lake, the forest community seems to be more homogeneous. Differences between day- and night-time catch

Table 3. Comparison of the catch distribution of the 50 most abundant white water fish species, expressed as biomass and percentage. Those species which represent 75% of the total biomass caught at the specific location are indicated by bold printed percentage values. Numbers marked by * indicate the two most abundant species captured at the specific location.

| Species | Biomass (g m ⁻² day ⁻¹) | Forest (%) | Lake (%) | Day (%) | Night (%) | Rising (%) | High (%) | Falling (%) | Low (%) |
|---------------------------------------|---|---------------|-------------|------------|--------------|---------------|-------------|----------------|------------|
| <i>Liposarcus pardalis</i> | 20311 | 29* | 71* | 43* | 57* | 4* | 0 | 25* | 70* |
| <i>Pygocentrus nattereri</i> | 9672 | 26* | 74* | 51* | 49* | 5* | 7* | 14* | 74* |
| <i>Pellona flavipinnis</i> | 4303 | 52 | 48 | 16 | 84 | 10 | 17 | 63 | 10 |
| <i>Colossoma macropomum</i> | 2986 | 75 | 25 | 66 | 34 | 3 | 4 | 79 | 14 |
| <i>Plagioscion squamosissimus</i> | 2743 | 42 | 58 | 12 | 88 | 14 | 12 | 48 | 26 |
| <i>Hoplosternum litorale</i> | 2328 | 87 | 13 | 5 | 95 | 3 | 1 | 88 | 8 |
| <i>Prochilodus nigricans</i> | 2250 | 57 | 43 | 67 | 33 | 10 | 10 | 30 | 50 |
| <i>Mylossoma duriventre</i> | 1834 | 100 | 0 | 3 | 97 | 2 | 1 | 96 | 1 |
| <i>Pseudodoras niger</i> | 1774 | 51 | 49 | 63 | 37 | 13 | 1 | 50 | 37 |
| <i>Serrasalmus spilopleura</i> | 1470 | 13 | 87 | 53 | 47 | 2 | 3 | 10 | 85 |
| <i>Potamorhina latior</i> | 1084 | 38 | 62 | 75 | 25 | 19 | 51 | 5 | 24 |
| <i>Potamorhina altamazonica</i> | 1075 | 82 | 18 | 63 | 37 | 16 | 33 | 13 | 38 |
| <i>Hypophthalmus edentatus</i> | 793 | 27 | 73 | 46 | 54 | 24 | 31 | 32 | 13 |
| <i>Cichla monoculus</i> | 739 | 87 | 13 | 88 | 12 | 44 | 4 | 47 | 6 |
| <i>Hemiodus microlepis</i> | 719 | 28 | 72 | 83 | 17 | 45 | 7 | 48 | 0 |
| <i>Potamorhina pristigaster</i> | 595 | 57 | 43 | 83 | 17 | 26 | 35 | 27 | 13 |
| <i>Pellona castelnaeana</i> | 553 | 41 | 59 | 53 | 47 | 43 | 28 | 21 | 8 |
| <i>Serrasalmus rhombeus</i> | 544 | 49 | 51 | 34 | 66 | 5 | 15 | 42 | 39 |
| <i>Osteoglossum bicirrhosum</i> | 520 | 91 | 9 | 84 | 16 | 34 | 0 | 50 | 16 |
| <i>Serrasalmus elongatus</i> | 480 | 67 | 33 | 55 | 45 | 10 | 10 | 12 | 67 |
| <i>Astronotus ocellatus</i> | 451 | 98 | 2 | 94 | 6 | 40 | 5 | 54 | 1 |
| <i>Schizodon fasciatus</i> | 449 | 74 | 26 | 63 | 37 | 30 | 33 | 15 | 22 |
| <i>Hypophthalmus marginatus</i> | 448 | 15 | 85 | 7 | 93 | 53 | 34 | 0 | 13 |
| <i>Acestrorhynchus falcistrostris</i> | 427 | 95 | 5 | 54 | 46 | 54 | 1 | 42 | 3 |
| <i>Hoplias malabaricus</i> | 418 | 81 | 19 | 16 | 84 | 5 | 2 | 84 | 9 |
| <i>Rhytioidus microlepis</i> | 389 | 83 | 17 | 77 | 23 | 22 | 49 | 29 | 0 |
| <i>Plagioscion montei</i> | 343 | 49 | 51 | 19 | 81 | 32 | 20 | 36 | 12 |
| <i>Heros</i> sp. | 314 | 93 | 7 | 92 | 8 | 16 | 7 | 73 | 4 |
| <i>Pimelodus blochi</i> | 307 | 66 | 34 | 62 | 38 | 63 | 18 | 17 | 1 |
| <i>Pterygoplichthys gibbiceps</i> | 296 | 67 | 33 | 50 | 50 | 11 | 2 | 18 | 69 |
| <i>Calophysus macropterus</i> | 281 | 32 | 68 | 12 | 88 | 18 | 23 | 6 | 53 |
| <i>Leporinus friderici</i> | 272 | 46 | 54 | 55 | 45 | 9 | 4 | 44 | 43 |
| <i>Triporthus angulatus</i> | 243 | 76 | 24 | 3 | 97 | 29 | 22 | 26 | 23 |
| <i>Psectrogaster rutiloides</i> | 212 | 91 | 9 | 35 | 65 | 88 | 3 | 0 | 9 |
| <i>Leporinus trifasciatus</i> | 183 | 79 | 21 | 84 | 16 | 18 | 14 | 57 | 12 |
| <i>Pseudoplatystoma fasciatum</i> | 164 | 68 | 32 | 23 | 77 | 34 | 6 | 23 | 37 |
| <i>Lycengraulis grossidens</i> | 162 | 33 | 67 | 77 | 23 | 46 | 19 | 28 | 7 |
| <i>Ageneiosus brevifilis</i> | 154 | 28 | 72 | 14 | 86 | 47 | 12 | 0 | 41 |
| <i>Rhaphiodon vulpinus</i> | 151 | 43 | 57 | 24 | 76 | 32 | 27 | 28 | 12 |
| <i>Hypostomus</i> sp. | 141 | 75 | 25 | 21 | 79 | 0 | 0 | 7 | 93 |
| <i>Anadoras gryphus</i> | 133 | 30 | 70 | 22 | 78 | 3 | 1 | 13 | 83 |
| <i>Parauchenipterus galeatus</i> | 128 | 64 | 36 | 1 | 99 | 8 | 6 | 55 | 31 |
| <i>Psectrogaster amazonica</i> | 127 | 96 | 4 | 32 | 68 | 18 | 28 | 3 | 51 |
| <i>Megalodoras irwini</i> | 121 | 62 | 38 | 6 | 94 | 6 | 76 | 19 | 0 |
| <i>Brycon cephalus</i> | 115 | 97 | 3 | 73 | 27 | 1 | 49 | 50 | 0 |
| <i>Loricariichthys acutus</i> | 115 | 31 | 69 | 47 | 53 | 28 | 12 | 36 | 24 |
| <i>Piaractus brachypomus</i> | 111 | 64 | 36 | 44 | 56 | 4 | 12 | 50 | 34 |

