

COMPARISON OF FISH ASSEMBLAGES IN FLOODED FOREST VERSUS  
FLOATING MEADOWS HABITATS OF AN UPPER AMAZON FLOODPLAIN  
(PACAYA SAMIRIA NATIONAL RESERVE, PERU)

By

SANDRA BIBIANA CORREA

A THESIS PRESENTED TO THE GRADUATE SCHOOL OF  
THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE  
REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2005

Copyright 2005

by

Sandra Bibiana Correa

To my parents and my family. During the course of my life their love and belief in my potential encouraged me to keep going and achieve my dreams. They supported me in all of my decisions even when they separated us for long periods of time. I also dedicate this thesis to Michael Goulding who inspired me to study Amazonian fishes and who is a pioneer in showing their beauty and fragility to the world.

## ACKNOWLEDGMENTS

This thesis would not have been possible without the support and commitment of my supervisory committee chair (Dr. James S. Albert) and my committee members (Dr. Lauren J. Chapman and Dr. William G.R. Crampton). All of them put lots of energy and time into the development of different aspects of this work. I thank James and Will for the outstanding time we spent in Peru during the field work that was the basis for this thesis. They were also crucial during the writing stage, and I enjoyed great discussions on Amazonian fish natural history and ecology. Lauren was my main support during the data analysis process. Without her, many of the results presented in this thesis may not have come out.

I also want to thank my field assistant; B.Sc. Mario Escobedo, who worked on this project as if it was his own; and with great dedication, made it possible to meet the goal of 18 hours of continuous sampling per day. I also thank the fishermen who collaborated on the sampling: Hitler Rodriguez, Wilson Lanza, and Marco from the village of Bretaña. I thank the Instituto Nacional de Recursos Naturales (INRENA) for the research permission (under J.S. Albert). I thank the graduate students of the Zoology Department at University of Florida (UF) for great interactions. I thank Ann Taylor from the Editorial Office at UF. Finally I want to thank N. Bynum, P. Coley, R. Prendeville, the Grunwald-Seibel family, and C. Chapman for the valuable support that finally put me in graduate school.

Last, I would like to acknowledge the support of the National Science Foundation (NSF-DEB 0215388, PI: J.S. Albert) which founded Project Ucamara and made possible the expedition for this thesis. This work was also supported with equipment donated by Idea Wild. I would also like to thank Fish Base, for the incredible resource that this data base represents to ichthyologists from all around the world.

## TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS .....	iv
LIST OF TABLES .....	vii
LIST OF FIGURES .....	viii
ABSTRACT .....	ix
INTRODUCTION .....	1
Characterization of Floodplains in the Amazon Basin .....	1
Importance of Flooded Forest and Floating Meadows for Fishes .....	3
Previous Studies on Amazonian Floodplain Fishes .....	3
Specific Objectives .....	6
MATERIALS AND METHODS .....	7
RESULTS .....	16
DISCUSSION .....	37
Species Richness and Abundance .....	37
Biomass and Size Distributions .....	39
Diel Variation in Species Richness, Abundance and Biomass .....	41
Fish Assemblages in Floodplains .....	42
Sampling Limitations .....	46
Conclusion .....	47
APPENDIX: SYSTEMATIC LIST OF SPECIES .....	48
LIST OF REFERENCES .....	51
BIOGRAPHICAL SKETCH .....	59

## LIST OF TABLES

<u>Table</u>		<u>page</u>
1	Abundance of 78 species in each of 10 locations in flooded forest and floating meadows of the Caño Yarina, Pacaya Samiria National Reserve.....	21
2	Mean values of different assemblage characteristics for flooded forest and floating meadows .....	25
3	Comparison of day and night captures between flooded forest and floating meadows.....	26
4	Principal food items for 78 species and their relative abundance as a percentage of the total abundance (n = 2793 individuals) in flooded forest and floating meadows, during May 2003 at Caño Yarina, Pacaya Samiria National Reserve ....	27
5	Systematic list of species organized by order, family, genus and species based on gill-netting sampling of the Caño Yarina floodplain, Pacaya Samiria National Reserve, during May 2003 .....	48

## LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1 Map of the study area in the Upper Amazon, Pacaya Samiria National Reserve, Peru.....	14
2 Sampling place in Location 1.....	15
3 Species richness saturation curves for flooded forest and floating meadows samples.....	30
4 Rank-ordered abundances (absolute number of individuals per species) of 78 species of fish captured during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru.....	31
5 Abundance per habitat of the 10 most abundant species (absolute number of individuals per habitat) captured during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. ....	32
6 Variation in abundance, biomass, and richness during three periods of capture (EN, LN, LD) during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru.....	33
7 Changes in abundance of the five most common species among three sampling periods in flooded forest and floating meadows.....	34
8 Size frequency distributions of fishes captured per habitat during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru.....	35
9 Nonmetric scaling ordination (NMS) of sampling locations in species space based on the abundances of 57 species that occurred in more than 5% of the sampling locations during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru.....	36

Abstract of Thesis Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Master of Science

COMPARISON OF FISH ASSEMBLAGES IN FLOODED FOREST VERSUS  
FLOATING MEADOWS HABITATS OF AN UPPER AMAZON FLOODPLAIN  
(PACAYA SAMIRIA NATIONAL RESERVE, PERU)

By

Sandra Bibiana Correa

May 2005

Chair: James S. Albert  
Major Department: Zoology

Flooded forests and floating meadows of Amazonian floodplains are important habitats for fishes and yet the distribution and abundance of fish in these habitats are poorly known. This study presents the first quantitative comparison of fish species richness and composition, abundance, biomass and body-size distributions between flooded forests and floating meadows in an Amazon floodplain. This study was conducted in the floodplain of Reserva Nacional Pacaya Samiria, in the Peruvian Amazon and sampled fish assemblages in both flooded forests and floating meadows, using matched sets of gill nets of different mesh sizes. This represents the only reliable method available of doing a quantitative assessment of fish assemblages in flooded forest.

Species richness was higher in flooded forest because of to a high percentage of unique species. Species abundances followed a hollow distribution in which three species accounted for 70 and 60 % of the total abundance in flooded forest and floating

meadows, respectively. Diel variation in the abundance and richness of fishes was observed in both habitats. Body-size distributions were very similar in the two habitats (in the range of 70 to 400 mm). In both flooded forests and floating meadows, most of the fishes caught were invertebrate feeders and frugivores (*i.e.*, *Dianema longibarbis* and *Triporthus angulatus*) in flooded forest; and detritivores (*i.e.*, *Psectrogaster rutiloides*) in floating meadows. Fish predators and frugivores were represented by few species.

Based on species composition and abundance, multivariate analysis suggested the presence of two subtly different fish assemblages in flooded forest *vs.* floating meadows. Water depth accounts for part of the differentiation in fish assemblages. However, the fact that many species (including all the common ones) were shared between the two habitats suggests movement of species between habitats in the floating meadows of Caño Yarina during the flood season.

## INTRODUCTION

Amazon fishes are strongly influenced by the inundation pulse (Goulding, 1980; Goulding *et al.* 1988; Junk, 1997). In the Amazon basin, floodplains are periodically inundated by the overflow of rivers and lakes, or precipitation (Junk, 1997). Floodplains offer a wide variety of resources for both plants and animals, and a complex nutrient and energy cycle integrates the aquatic and terrestrial phases (Junk, 1997). The powerful dynamics driven by the flood pulse make floodplains alternately suitable for aquatic and terrestrial organisms. Therefore, floodplains are believed to have a principal role in maintaining high biodiversity of both aquatic and terrestrial organisms (Goulding, 1980; Junk, 1997; Gopal & Junk, 2000). Furthermore, the Amazon basin contains the most diverse fish fauna (3,000 species) in the world (Val & Almeida-Val, 1995), which accounts for about 10 % of the global fish fauna (Groombridge & Jenkins, 1998). Besides the importance of floodplains in maintaining diversity, floodplains provide much of the carbon consumed by several commercially important species (Araujo-Lima *et al.* 1986a; Benedito-Cecilio *et al.*, 2000). And fishes represent the main sources of protein and commercial income to riverine people (Bayley, 1989; Crampton *et al.*, 2004).

### **Characterization of Floodplains in the Amazon Basin**

Floodplains are mosaics of lakes, channels (paraná), and levees (restingas), where flooded forest and floating meadows (patches of aquatic macrophytes) are the principal vegetation formations (Junk, 1984). Flooded forests are seasonally inundated by either nutrient-rich rivers (called várzea in Brazil), or by nutrient-poor rivers (called igapó in

Brazil) (Prance, 1980). Nutrient-rich rivers, originate in the Andes (Goulding *et al.* 2003). They have a high concentration of suspended solids, with a near-neutral pH (6 to 7 pH), and high electric conductivity (50 to 300  $\mu\text{S} \cdot \text{cm}^{-1}$ ) (Junk, 1984). Nutrient-poor rivers, originating in the Amazonian lowlands, have relatively high transparency, with water color depending on the soils that they drain, and the concentration of organic compounds in the water. The characteristic dark tea color of some waters is usually the result of local podzol-based soil geochemistry. Here there is little sequestering of organic matters, resulting in waters with a high concentration of humic substances (Leenheer, 1980). In this type of water, acidity varies between 2 and 5 pH, transparency ranges from 1.30 to 2.90 m (Sioli, 1984), and electric conductivity is low (5 to 30  $\mu\text{S} \cdot \text{cm}^{-1}$ ). In latosoils, the sequester of humic compounds on the clay matrix results in highly transparent drainage water (Leenheer, 1980) ranging from 1.10 to 4.30 cm (Sioli, 1984). Additionally, rivers that drain ancient upland regions of granite shields (i.e., Brazilian and Guiana Shields), where there is little erosion, are highly transparent (Goulding *et al.* 2003).

Chemical composition of each water type, nutrient levels, and the length of the flood season determine the vegetation present in each forest type (Prance, 1979). Biomass and local tree-species diversity ( $\alpha$ -diversity) is higher in várzea than in igapó; however at a regional scale ( $\beta$ -diversity), igapó forests are more diverse (Kubitzki, 1989). Flooded meadows are extensive rafts of floating macrophytes growing along the margins of rivers, lakes, and channels. The specific composition of these meadows changes from area to area, depending on water fluctuation. However, the most diverse macrophyte communities are present in floodplains of nutrient-rich rivers (Junk & Howard-Williams, 1984).

### **Importance of Flooded Forest and Floating Meadows for Fishes**

During the flood season, flooded forest and floating meadows are the most important habitats for a variety of Amazonian fish species. Flooded forests offer a wide variety of allochthonous food resources (*e.g.*, terrestrial herbaceous plants, leaves, flowers, seeds and fruits, and terrestrial invertebrates) (Goulding, 1980), while floating meadows offer autochthonous food resources (*e.g.*, phytoplankton, periphyton, aquatic herbaceous plants, and aquatic invertebrates) (Junk *et al.*, 1997). How fish species partition resources and microhabitats in floodplains is only partially known, partly because of the paucity of quantitative studies of fish assemblages in flooded forests. In general, small fish species and juveniles are the main components of the fish assemblage occupying floating meadows because of the availability of shelter and the abundance of food among meadows' roots (Saint-Paul & Bayley, 1979; Goulding, 1980; Goulding & Carvalho, 1982; Junk, 1984b; Sánchez-Botero & Araujo-Lima, 2001; Carvalho & Araujo-Lima, 2004). When fishes become larger, they move toward the flooded forest or into the main river channel (Junk, 1997).

### **Previous Studies on Amazonian Floodplain Fishes**

Given the extremely high diversity of fishes contained in the Amazon basin, one of the most striking questions in the study of Amazonian floodplains is the origin and maintenance of species diversity. Henderson *et al.* (1998) summarized historical and contemporary factors that aid in resolving this question in várzea floodplains. They speculated that the floodplain fish fauna is characterized by species with wide distributions and by low endemism. The spatial and temporal interconnection of habitats, the ephemeral character of habitats at large temporal scale, and the obligate migration during dry season, act as a group in limiting opportunities for speciation within

floodplains. They suggested that speciation may be occurring in river headwaters, with subsequent colonization of whitewater floodplains. Moreover, floodplain habitats would be selected for attributes of colonizing species resulting in more-simple body trends, and wide phenotypic plasticity.