Table 4. Comparison of the catch distribution of the 50 most abundant black water fish species, expressed as biomass and percentage. Those species which represent 75% of the total biomass caught at the specific location are indicated by bold printed percentage values. Numbers marked by * indicate the two most abundant species captured at the specific location.

| Species | Biomass (g m ⁻² d ⁻¹) | Forest (%) | Lake (%) | Day (%) | Night (%) | Rising (%) | High (%) | Falling (%) | Low (%) |
|--------------------------------------|---|---------------|-------------|------------|--------------|---------------|-------------|----------------|------------|
| <i>Plagioscion squamosissimus</i> | 1893 | 64* | 36* | 32* | 68* | 13* | 5 | 11* | 71* |
| <i>Serrasalmus rhombeus</i> | 956 | 86* | 14 | 64* | 36 | 16 | 24* | 45* | 15 |
| <i>Serrasalmus hollandi</i> | 874 | 83 | 17 | 61 | 39 | 23* | 6 | 5 | 66* |
| <i>Geophagus cf altifrons</i> | 652 | 94 | 6 | 87 | 13 | 7 | 3 | 9 | 81 |
| <i>Hemiodus immaculatus</i> | 650 | 70 | 30 | 74 | 26 | 2 | 17 | 29 | 52 |
| <i>Hypophthalmus marginatus</i> | 490 | 10 | 90* | 71 | 29 | 16 | 3 | 11 | 69 |
| <i>Serrasalmus serrulatus</i> | 458 | 89 | 11 | 53 | 47* | 26 | 14 | 35 | 25 |
| <i>Myleus rubripinnis</i> | 445 | 87 | 13 | 82 | 18 | 12 | 3 | 3 | 81 |
| <i>Pinirampus pirinampu</i> | 385 | 38 | 62 | 50 | 50 | 7 | 14 | 15 | 63 |
| <i>Ageneiosus brevifilis</i> | 384 | 53 | 47 | 15 | 85 | 40 | 6 | 10 | 44 |
| <i>Semaprochilodus taeniurus</i> | 350 | 87 | 13 | 64 | 36 | 8 | 0 | 59 | 33 |
| <i>Plagioscion monteí</i> | 318 | 49 | 51 | 17 | 83 | 10 | 2 | 41 | 47 |
| <i>Metynnis hypsauchen</i> | 308 | 77 | 23 | 45 | 55 | 5 | 15 | 5 | 76 |
| <i>Pseudoplatysoma fasciatum</i> | 298 | 91 | 9 | 45 | 55 | 0 | 0 | 0 | 100 |
| <i>Brachyplatystoma filamentosum</i> | 291 | 17 | 83 | 40 | 60 | 26 | 10 | 4 | 60 |
| <i>Osteoglossum bicirrhosum</i> | 258 | 100 | 0 | 81 | 19 | 8 | 4 | 2 | 86 |
| <i>Hypophthalmus fimbriatus</i> | 254 | 53 | 47 | 0 | 100 | 18 | 2 | 42 | 38 |
| <i>Uaru amphiacanthoides</i> | 251 | 100 | 0 | 94 | 6 | 3 | 4 | 37 | 56 |
| <i>Cichla temensis</i> | 199 | 92 | 8 | 98 | 2 | 26 | 33 | 24 | 17 |
| <i>Hoplias malabaricus</i> | 172 | 100 | 0 | 48 | 52 | 0 | 0 | 59 | 41 |
| <i>Pellona castelnaeana</i> | 169 | 14 | 86 | 20 | 80 | 5 | 0 | 7 | 88 |
| <i>Leporinus fasciatus</i> | 164 | 53 | 47 | 94 | 6 | 14 | 16 | 67 | 3 |
| <i>Serrasalmus cf. rhombeus</i> | 158 | 88 | 12 | 98 | 2 | 0 | 88* | 12 | 0 |
| <i>Ilisha amazonica</i> | 156 | 68 | 32 | 0 | 100 | 9 | 0 | 2 | 89 |
| <i>Hypophthalmus edentatus</i> | 146 | 53 | 47 | 12 | 88 | 24 | 12 | 59 | 4 |
| <i>Cyphocharax abramoides</i> | 145 | 96 | 4 | 55 | 45 | 0 | 1 | 65 | 34 |
| <i>Serrasalmus striolatus</i> | 145 | 96 | 4 | 78 | 22 | 9 | 68 | 4 | 20 |
| <i>Laemolita proximus</i> | 139 | 83 | 17 | 59 | 41 | 20 | 2 | 64 | 14 |
| <i>Myleus cf. torquatus</i> | 130 | 26 | 74 | 7 | 93 | 1 | 2 | 0 | 97 |
| <i>Cichla monoculus</i> | 125 | 96 | 4 | 94 | 6 | 24 | 8 | 62 | 6 |
| <i>Semaprochilodus insignis</i> | 119 | 97 | 3 | 85 | 15 | 0 | 11 | 70 | 19 |
| <i>Pellona flavipinnis</i> | 108 | 27 | 73 | 51 | 49 | 7 | 13 | 25 | 55 |
| <i>Rhaphiodon vulpinus</i> | 108 | 79 | 21 | 24 | 76 | 9 | 30 | 35 | 26 |
| <i>Leporinus falcipinnis</i> | 101 | 100 | 0 | 100 | 0 | 3 | 36 | 61 | 0 |
| <i>Agoniates anchovia</i> | 98 | 47 | 53 | 54 | 46 | 7 | 4 | 24 | 66 |
| <i>Pimelodina flavipinnis</i> | 97 | 10 | 90 | 33 | 67 | 25 | 15 | 0 | 59 |
| <i>Hemiodus unimaculatus</i> | 96 | 95 | 5 | 60 | 40 | 5 | 0 | 25 | 70 |
| <i>Anostomoides laticeps</i> | 85 | 84 | 16 | 71 | 29 | 8 | 17 | 74 | 0 |
| <i>Brycon cephalus</i> | 77 | 97 | 3 | 86 | 14 | 19 | 14 | 53 | 14 |
| <i>Acestrorhynchus guianensis</i> | 76 | 53 | 47 | 66 | 34 | 3 | 9 | 22 | 65 |
| <i>Phractocephalus hemiliopterus</i> | 75 | 100 | 0 | 100 | 0 | 0 | 0 | 0 | 100 |
| <i>Laemolita taeniata</i> | 70 | 54 | 46 | 87 | 13 | 83 | 4 | 7 | 6 |
| <i>Ageneiosus dentatus 2</i> | 67 | 77 | 23 | 7 | 93 | 21 | 8 | 0 | 72 |
| <i>Heros sp.</i> | 63 | 100 | 0 | 49 | 51 | 0 | 14 | 69 | 17 |
| <i>Hoplarchus psittacus</i> | 59 | 100 | 0 | 100 | 0 | 9 | 14 | 65 | 13 |
| <i>Argonectes scapularis</i> | 56 | 44 | 56 | 85 | 15 | 2 | 2 | 64 | 31 |
| <i>Calophysus macropterus</i> | 56 | 48 | 52 | 18 | 82 | 12 | 13 | 15 | 60 |
| <i>Leporinus agassizi</i> | 53 | 100 | 0 | 100 | 0 | 0 | 64 | 36 | 0 |
| <i>Potamorhina latior</i> | 52 | 88 | 12 | 22 | 78 | 4 | 0 | 30 | 66 |
| <i>Curimata kneri</i> | 51 | 73 | 27 | 47 | 53 | 4 | 0 | 19 | 77 |

seem to be minor. Looking at seasonal changes, there is a continuous decrease in species number from rising to low-water level. In other words, low-water catches are characterized by a fewer number of dominant species than catches obtained during rising water.