Other studies on Amazonian floodplain fishes, range from life history of economically key species (*e.g.*, *Arapaima gigas* (Hurtado, 1999), *Colossoma macropomum* (Goulding & Carvalho, 1982), *Cichla* sp. (Cala *et al.* 1996), and pimelodid catfishes (Arboleda, 1988; Rodriguez, 1991; Celis, 1994; Agudelo, 1994)) to community ecology (see below), ecophysiology (Junk *et al.* 1983; Val *et al.* 1986; Val & Almeida-Val, 1995), trophic ecology and nutrients flux (Araujo-Lima *et al.* 1986a; Forsberg *et al.* 1993; Yossa & Araujo-Lima, 1998; Benedito-Cecilio *et al.* 2000; Leite *et al.* 2002), migration (Vazzoler & Menezes, 1992; Barthem & Goulding, 1997), larval movement and recruitment (Araujo-Lima *et al.* 1994; Araujo-Lima & Oliveira, 1998; Carvalho & Araujo-Lima, 2004), and fisheries (Bayley & Petrere, 1989; Bayley, 1995; Bayley, 1996; Merona, 1990; Almeida *et al.* 2001; Crampton *et al.* 2004).

Most of the studies on community ecology of Amazonian fishes have focused on associations between floating meadows and fishes (Bayley, 1983; Soares *et al.*, 1986; Araujo-Lima *et al.*, 1986b; Henderson & Hamilton, 1995; Crampton, 1996; Henderson & Crampton, 1997; Henderson & Robertson, 1999; Petry *et al.*, 2003). In contrast, there are few studies on fishes from flooded forests. The most comprehensive study was Goulding (1980), who made a detailed account of feeding behavior (emphasizing the importance of seeds and fruits in fish diet). Later, Goulding *et al.* (1988) made the most-intensive survey of fish species in an Amazonian affluent (*i.e.*, Rio Negro). They did a

nonsystematic sampling of the Rio Negro's flooded forest and provided a list of 184 species, and food habits of 140 species in this habitat. Henderson and Crampton (1997) conducted a comparative study of fish richness and relative density in nutrient-poor and richer floodplain habitats in the Tefé region, Brazil. They sampled both floating meadows and flooded forests, at dry and flood season, and presented data on species abundance, distribution, and biomass. However, the fact that they used a different sampling technique at each habitat (seine nets in meadows, gill nets in flooded forest) did not allow direct quantitative comparisons of abundance and standing crop. Probably the most complete study of community ecology of fishes in flooded forests was conducted by Saint Paul *et al.* (2000). They compared fish assemblages in nutrient-poor and richer flooded forests near Manaus, Brazil, by using a wide range of gill-net mesh sizes. They reported 238 species; and contrasted species diversity, distribution, abundance, and biomass between the two habitats. In all of the studies mentioned above, gill nets were used as the only available method for quantitative sampling in flooded forests. Although fish length is related to net mesh size (Jensen, 1990) and gill-net effectiveness varies with fish behavior (Jensen, 1986), the structure of flooded forests does not allow the use of other sampling techniques. The only means to improve the efficiency of gill nets is to use a combination of nets of different mesh sizes (Jensen, 1990); usually arranged in batteries, with the largest mesh sizes downstream (if there is any flow).

Data on biomass and production of Amazonian fishes are almost nonexistent (Saint-Paul *et al.* 2000). There is an estimate of annual fish production of 31.2 g m<sup>-2</sup> in marginal floating meadows, and 19.2 g m<sup>-2</sup> in drifting islands of meadows. The study was conducted in Lake Mamirauá (Brazil), a nutrient-rich lake, during 8 days at the beginning

of the flood season (Henderson & Hamilton, 1995). Another study in the same lake estimated a mean of  $13.5 \text{ g fish m}^{-2}$ , based on 12 days of sampling during the flood season (Henderson & Crampton, 1997). Both of these estimates were based on seine-net sampling. In contrast, for flood forest there is an estimate of  $33 \text{ g fish m}^{-2}$  (of net area) per day for a nutrient-poor lake (Lago do Prato, Anavilhanas, Brazil), and  $104 \text{ g fish m}^{-2}$  (of net area) per day for a nutrient-rich lake (Lago do Inacio, Rio Manacapuru, Brazil) (Saint-Paul *et al.* 2000). These estimates were based on 48 hours of sampling (over 2 years) during the flood season, and were based on gill-net sampling; therefore the authors standardized by capture per unit effort (CPUE). The fact that all of the estimators mentioned above were obtained with different sampling protocols makes them noncomparable (e.g., seine nets give an estimator of biomass per  $\text{m}^2$  of meadow, whereas gill nets give an estimator of biomass per  $\text{m}^2$  of net surface area). Moreover, fish abundance and biomass differ from season to season in the same area (Henderson & Hamilton, 1995; Henderson & Crampton, 1997; Saint-Paul *et al.* 2000). Thus, to adequately compare fish biomass between habitats, sampling must be conducted during the same season and using the same fishing techniques.

### **Specific Objectives**

Given the apparent importance of flooded forest in maintaining fish diversity in Amazonian floodplains, and the lack of knowledge on how fish species partition resources and microhabitats in floodplains, the present study used a standardized sampling technique to compare species richness and composition, abundance, biomass, and size distribution of fishes in flooded forest with those of floating meadows in a floodplain of the Peruvian Amazon.

## MATERIALS AND METHODS

**Study site.** This study was conducted in the Caño Yarina, a tributary of the Río Pacaya in the Pacaya Samiria National Reserve (PSNR). This reserve is located at the confluence of the Marañon and Ucayali Rivers, in the Peruvian Amazon (5° 20.575' S; 74° 30.117' W). All specimens were collected within 10 km from one of the guard posts in the reserve (Puesto de Vigilancia 2 – “PV2”, Fig. 1).

The PSNR is the largest continuous area of protected várzea floodplain in the Amazon basin (21,500 km<sup>2</sup>) (INRENA, 2000) and therefore provides a good opportunity to survey fish communities that have not been highly perturbed as is the case in most of the lower and central Amazonian floodplains (with exceptions such as the Mamirauá Reserve, Brazil). The PSNR is located within the Ucamara Depression, an active deposit of marine and continental sediments dating back from the Late Tertiary to the present (Bayley *et al.*, 1992). Consequently, the area is an extensive floodplain that gets inundated most of the year with a short dry season from July to September (INRENA, 2000). Indeed, 86% of the area is represented by inundated forest (51%), seasonally flooded forest (34%), and rivers and oxbow lakes (1%) (Bayley *et al.*, 1992), making the landscape a complex mosaic of water bodies all interconnected during the inundation season. Extensive beds of floating macrophytes cover approximately 30-40% of the total open water surface area at high water (INRENA, 2000).

The taxonomic composition of macrophytes varies from one patch to another. The most abundant plant species occurring in the sampled patches were *Polygonium* sp.,

*Pistia stratiotes* (L.), *Eichhornia crassipes* Solms., *Paspalum* sp., and an unidentified legume species. Other taxa include *Azolla* sp., *Neptunia* sp., *Ludvigia* sp., *Salvinia* sp., *Utricularia* sp., and *Echinochloeta* sp. While most of these macrophyte species are buoyant and drift with wind and water currents, herbaceous species such as *Paspalum repens* Berg, and *Polygonium* sp.; and shrubs and trees such as *Sena* sp., and *Cecropia* sp. are rooted to the bottom. Rooted plants made the sampling effort with gillnet very difficult and in many occasions it was impossible to cut depth enough into the meadows to clear a patch for the nets.

Caño Yarina is a small affluent (no more than 100 m width) of the Rio Pacaya. Conductivity ranges from 100 to 200  $\mu$  siemens  $\text{cm}^{-1}$  in the Pacaya River, similar to that of “white” water, despite a dark coloration of the river which is more typical of blackwaters. Water depth varied from 0.6 to 2.5 m in the sampling places in the flooded forest and from 2.5 to 6.5 m in the floating meadows. Transparency was measured with a Secchi disk and ranged from 0.8 to 2.2 m in flooded forest and from 1.5 to 2.8 m in the floating meadows. Margins of the channel were covered by extensive beds of floating meadows. Behind these macrophytes were patches of shrubs, palms and *Cecropia* sp. trees which all together constitute the levee zone. The várzea flooded forest grows behind this zone.

**Fish sampling.** This study was designed to quantify fish assemblages in a way that would facilitate comparison between flooded forests and floating meadows. Fish collection was conducted during 9 to 21 May 2003 in two habitats: flooded forests and floating meadows. In each habitat 10 locations were chosen, separated by at least one km, with the exception of Locations 7 and 8.

At each location I selected three sampling positions, no further than 100 m apart. At each of these three positions a set of four gill nets of 25, 40, 80 and 120 mm mesh size were deployed. In the flooded forest, the nets were located from the edge of the dry land towards the open water, parallel to each other and with the bigger to the smaller mesh sizes facing the current direction (Jensen, 1990). In floating meadows nets were located around patches of vegetation and the order of mesh sizes was randomly assigned (Fig. 2). Nets were 20 m long and depth varied from 3.5 to 5 m. Fishing was conducted for a period of 18 h at each location. After selecting a location and recording its location with a Global Positioning System (GPS) receiver, one team of two people went inside the flooded forest and another team into the floating meadows to select the three sampling positions. Nets were deployed around 18:00 h. At midnight all captured fishes were removed from the nets and brought to the field station to be identified and measured. The nets were visited again at 06:00 h and at noon, and the same procedure was followed each time. Nets were removed at noon and brought to the field station to be repaired if necessary and all were deployed again at 18:00 h at the next sampling positions.

Standard length (SL), weight (W), time at capture, and mesh size for all captured fishes were recorded, and samples of each species were fixed in 10% formaldehyde and preserved in 70% ethanol. All preserved materials were deposited at the Florida Museum of Natural History (UF), University of Florida, USA.

**Data analysis.** Because of the low number of captures at individual sampling positions, the specimens collected at all three sampling positions for a single location were combined to produce a meaningful representation of the location. Therefore I considered locations as sample units, representing each habitat. Statistical analyses were

performed using Stat View 5.0 and JPM 5.0.1, except for Jackknife richness estimator and the multivariate analyses that were performed using PC-ORD software (McCune and Mefford, 1999).

Species accumulation curves for each habitat were constructed based on number of species caught per location. Each location represented 18 h of continuous sampling. Total species per habitat were estimated with a first and second order Jackknife estimator (Heltshel and Forrester, 1983) using PC-ORD.

Differences in assemblage characteristics between flooded forest and floating meadows were evaluated by conducting t-tests on abundance (total number of individuals), biomass (total weight of individuals), richness (total number of species), mean SL, maximum SL, mean weight, and maximum weight of fish from 10 locations of each habitat type. The same set of analyses was also conducted excluding individuals over 400 mm SL. Biomass was also estimated as “capture per unit of effort” (CPUE) by calculating the amount of grams of fish caught per meter square of net surface per day of sampling.

To compare the distribution of abundance of species between flooded forest and floating meadows, I ranked all species in a habitat based on abundance ( $n = 72$  species in flooded forest and  $n = 57$  species in floating meadows), giving the rank = 1 to the most abundant species and continuing the ranking in descending order. If more than one species presented the same abundance I gave the same rank to all of those species and then calculate the average rank (ties). I then plotted the ranks against the number of individuals. Differences in median abundance between habitats for the 10 most abundant species were also detected using the nonparametric Mann Whitney U test.

Temporal differences in abundance, biomass, and richness were explored using repeated measures ANOVA. This analysis allowed me to explore the effects of time of day, habitat, and their interaction on assemblage characters. Contrast analysis was performed to evaluate differences between time periods.

Distribution of body size of all fishes captured in flooded forest versus floating meadows was compared using the Kolmogorov-Smirnov test for frequency distributions. To study the distribution of species in the two habitats, multivariate procedures were performed with a matrix of species abundance per location. The original matrix contained 20 locations x 78 species. Eighteen species present in only one location (5% of the sampling units) were deleted from the matrix resulting in a new matrix of 20 locations x 60 species. This reduces the noise of uninformative rare species and is appropriate after species richness and diversity has been analyzed from with the data (McCune and Grace, 2002). However, after deleting the rare species, the coefficient of variance and average skewness for species were still very high (319.82%, and 2.55 respectively). Therefore the abundance matrix was transformed using  $\text{Log}_{10}(x + 1)$ . This transformation is useful in analyzing community data since it decreases the importance of highly abundant species that would skew cluster and ordination procedures (McCune and Grace, 2002).

An outliers analysis (PC-ORD) pointed out a location from floating meadows (FM5) as an outlier (standard deviation from average distance among sample units  $> 2$ ) (McCune and Grace, 2002). Similarly, a location from flooded forests (FF5) showed as an isolated point in exploratory ordination analysis (near to the point representing FM5). Although the standard deviation (Sd) value did not pointed out FF5 as an outlier (Sd = 1.77) I removed the two locations, based on the fact that these locations where highly

predated by piranhas, therefore the species richness and species abundances were remarkable low in both. These two locations produced an artificial clumping effect in the remaining 18 locations, over the axis correlated with species richness and diversity. Finally, I removed from the matrix three species present in only one location after the removal of locations FM5 and FF5.

The new matrix of 57 species and 18 locations of flooded forest and floating meadows was analyzed with a nonmetric multi-response permutation procedure (MRPP) in order to test the null hypothesis of no difference in species composition between the two habitats. The MRPP (Mielke, 1984) is a nonparametric multivariate procedure to test for differences between *a priori* defined groups (e.g., habitats). The nonmetric test transforms the distance matrix in ranks prior to calculating the test statistic ( $T$ ).  $T$  describes the separation between groups and is associated to a p-value. A more negative value of  $T$  means a stronger separation between groups. MRPP also provides a measure of “effect size” called  $A$ , which describes within group homogeneity, compared with the random expectation.  $A$  ranges from 0 to 1, therefore, when  $A=0$  the heterogeneity within groups is not different from that expected by chance, whereas, when  $A = 1$  all items are identical within each group (McCune & Grace, 2002). McCune *et al.* (2000) point out that in community ecology studies,  $A < 0.1$  is common, even when groups are obviously differ and  $A > 0.3$  is considered high.

To represent the similarities in species composition between locations, I used nonmetric multidimensional scaling (NMS; Kruskal, 1964; Mather, 1976). NMS is a nonparametric ordination technique; starting from a matrix of species abundance per sample, this procedure calculates coefficients of dissimilarity for each species, ranks

those coefficients, and “maps the samples in two or more dimensions, in which distance between samples reflects similarity in species composition” (Clarke, 1993). The aim of the analysis is to locate samples in positions (in the graph) that result in the lowest “stress”, stress been a measure of departure of sample positions in the graph from the initial dissimilarity matrix (Clarke, 1993). Therefore in PC-ORD stress is scaled from 0 to 100 where zero means perfect agreement in rank orders (McCune & Grace, 2002). NMS has advantages when analyzing community data by not assuming multivariate normality and by being robust to large numbers of zero values (Clarke, 1993; McCune & Grace, 2002). The analysis was performed through the autopilot slow-and-thorough option of NMS in PC-ORD. This option performed 40 runs with real data and 50 runs with randomized data to find a Monte Carlo test of significance for the best output.

The resulting ordination was rotated 15 degrees. Rotation maximizes the percentage of variance explained by each axis (McCune & Grace, 2002). The variance explained was expressed by the coefficient of determination between distances in the ordination space and distance in the original species space. Sorensen distance was selected in both cases since this distance measure has been recommended for analyzing community data (McCune & Grace, 2002). Environmental and assemblage variables were overlaid by using a joint plot, based on the individual correlations of those variables with the axes of community ordination (see Clarke, 1993; McCune *et al.*, 2000; and Peterson & McCune, 2001 for examples of applying this ordination technique on community data).

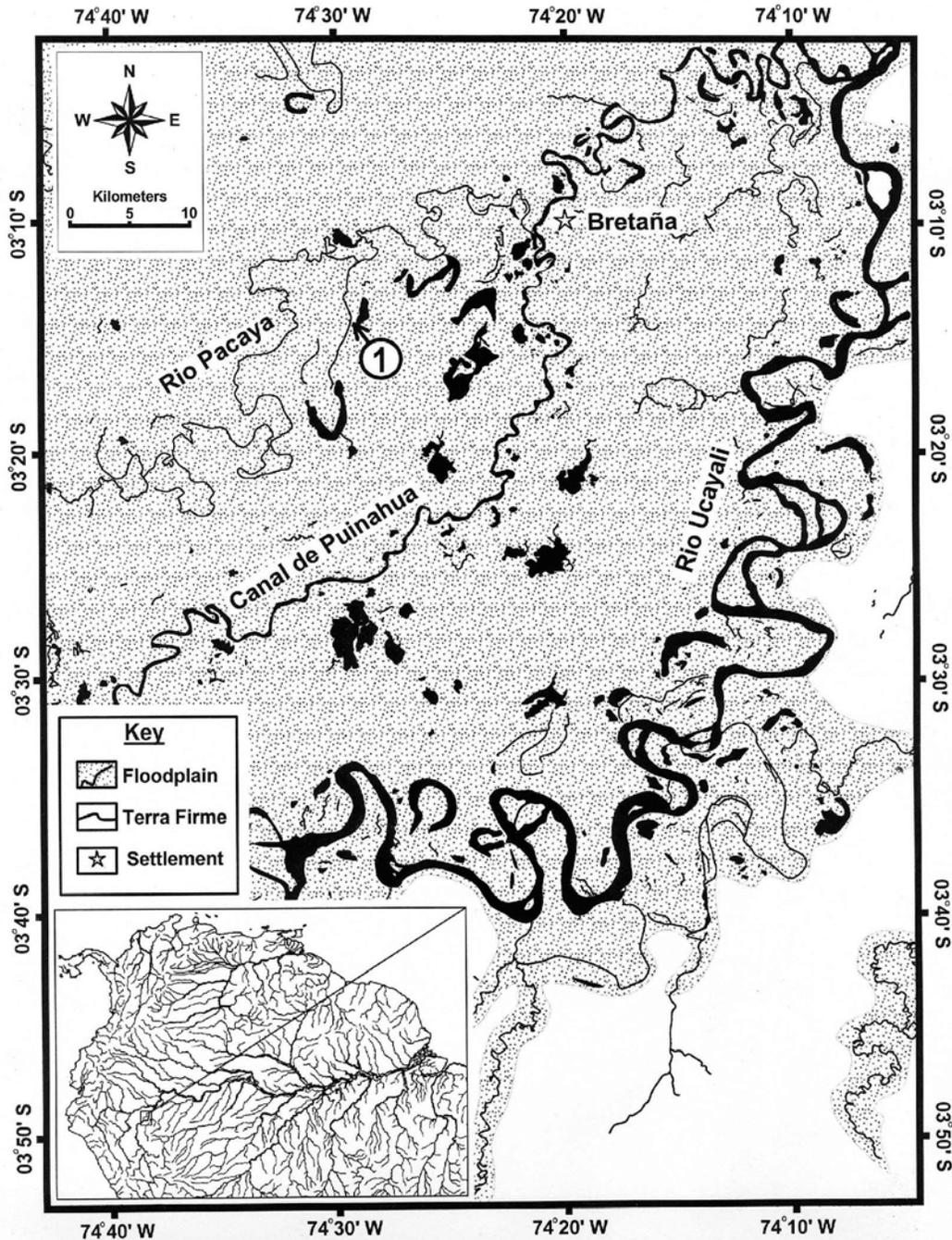


Figure 1. Map of the study area in the Upper Amazon, Pacaya Samiria National Reserve, Peru. Number one indicates the location of guard post, Puesto de vigilancia 2 (PV2), around which the sampling was conducted. Map was made by W.G.R. Crampton based on 1998 1:300,000 Landsat TM5 images; and used with his permission.

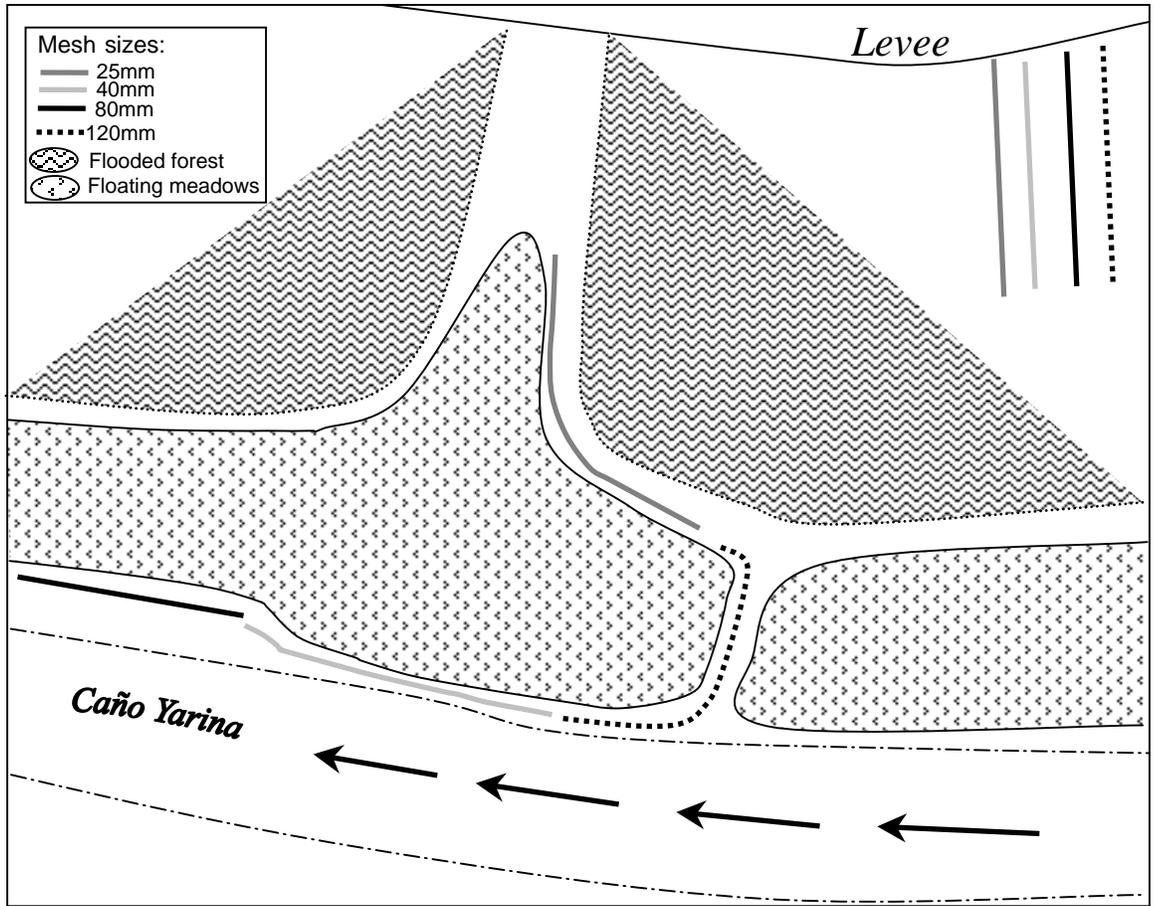


Figure 2. Sampling place in Location 1. Different mesh size nets are represented by shades. Nets closer to Caño Yarina, Pacaya Samiria National Reserve, Peru, are located in floating meadows whereas nets located next to the land edge, are placed into the adjacent flooded forest. Arrows represent the direction of the water current.