The number of species contributing to 75% of the biomass captured is higher in black than in white water (16.5 mean vs. 8.6). The most characteristic black-water species, in alphabetic order, were *H. marginatus* (lake), *P. squamosissimus* (site: forest, lake; time: day, night, rising, high, low), *S. cf. rhombeus* (time: high), *S. manuli* (time: rising, low), *S. rhombeus* (site: forest; time: day, high, falling), *S. serrulatus* (time: night). Differences in the number of characteristic species, comparing forest vs. lake and day-time vs. night-time catches, were much less pronounced than in white water, as well as seasonal differences, which could not be detected for this site.

Biomass based catch per unit of effort (CPUE)

To compare catches from different places and times, catch per unit of effort is used as an index. In white water, the average CPUE was 190 and in black water 41 g. Taking both areas into consideration, maximum catch was obtained at low water and minimum catch at high water (Figure 3). Comparing rising and falling water levels, a significantly higher quantity of fishes was captured at falling water level. In Figure 3, the data for each area, separated for floodplain forest and open water, are depicted separately, thus revealing distinct differences. In black water, the fish yield from floodplain forest exceeded the biomass of fish from open water (59 compared to 24 g), while the data for white water were rather similar (203 compared to 191 g). In black water, about 74% of the fishes were captured in floodplain forest and 26% in open water. Differences in white water were much smaller (60% from floodplain forest and 40% from open water). Seasonal differences are highest in black water, with maximum yields at low water obtained at the edge of floodplain forest.

Fish communities

The similarities between the samples were analyzed using PCA. Analysis focused firstly on similarities between the whitewater and blackwater samples. Due to the considerable differences between the two areas in the study (Figure 4), we also looked within each area for similarities between communities inside and

outside inundated forest, independently of water level. The results for white water provide the following, somewhat inconsistent picture:

Within inundated forest, there are major similarities between catches in November and March, i.e. between catches at low water and at rising water level. This group is followed, with decreasing similarity, by catches at falling and at high water level. Outside inundated forest, three catches (at rising, high and falling water levels) form a similar group, distinct from the catch at low water level. Taking all catches from white water, those from inundated forest at falling water level are markedly distinct from the remaining catches (Figure 5). Within this large group, there are certain similarities within the catches at low water and, as described above, between the fish communities caught in the inundated forest at low and at rising water levels.

In black water, the catches obtained inside inundated forest during high and falling water level are distinct from the large remaining body of catches (Figure 6). Within this group, there are clear similarities between catches from inundated forest and open water at low tide, also between the communities in inundated forest at rising water level and those in open water at falling water level.

Discussion

Following the recommendation of Legendre & Legendre (1998), the concept of fish community as used in this paper must not be confused with the concept of ichthyocenosis, from which it differs fundamentally. Fish species community is understood here as the possibly biased image given by the sampling of a group of fishes that can be caught in a particular environment at a given time. It thus describes an ecological entity, but is not this entity itself. The results obtained clearly demonstrate that fish community in the studied area is not stable. It has been reported, e.g. by Whitehead (1959), Lowe-McConnel (1975), Welcomme (1979) or Goulding (1980), that at the onset of floods some fish species migrate from the floodplains to the upper reaches of the river in order to breed, and then migrate downstream again after spawning as the water recedes. In other words, floodplain lakes connected with the river by channels are open systems which enable organismic exchanges. Hence, high water levels increase the size of the aquatic environment and also bring in nutrients which stimulate rapid growth of micro-organisms, invertebrates and plants, providing