## RESULTS

A total of 2789 individuals representing 6 orders, 20 families, 61 genera and 78 species of fishes were captured in this study (See appendix). Characiformes (35 species) was the most diverse taxon followed by Siluriformes (27 species), Perciformes (6 species of Cichlids), Gymnotiformes (7 species), Osteoglossiformes (2 species), and Synbranchiformes (1 species). Characiformes and Siluriformes alone accounted for 80% of the total number of species. Seventy three species were caught in flooded forest, 21 of which were exclusively found in this habitat. In floating meadows, 57 species were caught and only five were exclusively found in this habitat (Table 1). Species richness per location ranged from 9 to 33 in flooded forest (average  $19.3 \pm 7.6$ ) and from 14 to 30 in floating meadows (average  $19.0 \pm 5.1$ ).

Species richness approximates an asymptote in both habitats (Fig. 3), for the species with individuals ranging from 38 to 740 mm SL. Total species estimates were 102 (first order jackknife) and 117 (second order jackknife) for flooded forest. In this habitat, 32 species (44%) occurred in only one location. In floating meadows total species was estimated in 74 (first order jackknife) and 79 (second order jackknife). In this habitat, 19 species (33%) occurred in only one location.

Assemblage characters, averaged across locations and including abundance (total number of individuals), biomass (total weight of individuals), richness (total number of species), mean SL, maximum SL, mean weight, and maximum weight of fish were

similar in between flooded forest and floating meadows (Table 2). Similar results were found when individuals over 400 mm SL were excluded from the analysis.

Total biomass was higher in flooded forest than in floating meadows (71.0 kg vs. 49.9 kg respectively). A total of 1000.22 m<sup>2</sup> gill net surface area was deployed at each habitat. Capture per unit effort was estimated as 7.10 g fish m<sup>-2</sup> per day in flooded forest and 4.99 g fish m<sup>-2</sup> per day in floating meadows for fishes ranging between 38 to 740 mm (n = 2789 individuals).

Species abundances at each habitat followed an expected hollow distribution (Hubbell, 2001) where few species were very abundant and most of the remaining species were represented by few individuals (Fig. 4). Indeed, in flooded forest 70% of the total abundance was accounted for by three species: *Dianema longibarbis*, *Psectrogaster rutiloides*, and *Triportheus angulatus*, while 25 species (35% of the total richness) occurred only once. In floating meadows 60% of the total abundance was represented by *D. longibarbis*, *P. rutiloides*, and *Psectrogaster amazonica* (Fig. 5), and 12 species (21% of the total richness) occurred only once. Among the 10 most abundant species, only *T. angulatus* was significantly more abundant in flooded forest than in floating meadows (Mann Whitney,  $U = 6.0$ ,  $P < 0.001$ ; FF  $30.9 \pm 19.0$ ; FM  $4.8 \pm 3.4$ ), whereas *Hoplias malabaricus* ( $U = 15.5$ ,  $P < 0.01$ ; FF  $0.6 \pm 1.1$ ; FM  $3.2 \pm 2.7$ ), *Cichlasoma amazonarum* ( $U = 24.50$ ,  $P < 0.05$ ; FF  $0.7 \pm 1.6$ ; FM  $3.0 \pm 2.8$ ), and *Mesonauta mirificus* ( $U = 20.50$ ,  $P < 0.05$ ; FF  $0.4 \pm 0.7$ ; FM  $3.0 \pm 2.8$ ) were significantly more abundant in floating meadows (Fig. 5).

Numbers of individuals and species richness were higher at night; however biomass did not show diel differences (Table 3). Abundance and richness were highest at the

18:00 to 24:00 period and the lowest at the 6:00 to 12:00 period (Fig. 6). Moreover, there were temporal differences in abundance within each habitat, as well. In flooded forest the abundance was highest during the 18:00 to 24:00 period and lowest at the 6:00 to 12:00 period (Contrast analysis for: 18:00 to 24:00 vs. 6:00 to 12:00,  $F = 45.31$ ,  $df = 1$ ,  $P < 0.0001$ ; 24:00 to 6:00 vs. 6:00 to 12:00,  $F = 9.72$ ,  $df = 1$ ,  $P < 0.01$ ; Fig. 6). In floating meadows the abundance was also highest at the 18:00 - 24:00 period, but it was equally lower in the other two periods of time (Contrast analysis for: 18:00 - 24:00 vs. 6:00 to 12:00,  $F = 12.36$ ,  $df = 1$ ,  $P < 0.01$ ; 24:00 to 6:00 vs. 6:00 to 12:00,  $F = 0.36$ ,  $df = 1$ ,  $P = \text{NS}$ ; Fig. 6). At the species level, the five most common species (*D. longibarbis*, *P. rutiloides*, *T. angulatus*, *P. amazonica*, and *Ctenobrycon spilurus*) represented highest abundances during the nocturnal samples (18:00 to 24:00 and 24:00 to 06:00) in both flooded forests and floating meadows (Fig. 7). There were no temporal differences in species richness within each habitat. Biomass was similar at day and night samples with approximately 2 kg of fish per net area (2000.4 m<sup>2</sup>) in a 6 h period (Fig. 6).

Body size distributions were very similar in the two habitats. There were no significant differences in the frequencies of SL intervals (Kolmogorov-Smirnov,  $X^2 = 0.667$ ,  $P = \text{NS}$ ) (Fig. 8).

**Community-structure patterns.** Flooded forest locations differed from floating meadows locations in species composition (MRPP  $A = 0.15$ ,  $P < 0.001$ , where  $A$  describes within group homogeneity compared to the random expectation). Although the  $A$  value was small, it is significantly different from zero and indicates that the homogeneity within groups is higher than expected by chance, meaning that there is a different assemblage at each habitat type.

Flooded forest locations separates from floating meadows locations along the vertical ordination axis (Fig. 9). After rotation, the vertical axis explained 32% of the variation in fish assemblages and was correlated with water depth (Pearson Correlation,  $r = 0.68$ ,  $P < 0.01$ ), but not significantly correlated with water transparency ( $r = 0.40$ ,  $P = NS$ ). The vertical axis was also positively correlated with the abundance of *C. amazonarum* ( $r = 0.65$ ,  $P < 0.005$ ), *H. malabaricus* ( $r = 0.65$ ,  $P < 0.005$ ), *Crenicichla proteus* ( $r = 0.59$ ,  $P < 0.01$ ), *M. mirificus* ( $r = 0.53$ ,  $P < 0.05$ ), and negatively correlated with the abundance of *T. angulatus* ( $r = -0.86$ ,  $P < 0.001$ ), *Callichthys callichthys* ( $r = -0.71$ ,  $P < 0.001$ ), *Gymnotus ucamara* ( $r = -0.67$ ,  $P < 0.005$ ), *Ancistrus* sp. PUA ( $r = -0.62$ ,  $P < 0.01$ ), and *Hoplerythrinus unitaeniatus* ( $r = -0.60$ ,  $P < 0.01$ ).

The horizontal axis explained 30% of the variation in fish assemblages and was positively correlated with the abundance of *P. rutiloides* ( $r = 0.85$ ,  $P < 0.001$ ), *P. amazonica* ( $r = 0.82$ ,  $P < 0.001$ ), *Potamorhina altamazonica* ( $r = 0.68$ ,  $P < 0.005$ ), *Curimatella meyeri* ( $r = 0.58$ ,  $P < 0.05$ ), *Doradidae* sp. PUA ( $r = 0.51$ ,  $P < 0.05$ ), and negatively correlated with the abundance of *Colossoma macropomum* ( $r = -0.50$ ,  $P < 0.05$ ) and *Liposarcus pardalis* ( $r = -0.49$ ,  $P < 0.05$ ). A third axis and explained 20% of the variation in fish assemblages and was correlated with overall species richness ( $r = 0.84$ ,  $P < 0.001$ ),

The coefficients of correlation with environmental and assemblage variables were obtained from a joint plot and are in accordance with the highest values of depth ( $t = -8.31$ ,  $P < 0.0001$ ; 144 cm  $\pm$  47.8 in flooded forest vs. 403 cm  $\pm$  85.8 in floating meadows). Species richness was similar in both habitats ( $t = 0.1$ ,  $P = NS$ ; 19.3 species  $\pm$  7.6 in flooded forest vs. 19.0 species  $\pm$  5.1 in floating meadows).

Literature review and personal observations by the author and W.G.R. Crampton, were used to categorize the diet of caught species. In flooded forest, invertebrate feeders (30% of 73 species) was the trophic guild with higher number of species, followed by detritivores (20%), piscivores (15%), and frugivores (7%). Relative abundance, showed a similar pattern, but in each guild, there was a single species that accounted for most of the abundance in this habitat. These species were *D. longibarbis* (39% of the total abundance), *T. angulatus* (20%), and *P. rutiloides* (13%) (Table 4).

In floating meadows, a similar pattern to the one found in flooded forest was observed. Invertebrate feeders (40% of 57 species), detritivores (28%), and piscivores (16%) were the trophic guilds with higher number of species. However the relative abundance of invertebrate feeders, detritivores and piscivores was higher. Again a single species accounted for most of the abundance in each guild. *Dianema longibarbis* (36% of the total abundance), was the most abundant species, *P. rutiloides* (17% of the total abundance), was the second most abundant species and the abundance of *T. angulatus* (4% of the total abundance), was much lower than in flooded forest.

Table 1. Abundance of 78 species in each of 10 locations in flooded forest and floating meadows of the Caño Yarina, Pacaya Samiria National Reserve.

<b>Taxon</b>	FM 1	FM 2	FM 3	FM 4	FM 5	FM 6	FM 7	FM 8	FM 9	FM 10	FF1 2	FF 3	FF 4	FF5 6	FF 7	FF 8	FF9 0	FF1 0	Total		
<i>Acestrorhynchus falcatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1		
<i>Acestrorhynchus falcirostris</i>	0	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0	0	7		
<i>Acestrorhynchus microlepis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1		
<i>Adontosternarchus sp. A</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1		
<i>Agamyxis pectinifrons</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2		
<i>Anadoras grypus</i>	0	0	0	1	1	0	0	0	0	0	0	0	3	0	0	1	4	0	11		
<i>Ancistrus sp. PUA</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2		
<i>Arapaima gigas</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1		
<i>Astyanax bimaculatus</i>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3		
<i>Auchenipterichthys longimanus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2		
<i>Brochis splendens</i>	0	0	0	0	0	0	14	5	0	0	0	0	0	0	0	2	0	0	21		
<i>Brycon cephalus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
<i>Callichthys callichthys</i>	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0	1	1	0	6		
<i>Charax gibbosus</i>	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	3		
<i>Cichlasoma amazonarum</i>	7	3	0	4	0	2	4	0	2	8	0	5	0	0	0	1	0	1	37		
<i>Colossoma macropomum</i>	1	0	0	0	0	0	0	5	0	1	1	0	0	0	3	1	3	0	18		
<i>Crenicichla proteus</i>	1	0	0	5	2	0	3	0	5	2	0	0	1	0	0	0	0	0	19		
<i>Ctenobrycon spilurus</i>	1	0	9	9	0	3	1	0	1	1	0	23	9	20	1	12	5	3	100		
<i>Curimata vittata</i>	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0	0	0	0	5		
<i>Curimatella alburna</i>	0	2	0	4	0	0	0	0	0	0	0	6	1	10	0	0	3	0	26		
<i>Curimatella meyeri</i>	9	2	2	3	0	0	0	2	0	0	0	8	0	1	0	0	2	0	29		
<i>Cyphocharax cf. festivus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		
<i>Dianema longibarbis</i>	105	46	15	29	1	56	52	46	23	63	29	124	226	57	8	50	22	22	16	42	1032

Table 1. Continued

<b>Taxon</b>	FM	FF1	FF	FF	FF	FF5	FF	FF	FF	FF9	FF1	Total									
	1	2	3	4	5	6	7	8	9	10		2	3	4		6	7	8		0	
<i>Doradidae sp. PUA</i>	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	5
<i>Doradidae sp. PUB</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eigenmannia limbata</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Doradidae sp. PUA</i>	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	5
<i>Doradidae sp. PUB</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eigenmannia limbata</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Electrophorus electricus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2
<i>Erythrinus erythrinus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2
<i>Gasteropelecus sternicla</i>	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
<i>Gymnocorymbus thayeri</i>	1	0	0	1	0	0	2	0	0	2	0	0	4	6	0	0	4	0	0	0	20
<i>Gymnotus carapo</i>	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	4
<i>Gymnotus ucamara</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	4
<i>Gymnotus varzea</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Heros appendiculatus</i>	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2
<i>Hoplerythrinus unitaeniatus</i>	0	0	0	0	0	0	0	0	0	0	4	0	1	1	0	1	0	3	0	1	11
<i>Hoplias malabaricus</i>	4	2	1	7	0	1	8	4	1	4	0	0	0	3	0	2	0	1	0	0	38
<i>Hoplosternum littorale</i>	3	1	0	0	0	1	0	2	1	3	1	3	4	5	0	3	3	0	0	0	30
<i>Hypoptopoma gulare</i>	0	0	0	3	7	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	12
<i>Hypselacara temporalis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3
<i>Leporinus trifasciatus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	3
<i>Lepthoplosternum sp. PUA</i> (black belly)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lepthoplosternum sp. PUB</i> (pepper belly)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Liposarcus pardalis</i>	0	1	0	0	0	3	1	9	8	2	9	1	2	4	0	1	1	0	0	1	43
<i>Loricariichthys cf. acutus</i>	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	2	1	0	0	9

Table 1. Continued

<b>Taxon</b>	FM	FF1	FF	FF	FF	FF5	FF	FF	FF	FF9	FF1	Total									
	1	2	3	4	5	6	7	8	9	10		2	3	4	6	7	8		0		
<i>Loricariichthys cf. maculatus</i>	0	0	0	1	0	0	2	0	0	0	0	1	0	1	0	4	1	0	0	0	10
<i>Loricariichthys cf. nudirostris</i>	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	2	0	0	0	7
<i>Loricariichthys</i> sp.1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	5
<i>Loricariichthys</i> sp.2 (possibly juvenile of <i>maculatus</i> )	0	5	3	0	0	1	0	0	1	17	0	1	2	0	0	0	0	0	0	0	30
<i>Loricariinae</i> sp. Indet. TF03	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Megalechis thoracata</i>	0	1	0	0	0	3	1	0	0	1	0	4	4	0	0	9	0	5	1	3	32
<i>Mesonauta mirificus</i>	8	0	2	4	3	5	0	0	2	6	1	1	0	0	2	0	0	0	0	0	34
<i>Moenkhausia cf. chrysagyrea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2
<i>Mylossoma duriventre</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Osteoglossum bicirrosum</i>	0	0	0	1	0	0	3	1	0	2	0	2	0	1	0	2	0	0	0	1	13
<i>Parapteronotus hasemani</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Potamorhina altamazonica</i>	5	3	4	2	0	4	1	0	2	1	0	18	1	5	0	1	7	1	0	0	55
<i>Potamorhina latior</i>	13	3	0	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	21
<i>Prochilodus nigricans</i>	0	0	0	0	0	4	3	0	0	0	4	0	0	0	0	0	5	0	0	0	16
<i>Psectrogaster amazonica</i>	7	14	39	2	2	9	1	5	3	0	0	21	0	0	1	0	12	8	7	0	131
<i>Psectrogaster essequibensis</i>	0	3	0	0	0	0	0	0	0	0	0	7	0	0	0	0	2	0	0	0	12
<i>Psectrogaster rutiloides</i>	65	56	23	17	1	20	2	5	5	15	1	140	1	3	0	2	26	4	24	1	411
<i>Pseudorinelepis genibarbis</i>	0	0	0	0	2	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	5
<i>Pterodoras granulosus</i>	0	2	0	2	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	20
<i>Pterygoplichthys scrophus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Pygocentrus nattereri</i>	4	0	2	4	10	0	7	0	0	0	0	0	0	1	1	0	0	0	0	0	29

Table 1. Continued

<i>Taxon</i>	FM 1	FM 2	FM 3	FM 4	FM 5	FM 6	FM 7	FM 8	FM 9	FM 10	FF1 2	FF 3	FF 4	FF5 6	FF 7	FF 8	FF9 0	FF1 0	Total	
<i>Rhamdia quelen</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
<i>Rhytiodus microlepis</i>	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	1	0	0	0	5
<i>Roeboides biserialis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Satanoperca jurupari</i>	0	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	2	0	0	9
<i>Schizodon fasciatus</i>	0	0	1	2	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0	8
<i>Serrasalmus rhombeus</i>	0	0	3	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6
<i>Sorubim lima</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
<i>Synbranchus marmoratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Tetragonopterus argenteus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
<i>Tetragonopterus chalceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Trachelyopterus galeatus</i>	2	2	0	0	0	0	1	0	0	2	1	5	2	4	0	0	1	2	0	22
<i>Triportheus albus</i>	0	1	1	0	1	1	0	0	2	0	0	0	0	0	1	0	0	1	0	8
<i>Triportheus angulatus</i>	3	10	1	10	3	5	0	7	4	5	37	43	55	22	5	20	63	33	23	357
Total	244	159	107	129	40	119	121	95	60	138	99	439	318	169	27	115	174	100	76	2789

Abbreviations: FM - floating meadows; FF - flooded forest. The numbers following the abbreviations correspond to the sampling location in each habitat (1-10).

Table 2. Mean values of different assemblage characteristics for flooded forest and floating meadows.

	FF	FM	P
Mean abundance (total number of fish)	157.9 ± 128	121.4 ± 56	0.4189
Mean biomass (g)	7099.5 ± 4510	4994.1 ± 4516	0.3107
Mean richness (species)	19.4 ± 8	19.3 ± 5	0.9731
Mean standard length (mm)	97.6 ± 15	94.6 ± 15	0.6474
Maximum standard length (mm)	527.8 ± 164	366.4 ± 196	0.0806
Mean weight (g)	62.9 ± 50	45.7 ± 47	0.4368
Maximum weight (g)	1717.0 ± 1283	1156.1 ± 1242	0.3339

Calculations are based on totals, means, or maximum values averaged across 10 locations in each habitat type. Abbreviations: FF - flooded forest, FM - floating meadows. A t-test was used to detect differences between the two habitats in Caño Yarina, Pacaya Samiria National Reserve.

Table 3. Comparison of day and night captures between flooded forest and floating meadows. Repeated measures ANOVA was used to detect effects of time, habitat and their interaction on abundance ( $\log_{10}x+1$  transformed), richness ( $\log_{10}x+1$  transformed), and biomass ( $\log_{10}x+1$  transformed) of fishes with three times of capture (18:00 - 24:00h, 24:00 - 6:00h, 6:00 - 12:00h) and two habitats in Caño Yarina, Pacaya Samiria National Reserve. For abundance, Mauchley's criterion indicated rejection of the compound symmetry assumption, therefore adjusted probability values (G, Greenhouse-Geisser and H-F, Huynh-Feldt) are provided.

SOURCE OF VARIATION	df	SS	F	P	Adj. G-G	H-F
<b>Abundance</b>						
Between-subjects effect						
Habitat	1	0.117	0.452	NS		
Error	18	4.641				
Within-subjects effect						
Time	2	4.222	24.894	<0.001		
Time*habitat	2	1.094	6.453	<0.005	<0.05	<0.01
Error (time)	36	3.053				
<b>Biomass</b>						
Between-subjects effect						
Habitat	1	0.018	0.023	NS		
Error	18	14.092				
Within-subjects effect						
Time	2	1.478	1.754	NS		
Time*habitat	2	0.987	1.172	NS		
Error (time)	36	15.167				
<b>Richness</b>						
Between-subjects effect						
Habitat	1	0.169	1.963	NS		
Error	18	1.550				
Within subjects effect						
Time	2	0.820	10.419	<0.001		
Time*habitat	2	0.164	2.087	NS		
Error (time)	36	1.416				

Table 4. Principal food items for 78 species and their relative abundance as a percentage of the total abundance (n = 2793 individuals) in flooded forest and floating meadows, during May 2003 at Caño Yarina, Pacaya Samiria National Reserve. Food items were extracted from literature. Diet of species in which a reference is not provided was assessed by W.G.R. Crampton and S.B. Correa.

<b>Taxon</b>	<b>Diet</b>	<b>Reference</b>	<b>Relative abundance</b>
<i>Acestrorhynchus falcatus</i>	Fish	Planquette <i>et al.</i> (1996)	0.04
<i>Acestrorhynchus falcirostris</i>	Fish	Goulding <i>et al.</i> (1988)	0.25
<i>Acestrorhynchus microlepis</i>	Fish	Planquette <i>et al.</i> (1996)	0.04
<i>Adontosternarchus sp. A</i>	Invertebrates		0.04
<i>Agamyxis pectinifrons</i>	Invertebrates		0.07
<i>Anadoras grypus</i>	Invertebrates		0.39
<i>Ancistrus sp. PUA</i>	Detritus		0.07
<i>Arapaima gigas</i>	Fish		0.04
<i>Astyanax bimaculatus</i>	Zooplankton	Planquette <i>et al.</i> (1996)	0.11
<i>Auchenipterichthys longimanus</i>	Fruits Aquatic	Manheimer <i>et al.</i> (2003)	0.07
<i>Brochis splendens</i>	invertebrates	Burgess (1989) Goulding (1980), Anonymous (1981)	0.75
<i>Brycon cephalus</i>	Fruits		0.04
<i>Callichthys callichthys</i>	Zooplankton	Mol (1995)	0.21
<i>Charax gibbosus</i>	Fish	Winemiller (1989) Stawikowski & Werner (1998)	0.11
<i>Cichlasoma amazonarum</i>	Plants		1.32
<i>Colossoma macropomum</i>	Fruits	Goulding (1980)	0.64
<i>Crenicichla proteus</i>	Fish	Kullander (1986) Mills & Vevers (1989)	0.68
<i>Ctenobrycon spilurus</i>	Zooplankton	Val & de Almeida-Val (1995) Goulding <i>et al.</i> (1988)	3.59
<i>Curimata vittata</i>	Detritus		0.18
<i>Curimatella alburna</i>	Detritus		0.93
<i>Curimatella meyeri</i>	Plants	Soares <i>et al.</i> (1986)	1.04
<i>Cyphocharax cf. festivus</i>	Detritus		0.04
<i>Dianema longibarbis</i>	Invertebrates		36.95
<i>Doradidae sp. PUA</i>	Invertebrates		0.18
<i>Doradidae sp. PUB</i>	Invertebrates		0.04
<i>Eigenmannia limbata</i>	Invertebrates		0.04
<i>Electrophorus electricus</i>	Fish		0.07

Table 4. Continued

<b>Taxon</b>	<b>Diet</b>	<b>Reference</b>	<b>Relative abundance</b>
<i>Erythrinus erythrinus</i>	Fish	Planquette <i>et al.</i> (1996)	0.07
<i>Gasteropelecus sternicla</i>	Aquatic invertebrates	Mills & Vevers (1989)	0.07
<i>Gymnocorymbus thayeri</i>	Invertebrates		0.72
<i>Gymnotus carapo</i>	Invertebrates		0.14
<i>Gymnotus ucamara</i>	Aquatic invertebrates	Crampton <i>et al.</i> (2003)	0.14
<i>Gymnotus varzea</i>	Aquatic invertebrates		0.04
<i>Heros efasciatus</i>	Plants		0.07
<i>Hoplerythrinus unitaeniatus</i>	Aquatic invertebrates		0.39
<i>Hoplias malabaricus</i>	Fish	Planquette <i>et al.</i> (1996)	1.36
<i>Hoplosternum littorale</i>	Aquatic invertebrates	Boujard <i>et al.</i> (1997)	1.07
<i>Hypoptopoma gulare</i>	Detritus		0.43
<i>Hypselacara temporalis</i>	Fish		0.11
<i>Leporinus trifasciatus</i>	Periphyton		0.11
<i>Lepthoplosternum sp. PUA</i> (black belly)	Invertebrates		0.04
<i>Lepthoplosternum sp. PUB</i> (pepper belly)	Invertebrates		0.04
<i>Liposarcus pardalis</i>	Detritus	Yossa & Araujo-Lima (1998)	1.54
<i>Loricariichthys cf. acutus</i>	Aquatic invertebrates	Goulding <i>et al.</i> (1988)	0.29
<i>Loricariichthys cf. maculatus</i>	Detritus		0.39
<i>Loricariichthys cf. nudirostris</i>	Detritus		0.25
<i>Loricariichthys sp.1</i>	Detritus		0.18
<i>Loricariichthys sp.2</i> (may be <i>maculatus</i> juvenile)	Detritus		1.07
<i>Loricariinae sp. Indet. TF03</i>	Detritus		0.04
<i>Megalechis thoracata</i>	Zooplankton	Mol (1995)	1.15
<i>Mesonauta mirificus</i>	Periphyton		1.22
<i>Moenkhausia cf. chrysagyrea leucopomis</i>	Invertebrates		0.07
<i>Mylossoma duriventre</i>	Fruits	Goulding (1980)	0.07