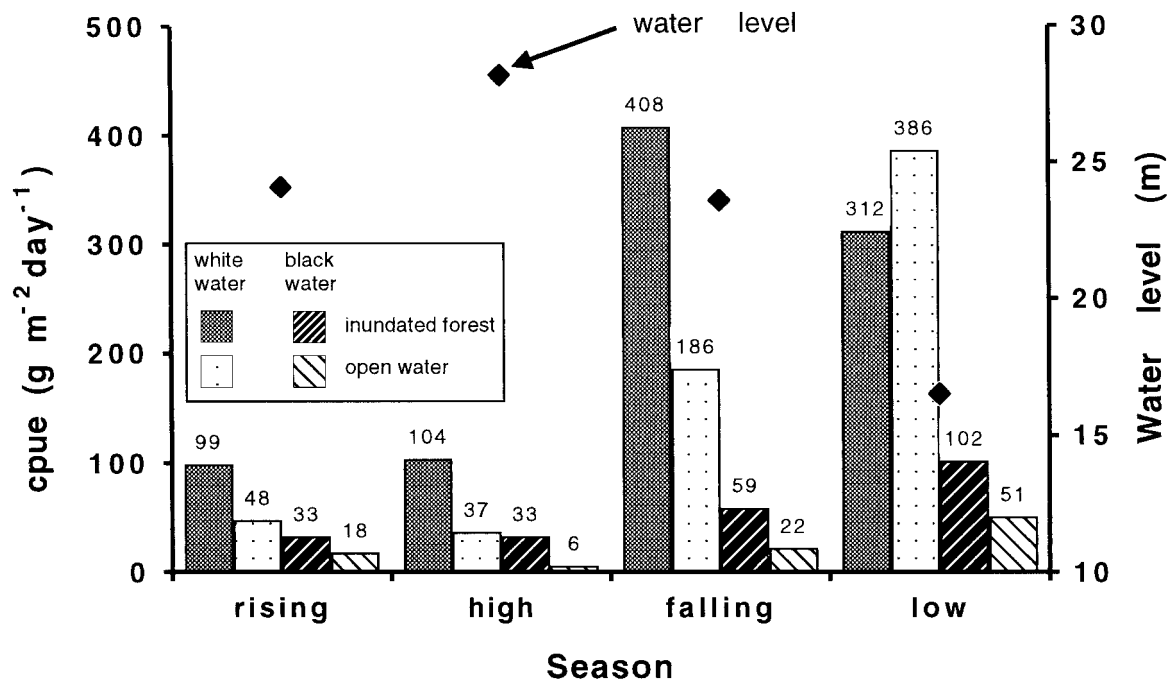


Figure 3. Seasonal changes in catch per unit of effort of white- and blackwater sampling sites, separated by inundated forest and open water. Water-level data are averaged over both years and provided by the Manaus Harbor Authorities.

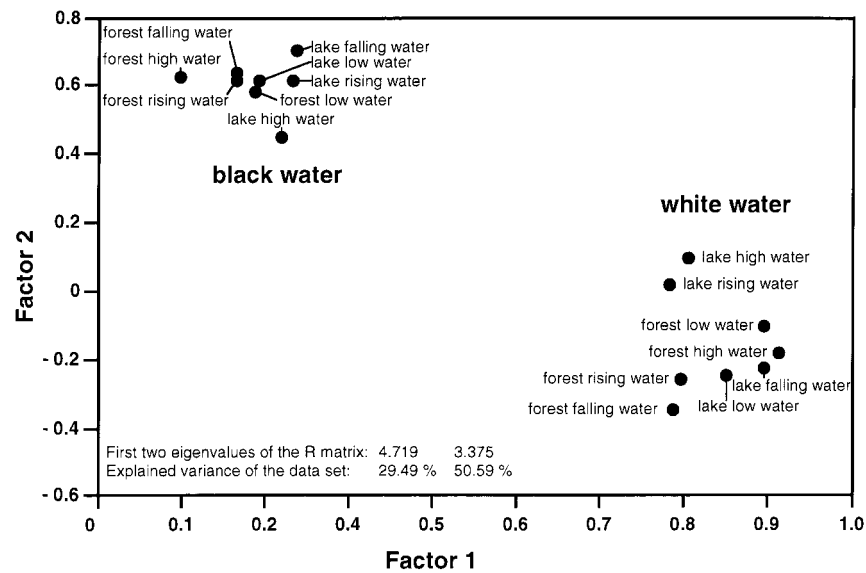


Figure 4. Principle component analysis (PCA) of 16 fish samples from Amazonian black and white waters. The positions of the 16 SUs on the main components I and II are demonstrated. Biomass data of 238 fish species are used.