Table 4. Continued

<b>Taxon</b>	<b>Diet</b>	<b>Reference</b>	<b>Relative abundance</b>
<i>Osteoglossum bicirrosom</i>	Terrestrial invertebrates	Goulding (1980)	0.47
<i>Parapteronotus hasemani</i>	Invertebrates		0.07
<i>Potamorhina altamazonica</i>	Detritus	Soares <i>et al.</i> (1986) Goulding <i>et al.</i>	1.79
<i>Potamorhina latior</i>	Detritus	(1988)	0.75
<i>Prochilodus nigricans</i>	Detritus	Soares <i>et al.</i> (1986)	0.57
<i>Psectrogaster amazonica</i>	Detritus		4.87
<i>Psectrogaster essequibensis</i>	Detritus		0.43
<i>Psectrogaster rutiloides</i>	Detritus		14.72
<i>Pseudorinelepis genibarbis</i>	Detritus		0.18
<i>Pterodoras granulosus</i>	Fruits		0.72
<i>Pterygoplichthys scrophus</i>	Detritus		0.04
<i>Pygocentrus nattereri</i>	Fish	Sazima & Machado (1990) Boujard <i>et al.</i>	1.04
<i>Rhamdia quelen</i>	Fish	(1997)	0.11
<i>Rhytiodus microlepis</i>	Plants	Soares <i>et al.</i> (1986)	0.18
<i>Roeboides biserialis</i>	Fish scales		0.04
<i>Satanoperca jurupari</i>	Invertebrates	Keith <i>et al.</i> (2000) Planquette <i>et al.</i>	0.32
<i>Schizodon fasciatus</i>	Plants	(1996)	0.29
<i>Serrasalmus rhombeus</i>	Fish	Correa (1999)	0.21
<i>Sorubim lima</i>	Fish	Goulding (1981)	0.11
<i>Synbranchus marmoratus</i>	Terrestrial invertebrates	Soares <i>et al.</i> (1986) Silvano <i>et al.</i>	0.04
<i>Tetragonopterus argenteus</i>	Invertebrates	(2001)	0.07
<i>Tetragonopterus chalcus</i>	Aquatic invertebrates	Goulding <i>et al.</i> (1988) Le Bail <i>et al.</i>	0.04
<i>Trachelyopterus galeatus</i>	Fish	(2000)	0.79
<i>Triportheus albus</i>	Invertebrates		0.29
<i>Triportheus angulatus</i>	Fruits	Goulding (1980)	12.80

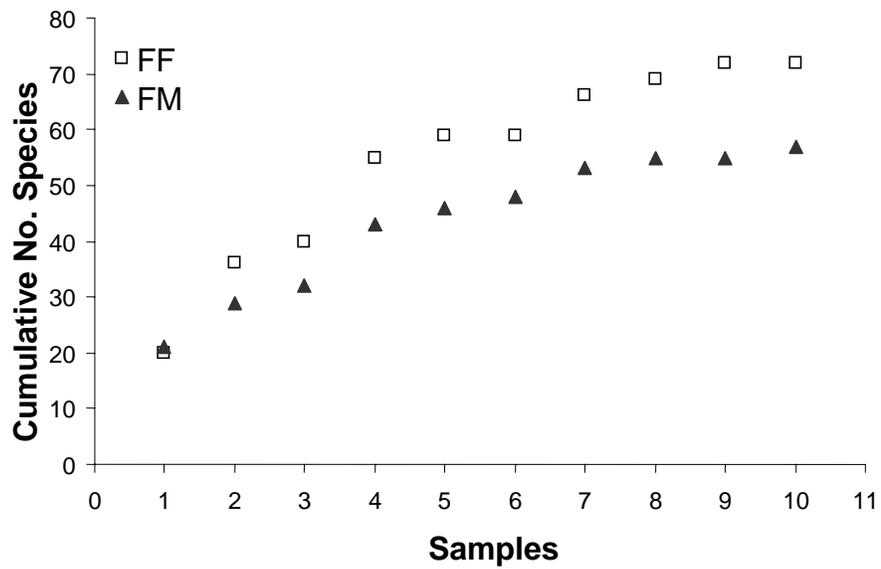


Figure 3. Species richness saturation curves for flooded forest and floating meadows samples. Fish ranged from 38 mm to 740 mm ( $n=2789$  individuals) and were caught with gill nets of 25, 40, 80, and 120 mm mesh size. Sampling was conducted during May 2003 at Caño Yarina, Pacaya Samiria National Reserve, Peru.

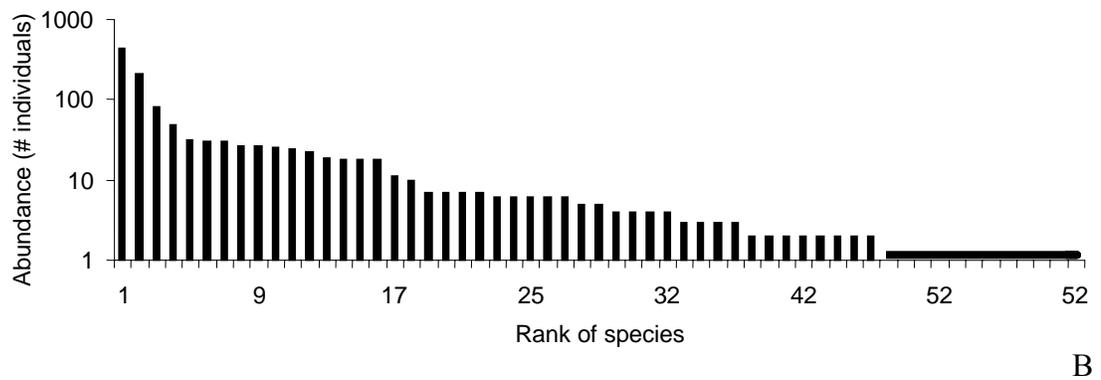
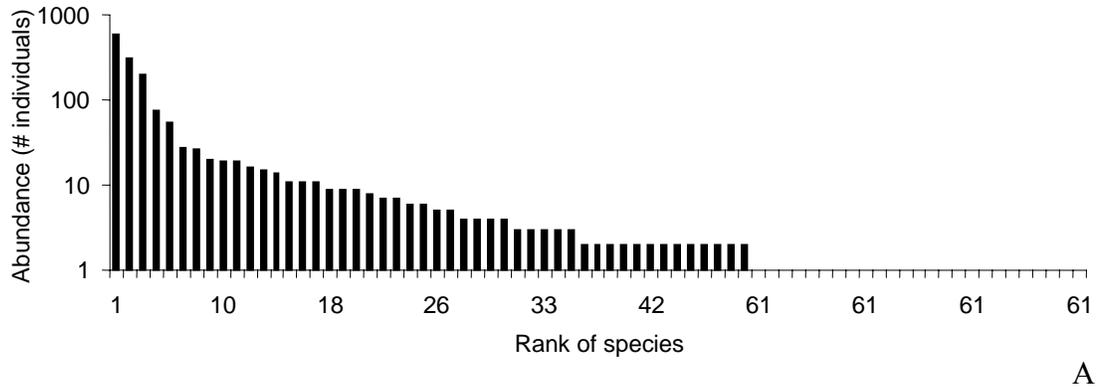


Figure 4. Rank ordered abundances (absolute number of individuals per species) of 78 species of fish captured during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. A) flooded forest (72 species). B) floating meadows (57 species). Mean species richness was equal in the two habitats ( $P = 0.9731$ ). P value originated by t-test. Note the hollow curve where only three species account for 70% and 60% of the total abundance in flooded forest and floating meadows, respectively. See text for method of ranking species.

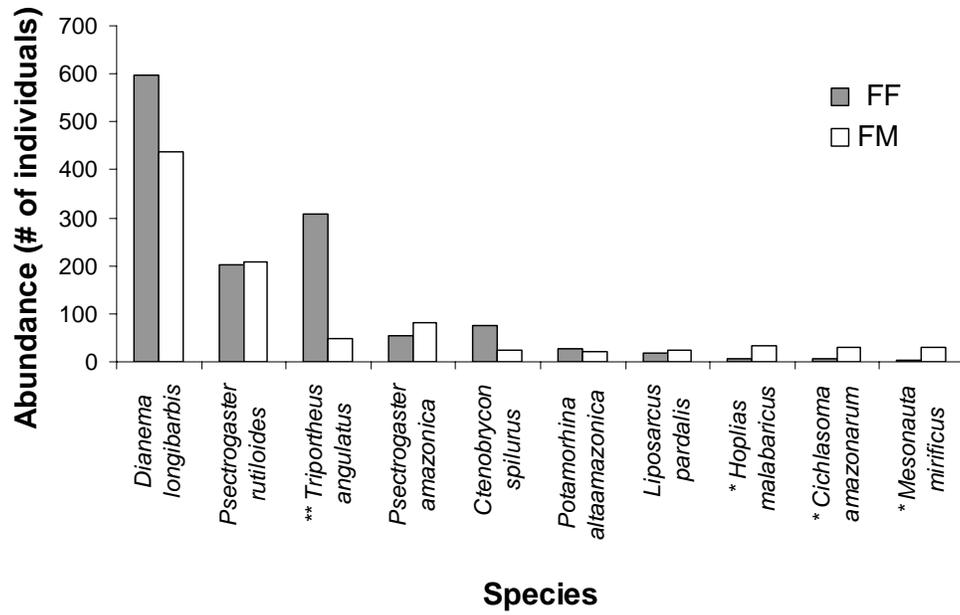


Figure 5. Abundance per habitat of the 10 most abundant species (absolute number of individuals per habitat) captured during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. \*\* indicates  $P > 0.001$ , \* indicates  $P > 0.05$ . Abbreviations: FF - flooded forest, FM - floating meadows.

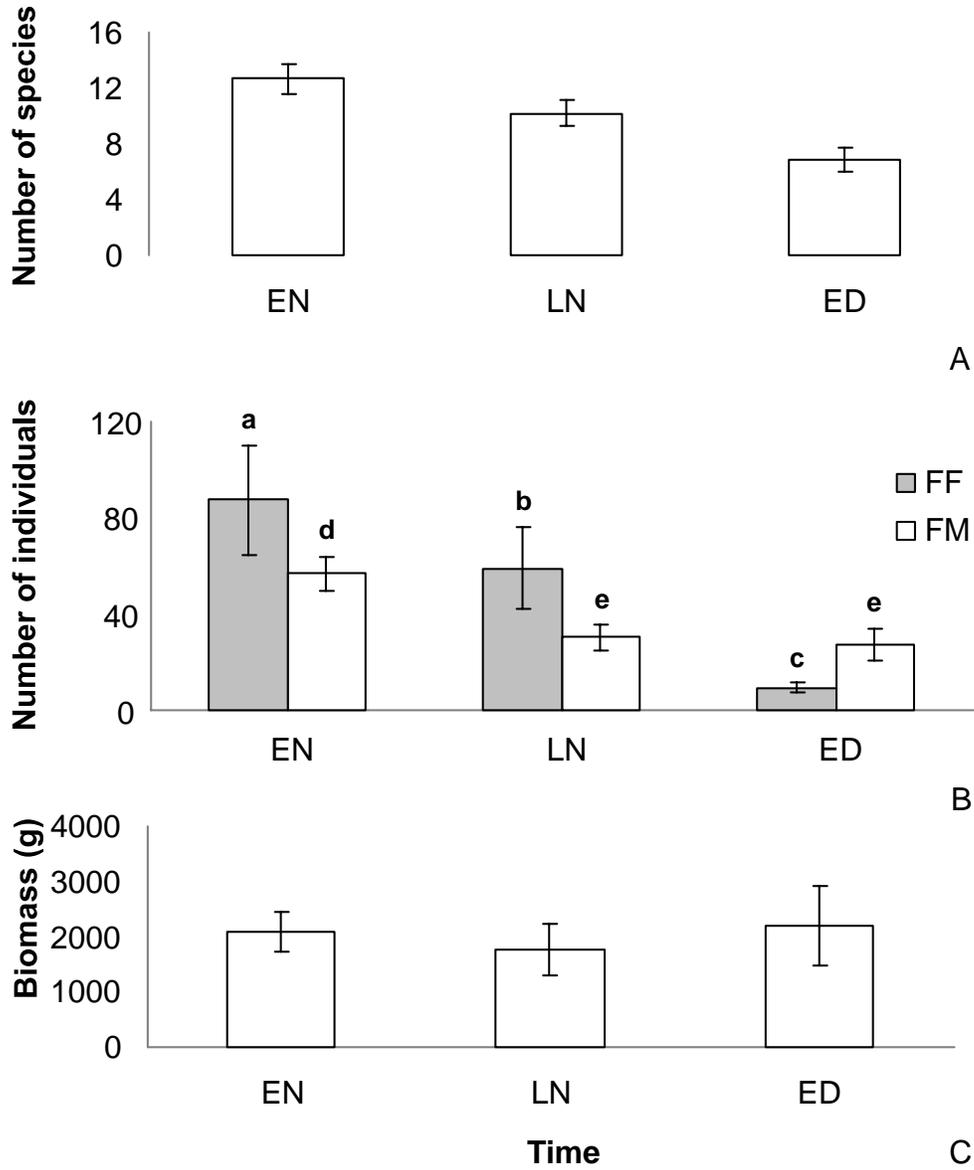


Figure 6. Variation in abundance, biomass, and richness during three periods of capture (EN, LN, LD) during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. Graphs A and C represent means combining the two habitats, graph B shows variation between habitats. Bars represent standard error. Abbreviations: EN – early night: 18:00 – 24:00; LN – late night: 24:00-06:00; ED – early day: 06:00 – 12:00; FF - flooded forest, FM - floating meadows.

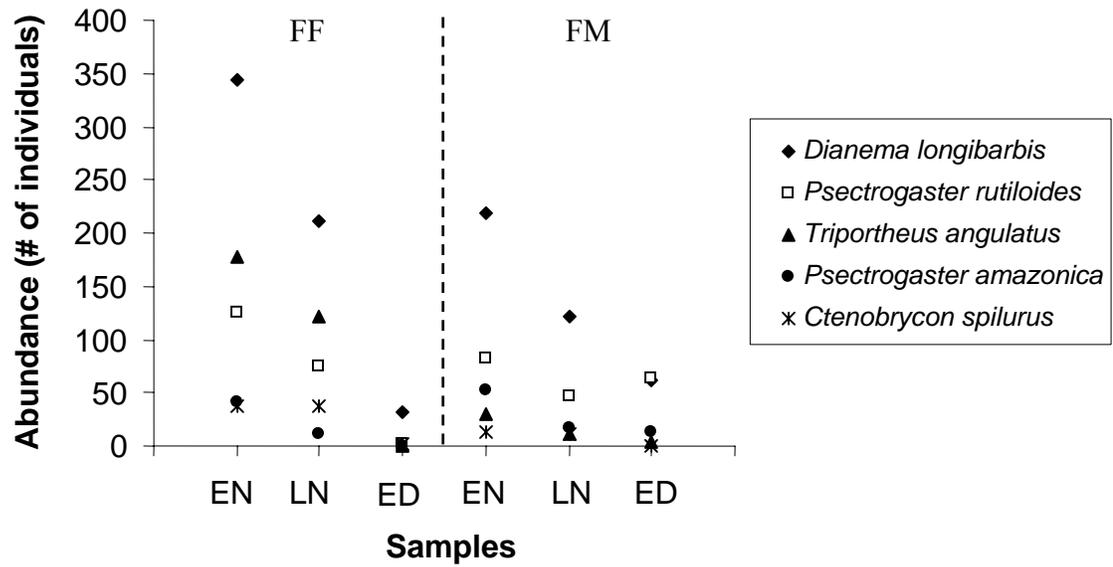


Figure 7. Changes in abundance of the five most common species among three sampling periods in flooded forest and floating meadows. Sampling was conducted during May 2003 at Caño Yarina, Pacaya Samiria National Reserve, Peru. Abbreviations as in Figure 6.

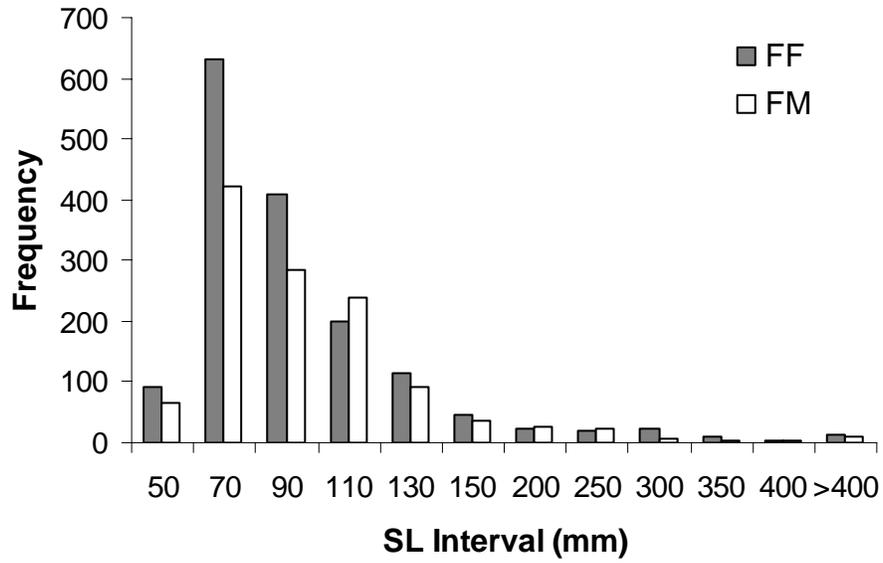


Figure 8. Size frequency distributions of fishes captured per habitat during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. Abbreviations: SL - standard length, FF - flooded forest, FM - floating meadows.

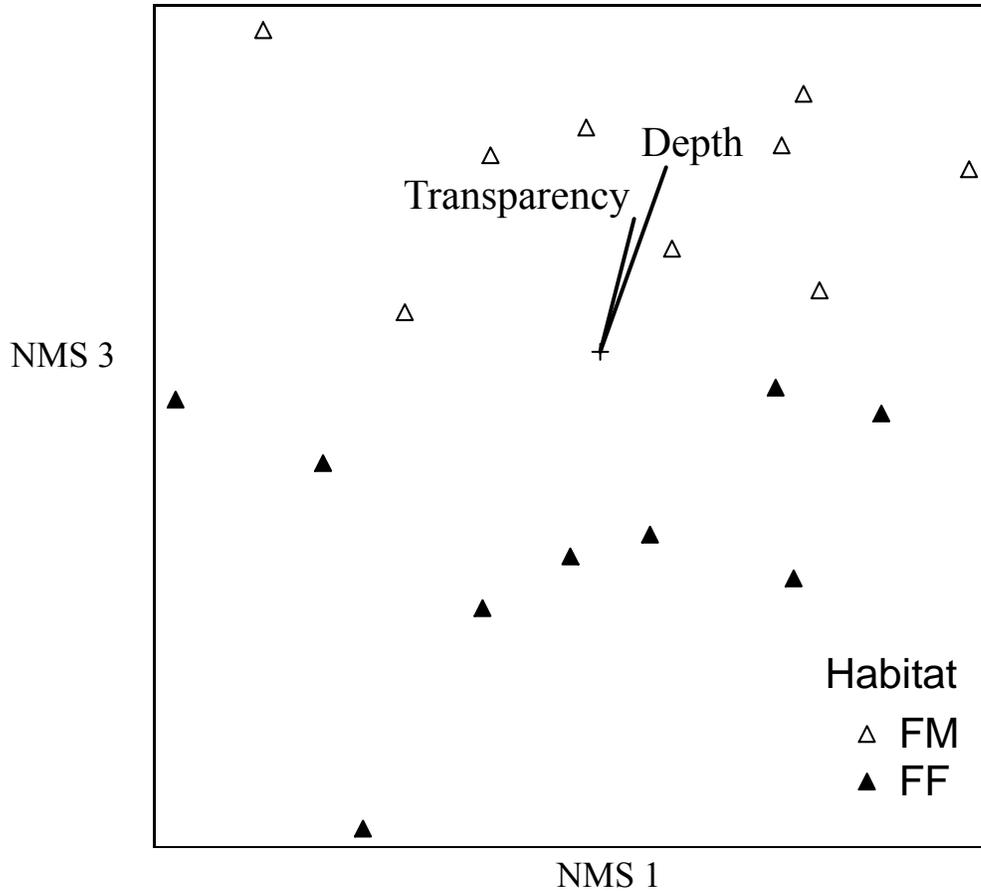


Figure 9. Non metric scaling ordination (NMS) of sampling locations in species space based on the abundances of 57 species that occurred in more than 5% of the sampling locations during May 2003 in Caño Yarina, Pacaya Samiria National Reserve, Peru. The vertical axis accounts for 32% while the horizontal axis accounts for 30% of the variation in the data. Filled triangles represent sampling locations in flooded forest (FF) and open triangles represent sampling locations in floating meadows (FM). The distances between triangles in the ordination are approximately proportional to the dissimilarities between the sampling locations. Environmental variables are join-plotted expressing its relationship with ordination scores. Length and angle of correlation vectors represents the strength of the correlation. The final stress value for a three dimensional representation was 11.367. Instability (0.000001) was the lowest out of the 10 repetitions.

## DISCUSSION

### **Species Richness and Abundance**

The present study provides the first empirical data on the relative species abundance in an Amazonian flooded forest. Relative abundances of species often follow a hollow distribution with very few dominant species and a long tail of rare species (Hubbell, 2001; Magurran & Henderson, 2003). This hypothesis was corroborated in a study of fish assemblages in Amazonian floating meadows (Henderson & Crampton, 1997). In flooded forests of Caño Yarina, 70% of the total abundance was represented by three species: *D. longibarbis*, *P. rutiloides* and *T. angulatus*; while 25 species (35% of the total richness) only occurred once. In floating meadows 60% of the total abundance was represented by *D. longibarbis*, *P. rutiloides* and *P. amazonica*; while 12 species (21% of the total richness) occurred only once.

What allows a species to be abundant in a habitat depends on characteristics of the habitat such as food resources and habitat structure, on ecological processes such as competition and predation, and on stochastic factors. Moreover, the identity of the dominant species in a habitat may change from place to place and year to year depending on migration and recolonization of the habitats (Hubbell, 2001). The reproductive biology of the callichthyid *D. longibarbis*, the dominant species in both habitats, is not well known. Callichthyids in general are reported as K- strategists (sensu Pianka, 1970) (Junk *et al.*, 1997) and Riehl & Baensch (1991) reported bubble nest-building behavior in *D. longibarbis*. Other species with nesting behaviors are defined as “equilibrium” life

history strategist (*sensu* Winemiller, 1989), characterized also by prolonged breeding seasons, and parental investment in individual offspring, probably resulting in enhanced juvenile survivorship. This type of species usually has relatively stable sedentary local populations (Winemiller, 1989). This fact allows me speculate that *D. longibarbis* may be a year round resident of floating meadows that sends colonizers to adjacent flooded forest during the rise of the waters. To prove this hypothesis, a multiseason study in these habitats would be necessary.