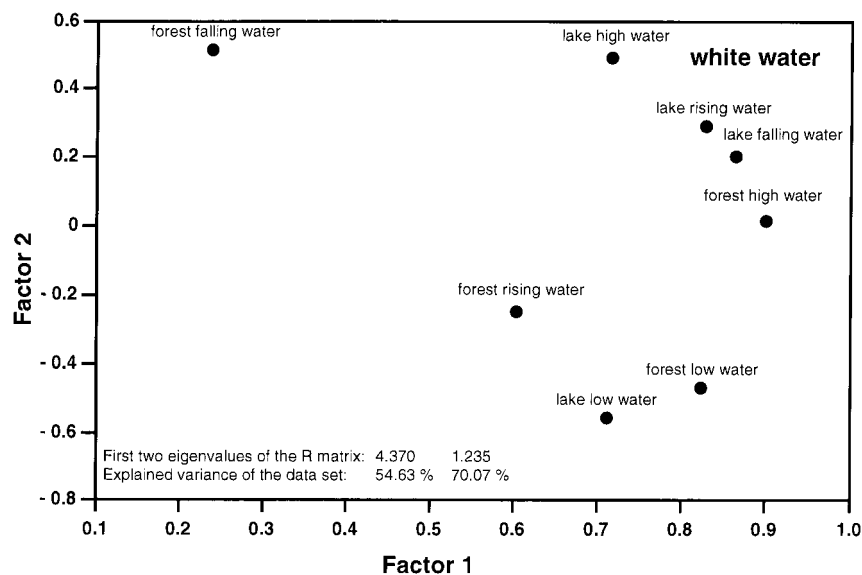


Figure 5. Principle component analysis (PCA) of 7 fish samples from Amazonian white waters. The positions of the 7 SUs on the main components I and II are demonstrated. Biomass data of the 50 most abundant fish species are used. Because of the extremely low number of fishes, the high water sampling site in the lake was not taken into consideration.

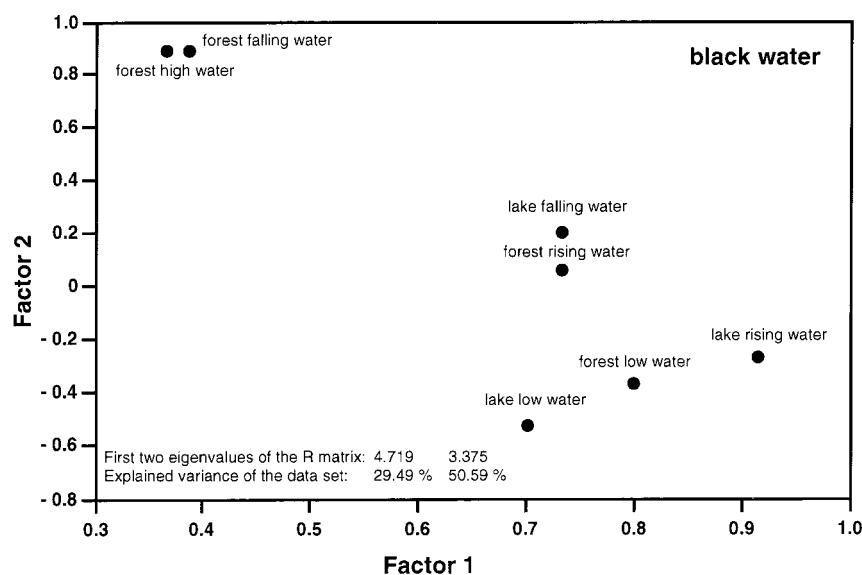


Figure 6. Principle component analysis (PCA) of 8 fish samples from Amazonian black waters. The positions of the 8 SUs on the main components I and II are demonstrated. Biomass data of the 50 most abundant fish species are used.

abundant food and coverage for fishes during the high-water season (Lowe-McConnell 1979).

As floodplains periodically expand and shrink because of natural water level fluctuations, with concomitant changes in living conditions, many fishes are

migratory and live in both floodplain and river-channel waters. Especially during low water, many fishes leave the floodplains and migrate into the main river channels. Migratory movements between flooded zones and the river make description and interpretation of lake

community structure more difficult, because species composition inside the floodplains may change. Compared to the temperate zone, flooding of the river is a completely different form of seasonality than changes in temperature and daylight, because it does not change the abiotic factors of the environment but enlarges the aquatic environment seasonally available to the fishes (Lowe-McConnell 1979).

Within the last two decades, traditional fishing gear has greatly declined in importance because of the widespread introduction of gillnets (Meschkat 1958) made from synthetic materials which can be used in flooded forest. Nowadays, gillnets are the most important gear used by small-scale fishermen (Petrere Jr. 1978). Gillnet fishing has serious drawbacks, because it does not permit biomass to be calculated and provides only relative abundance indices. In practical terms, however, gillnet fishing exhibits a number of major advantages, since it is one of the few methods that can be used in the floodplain forest (except traps, ichthyotoxins or hook fishing, which are less suitable for this kind of study) and all other lake environments throughout the year. Local fishermen also seem to be familiar with this method of fishing. However, because of gear selectivity the catches do not provide a complete and accurate picture of the entire community. This is why we referred at the beginning of this section to ecological entity. Given that fish abundance inside and outside the floodplain forest needs to be compared on a spatio-temporal basis, gill netting remains justified because it permits the analysis of relative abundance. Similar studies on diurnal migrations of whitewater fishes have been carried out by Barthem (1981, 1987).

Fish belong to the best studied group of animals in Amazonian waters. About 2000 species have been described so far, but the total number may reach 2500–3000. Monographs by Goulding (1980) and by Goulding et al. (1988) provide a general review of the food and feeding habits of Amazonian fish species and indicate the importance of the floodplain forest as a source of food for fishes. Lowe-McConnell (1975, 1987) considers the Amazonian fish fauna in the context of tropical fish communities.

Comparing both sample sites, the number of species in black water was found to be some 10% higher than in white water and is characterized by 54% similarity. The number of species is similar to that in other studied regions, for example Lago Camaleão (Ilha de Marchantaria, close to Manaus), where 132 species belonging to 94 genera, 31 families and 10 orders were identified

by Soares et al. (1986). Bayley (1982), collecting fishes in the mouth bay of the same lake, recorded more than 226 species, belonging to 40 families and 132 genera. Goulding et al. (1988) made the most intensive collection of fish species in the lower and middle Rio Negro, finding a total of 450 species belonging to 202 genera and 39 families. This number is much higher, because his aim was not to analyze community structure, but rather to conduct a complete faunistic investigation using different fishing methods. However, for the flooded forests of the Anavilhanas a species quantity of 140 captured by gillnet, seine, dipnet and line-and-pole is described by Goulding et al. (1988).

Despite the high degree of similarity and diversity of the fish fauna in both areas, it was possible to identify those species which are associated in terms of biomass with white and with black waters. However, differences in space and time were great. The most abundant white-water species are *L. pardalis*, *P. nattereri* and *P. flavipinnis*. The first is a detritus grazer, whereas the two other species are predators. Looking for site differences, a much higher quantity of species makes up the catch in the inundated forest than in the open water of the lake. Diurnal differences are not very clear when taking only the most abundant species into consideration. Taking a more detailed look, a significant number of the 50 most abundant species occurred only at day or at night. Thus, catch composition is characterized by the by-catch composition rather than by frequency. What is interesting are the seasonal differences. From rising to low water level, predominant species number decreases due to the reduction in space. Many species have to leave the floodplains during falling water level. Only those featuring special respiratory adaptations, such as facultative areal respiration (*L. pardalis*) or ecological resistance (*P. nattereri*), are able to survive the unfavorable environmental conditions of limited space and oxygen during the low-water period (Saint-Paul 1996).

The most abundant blackwater species are predators: *P. squamosissimus*, *S. rhombeus*, and *S. manuli*. Compared to the whitewater site, the number of species contributing to the main catch is much higher. This correlates with the lower dominance index for black as compared to white water. Even seasonal differences are less pronounced, or do not even exist since blackwater floodplains do not exhibit any significant reduction in surface area during low water, fishes do not leave the system due to topographic differences between the two sample sites. They become rather concentrated, which is the reason for a much higher catch during low water

compared to the rest of the year. Analyzing the abundant species of the floodplain forest, only some are fruit feeders. This suggests that many fishes may move into the floodplain forest to find shelter or for predating.

Studies on diurnal activities by gillnet of white water fish by Barthem (1981, 1987) suggest a bimodal pattern of activity. He distinguished *Acestrorhynchus falcistrostris* and *Laemolita* sp. as dawn, *Rhaphiodon vulpinus*, *Plagioscion* spp. and *Auchenipterus nuchalis* as night and *Hemiodus microepis* and *H. immaculatus* as day active. Similar diurnal activities were also observed in the present study, although data have not yet been analyzed in detail with regard to this aspect. Similar studies on black water have not been carried out so far.

There are very few data on biomass, growth and production of Amazonian fish communities. Bayley (1982), from his quantitative study in the mouth bay of Lago Camaleão, estimates an overall mean biomass for the várzea of about 1.6 t ha^{-1} and a total fish production of $280 \text{ g m}^{-2} \text{ yr}^{-1}$. However, these data are difficult to compare with the catch per unit of effort data from the present study because of the different fishing methods applied. It is interesting to see that the most abundant species are not necessarily of commercial interest. Within the 20 most important species in terms of biomass, only *C. macropomum* is of high market value, followed, to a certain extent, by *L. pardalis*, *P. squamosissimus*, *P. nigricans* and *C. monoculus*. Catches in black water are so low that no commercial fishery is carried out in this area. The data on fish biomass in black and white water using the same gear and the same fishing effort show that in the Amazon floodplains, fish biomass was about five times higher than in the Rio Negro, indicating a better food supply in the várzea. In both areas, seasonal variations in biomass are similar, showing minimum catches during high and maximum catches during low water. This is not a consequence of biomass change during the year but is caused by habitat changes due to water-level fluctuations. During high water, large areas become flooded, so fishes are spread out as a result. During low water, some fish species leave the floodplains and stay in the rivers, mainly for reproduction. However, those which remain are concentrated in restricted areas and can be captured easily. This demonstrates the strong influence of the flooding regime on fish communities, as already pointed out by Junk et al. (1997) in a general paper on river floodplain ecology. The effect of flooding on fishing

habits is also confirmed by Merona (1990) in a study of fish communities and fishing in a Central Amazonian floodplain.

Community similarity was compared by running a PCA. As would be expected, there are clear differences between the results for black and for white water. Since fishes use the inundated forest as a food source, it is understandable that community composition correlates with food demand. This is why, for white water, we can separate low and rising water level (no fruit offer) from high and falling water (high fruit offer) (Ziburski 1990). The clear separation of the low-water community in the lake is clear because of the unfavorable conditions, which can be withstood by only a few resistant species. The hypoxia problem is discussed later.

In black water, similarities are less distinct. Two main groups can be distinguished: inundated forest communities during high and falling water level, and the remainder. As black water obviously has less habitats than white water, due to the lack of floating meadows (Junk & Piedad 1997), fishes just leave the forest during falling water and stay in the open water. Given that these lakes are not liable to dry out, the fishes do not have to leave these areas, as they do in the várzea lake. These reduced migration dynamics in black water may be the reason why fish communities outside the inundated forest are more similar in black water.

In an analysis of the multispecies fisheries of the Orinoco River, Novoa (1989) reports that flood intensities have remarkable effects on fish species' abundance and catch. This is confirmed by Quirós & Cuch (1989), who show that that fish catches in the lower Plata Basin are related to the flood regime and are regulated by fish movements between the main channel and the floodplain. In a study on hydrology and fisheries in Lake Kariba, Central Africa, Karenga & Kolding (1994) found a greater immediate impact on fish catch with positive changes in the delta lake levels. These results match the analytical findings obtained by Welcomme & Hagborn (1977) from their model simulation of floodplain fishery. However, comparing the result of the present study, fish catch is correlated not only with the mean flooded area. During falling water, the quantity of fish captured was always significantly higher than during rising water. As fishes are prepared to leave the floodplain to escape draining, stocks probably become more concentrated and can be captured more easily.

Partial extinction of species during low water can be compensated by immigration from other connected

habitats, making Amazonian river floodplains species-rich habitats despite the severe impacts of annual droughts. Inter-species competition for food is reduced by the large annual mortality during the dry season, which does not permit the exclusive development of an extremely competitive species eliminating other minor aggressive ones. Great structural complexity in the floodplain provides great habitat diversity to fishes at high water, allowing a great number of species to occur together in the same area (Junk et al. 1997). The hydrological dynamics of the river-floodplain system favors the occurrence of stochastic communities of species, as postulated by Lowe-McConnell (1975, 1987) and Goulding et al. (1988), provided no other factors, e.g. severe hypoxia, generate a community structure based on the level of tolerance against oxygen deficiency, or other restricted factors. However, Welcomme (1979) has pointed out that species diversity and average size of species can increase with waterbody size. Bonetto et al. (1970a,b) have found considerable interannual variability in lakes of the Paraná system, and have not detected any relationship between community structure and lake characteristics. Cordiviola de Yuan (1980) found great spatial variability in species abundance in several lakes along the Paraná River. In contrast, most of the spatial variation in species composition was due to differences between black- and whitewater regions along the Orinoco River (Rodríguez & Lewis 1990). Fish community studies in another Central Amazonian floodplain lake showed high values of species richness and diversity. Main source of variability was interannual while seasonal variability has been related to the water level of the system (Merona & Bittencourt 1993). This relation between flood regime parameters and fish abundance, which was found in the present investigation and is confirmed by many other authors, is rendering it difficult to detect overfishing of certain species, because, as shown by the findings of Merona & Gascuel (1993), abundance is largely determined by the hydrological events of previous years. This makes biomass determination difficult in floodplains. The authors therefore recommend using only the estimated biomass during high water as an accurate reflection of the mean biomass in the environment.

The importance of site-specific environmental attributes has been confirmed by the present study, which showed certain distinctions between community structure of fish captured in floodplain forest compared to those from open water. Differences between white and black water were even higher than between

floodplain forest and open water. However, even considering spatial, seasonal and annual variability, as in this study, community structure was rather deterministically assembled. Differences between white and black water are obvious, but less clear between the other sample sites. Based on abundance only, certain site-specific species could be identified. Since conditions such as food availability and space are mainly influenced by water-level fluctuations, this can be seen as the critical habitat factor affecting most fish community diversity in Amazonian floodplains. Flooding seems to be the most important seasonal factor, thus being responsible for fluctuations in fish communities, both throughout the year and interannually. However, the data presented allow conclusions between these two lakes, but not between black- and whitewater lakes in general. In order to study spatial composition in more detail, replicates are necessary.

Acknowledgements

This paper resulted from collaboration between the Max-Planck-Institute für Limnologie, Arbeitsgruppe für Tropenökologie, Plön and the Instituto Nacional de Pesquisa da Amazonia, INPA, Manaus, under the Governmental Agreement on Cooperation in the field of Scientific Research and Technological Development between Germany and Brazil as part of the SHIFT program financed by the German Ministry for Science and Technology (BMBF) [Project number: 0339366A, The Neotropical floodplain forest: relations between fish and environment], the Conselho Nacional de Pesquisa e Tecnologia (CNPq), and the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis (IBAMA). Thanks are extended to John Kennedy and Volker Koch for their help with the statistical elaboration of the data.

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