In this study, species richness was similar in both flooded forest and floating meadows (72 and 57 species respectively). First and second order Jackknife estimators (Heltsh & Forrester, 1983) estimate the number of species to be higher in both habitats than my absolute accounts and the number of species in flooded forest as higher (102 and 117 species respectively) than in floating meadows (74 and 79 species respectively). First order Jackknife estimators has been considered as the most accurate method for estimating species richness (Palmer 1990; Palmer 1991), however, it is susceptible to high number of rare species in the data set (Palmer 1990); indeed I found four times more rare species in flooded forest than in floating meadows. A higher species richness and biomass in flooded forest was expected because the flooded forest constitutes an expansion of available habitat in the floodplain during the flooded season, therefore is expected that many species would colonize this habitat with the rise of the water. The diversity and abundance of resources provided by flooded forests (Goulding 1980, Junk *et al.*, 1997b) seems to be the driving force for colonization. For migratory fishes, flooded forests are a key habitat that provides enough food for them to accumulate fat reserves as

preparation for subsequent reproductive migration at the low waters season (Junk *et al.*, 1997b, Carvalho & Araujo-Lima, 2004).

### **Biomass and Size Distributions**

Higher biomass along with higher species richness was expected in flooded forest because of increased availability of habitat during the flooded season. Total biomass was similar in the two habitats (73.3 kg *vs.* 51.1 kg for flooded forest and floating meadows respectively) and there was no difference in average biomass between habitats. Flooded forest however had a slightly higher CPUE than floating meadows (7.33 and 5.11 g fish m<sup>-2</sup> net surface per sampled day, respectively). A comparable estimate of CPUE in flooded forest was much higher (104 g m<sup>2</sup> per day; Saint-Paul *et al.*, 2000) than the CPUE value reported in the present study. Although the area covered during sampling in Caño Yarina was higher than the sampled area covered by Saint-Paul *et al.* (2000) (*i.e.*, 1000.15 m<sup>2</sup> *vs.* 772 m<sup>2</sup>, respectively), their study used a wider range of mesh sizes (13 different sizes, ranging from 12 to 200 mm) which in turn could caught a wider range of fish sizes, and therefore a highest biomass. For floating meadows, there is not comparable data since the data available are estimations of standing crop (Bayley 1983; Henderson & Hamilton 1995; Henderson & Crampton 1997).

Body size distributions were highly similar between the two habitats, although differences were expected. A higher number of small fishes in floating meadows were expected, since this habitat is recognized as nursery habitat for juveniles of many species (Saint-Paul & Bayley 1979; Goulding 1980; Junk 1984, Sánchez-Botero & Araujo-Lima 2001), whereas in flooded forest small fishes could be more susceptible to predation; therefore bigger-sized fish were expected.

The body size range found in Caño Yarina was truncated at the extremes (38 to 740 mm SL). This range most likely reflect the chosen mesh sizes (*i.e.*, 25 to 120 mm) leading to under sample juveniles, small fish, and very large fish. Nevertheless, the shape of the distribution of body size frequencies of fishes in the sampled range was similar in both habitats. This result suggest that juveniles and small fishes (over 38 mm) of the species caught at Caño Yarina are using both flooded forest and floating meadows habitats in the same proportion. This contrast with previous hypothesis of floating meadows been a preferred habitat for juveniles because the availability of food and shelter (Junk, 1997). Large fishes (under 740 mm) seem also to be using both habitats in similar proportions despite the differences in habitat complexity.

It is difficult to estimate what percentage of the community falls in and out of this range of body sizes found in Caño Yarina (38 to 740 mm SL). For example, in sandy beach communities in the Orinoco basin, Layman & Winemiller (2004) found that around 50% of the fishes were  $\leq 50$  mm SL. In a nutrient-poor river in the Amazon basin, Goulding *et al.* (1988) found that around 100 species (approximately 20% of total species richness) reach maturity at 30 mm, and all dominant species were adults  $\leq 40$  mm. In contrast, in the nutrient rich floodplain of the Solimoes-Amazonas River, juveniles of the medium sized fishes tend to dominate (Goulding *et al.*, 1988). Goulding *et al.* (1988) hypothesize that in nutrient rich systems, the abundance of juveniles of bigger sized fishes would be higher compared with low nutrient systems, where early maturation seems to be a strategy due to competitive exclusion in food limited habitats. Indeed, in Caño Yarina (a nutrient rich system), the four dominant species were adults of medium

sized fishes: *D. longibarbis* (46 to 103 mm), *P. rutiloides* (53 to 204 mm), *T. angulatus* (56 to 150 mm), and *P. amazonica* (54 to 131 mm).

### **Diel Variation in Species Richness, Abundance and Biomass**

Diel changeover in species composition is known to occur in Neotropical fish assemblages (Arrington & Winemiller, 2003). In a study in the Orinoco floodplain, Arrington & Winemiller (2003) found nocturnal samples to be higher in number of species and individual abundances and explained the phenomenon as “morphological trade-offs in foraging and anti-predator defenses”. In Caño Yarina, the differences in species richness and abundance between day and night samples were impressive. In both flooded forest and floating meadows, species richness and abundance were much higher at night samples.

While in flooded forest abundance was much higher at night samples (both early night and late night), in floating meadows abundance was higher at the early night samples but similar at both late night and early day samples species. Moreover, abundance at these time periods was higher than abundance at the early day samples in flooded forest.

Differences in structural complexity between the flooded forest and floating meadows could be the mechanism allowing the higher abundance caught at day samples in floating meadows. The submerged portions of floating meadows are composed of a very dense matrix of stems and roots that may limit the pass of light during the day, whereas flooded forests, despite of having lots of stems and submerged branches, is a more open habitat. Consequently light penetration during the day time could be higher than in floating meadows. Therefore, predation risk at day time could be higher in flooded forests. It has been demonstrated that fishes are able to assess predation risk and

modify their foraging behavior through foraging rate/mortality risk tradeoff mechanisms (Mittelbach, 1981; Werner *et al.*, 1983; Mittelbach, 1984). Therefore predation avoidance behaviors may lead susceptible individuals to limit the use of rich habitats (Werner *et al.*, 1983) as could be happening in flooded forest during the day time, but probably not in floating meadows where a more dense vegetation could reduce the risk of predation. However, the reduced abundance of fish predators in the samples does not provide evidence to support this hypothesis.

The absence of diel change in biomass between habitats, despite of the differences in abundance, leads one to expect that a high amount of small fishes caught during night samples could weight as much as a few large fishes caught in day samples. Indeed, this was observed in flooded forest, where 21 individuals (23% of the total abundance) of 5 species (*Arapaima gigas*, *C. macropomum*, *H. unitaeniatus*, *H. malabaricus*, and *L. pardalis*) accounted for 85% of the total biomass in the day samples. In floating meadows, the trend was more dramatic. Twenty individuals (7% of the total abundance) of five species (*C. macropomum*, *Electrophorus electricus*, *Leporinus trifasciatus*, *L. pardalis*, and *Osteoglossum bicirrhosum*) accounted for 75% of the total biomass in the day samples.

### **Fish Assemblages in Floodplains**

All quantitative analyses of community variables (*i.e.* abundance, biomass, species richness, and body size), without accounting for the species identity, did not provide evidence to separate the ichthyofauna of Caño Yarina in two assemblages. However, multivariate analysis of species abundances (*i.e.*, MRPP and NMS ordination) suggested the presence of two subtly different fish assemblages in flooded forest *vs.* floating meadows. Floating meadows locations were characterized by deeper and more

transparent waters than flooded forest. However, these habitats differ also in many other characteristics such as type of vegetation, structural complexity of the submerged portion of the vegetation, but especially in food resources. These variables are difficult to quantify and therefore it is hard to determine the individual effect on particular fish species. Specific habitat selection has been reported before in floodplain fish communities related to abiotic factors such as type of water (Saint-Paul *et al.*, 2000), oxygen concentration (Junk *et al.*, 1983; Winemiller, 1996), and water depth and transparency (Rodriguez & Lewis, 1994; Tejerina-Garro *et al.*, 1998). In this last case, abundance of visually oriented predators (e.g., characids and cichlids) was positive correlated to water depth and transparency.

In the present study, fish predators were scarce (19 and 4.6 % of the total species richness and abundance, respectively). Species of important predatory families such as Serrasalminidae were very scarce in the samples, indeed only two species were caught, *Serrasalmus rhombeus* and *Pygocentrus nattereri*. Only six juvenile specimens (45 to 76 mm) of *S. rhombeus* and 29 juvenile and adult specimens (63 to 205 mm) of *P. nattereri* were caught, mostly in the floating meadows. Pimelodids, another common family of silurid predators, was only represented by few specimens of *Sorubim lima* (n=3, 168 to 196 mm). Other common predators inhabiting flooded forest such as *Cichla monoculus* (Correa, 1999), were completely absent from the samples. *Hoplias malabaricus*, the most abundant predator species in Caño Yarina (1.4%), was scarcely found, mainly in floating meadows. A partial explanation for the low abundance of some large sized predator fishes is based on the limited efficiency of the gill nest. Surprisingly one individual of *Arapaima gigas* (a sub adult of 600 mm SL) was caught in this study when usually

*A. gigas* are caught with harpoons or nets of mesh sizes bigger than 120 mm. However, it is unlikely that if other predator species, especially medium sized ones, were present in the system not even single individuals of each of those species were caught.

Consequently an alternative explanation could be based on low productivity of the floodplain of Caño Yarina. CPUE in both flooded forest and floating meadows was low; therefore it is possible that low prey abundance could be limiting predators' abundance as predicted by the Lotka-Volterra predation model (Begon *et al.*, 1996). CPUE was low in the present study, but this fact alone does not provide sufficient evidence to support a low productivity hypothesis for Caño Yarina. Another possible explanation for the scarcity of some predator species (*e.g.*, *Cichla monoculus* and Pimelodid species) could be based on over fishing in the area before the reserve was established. At the time this study was conducted, signals of illegal fishermen in the area were observed and indeed some of the gill nets used in this study were stolen.

Variable food resources could also lead to differences in species composition between habitats. In both flooded forests and floating meadows, the majority of the species caught feed on invertebrates (aquatic and/or terrestrial), detritus, or fish. In flooded forest, invertebrate feeders and frugivores were dominant; whereas in floating meadows, invertebrate feeders and detritivores were dominant. These patterns were predicted, based on the differential food availability of flooded forests and floating meadows (seeds, fruits, and periphyton, *vs.* macrophytes, detritus, and autochthonous invertebrates) (Junk, 1997).

Invertebrate feeders were expected to be an important guild in both habitats. Aquatic invertebrates are abundant in floating meadows (Junk, 1997) and terrestrial

invertebrates are an important input of the terrestrial vegetation of the flooded forest (Goulding, 1980). The diversity of invertebrate feeders was high in both habitats but each species (except for *D. longibarbis*) presented a low abundance. It is possible that the ability of gymnotiform fishes to detect gill nets with their electric sense (W.G.R. Crampton, pers. commun.) may undermine the efficiency of gill nets in capturing them. Gymnotiforms are important components of floating meadows ichthyofauna (Crampton, 1996) but only seven species were found in this study, five of them been invertebrate feeders.

Although a frugivore species (*T. angulatus*) was the second most abundant species in flooded forest, the total number of frugivore species found in Caño Yarina was surprising low. Serrasalminae, a sub-family with highly specialized frugivorous fishes (Goulding, 1980), was only represented by few individuals of *Colossoma macropomum*, and *Mylossoma duriventre*. Other frugivores found in flooded forest were *Pterodoras granulosus*, *Auchenipterichthys longimanus*, and *Brycon cephalus* all with low abundances as well (Table 4). The present study was conducted at the end of the high waters season; although fruit phenology of many species in Amazon flooded forests is strongly linked with the flooded season (Kubitzki & Ziburski, 1994), it is possible that the abundance of fruits in the flooded forests around Caño Yarina may have been low during the study period. If that was the case, then frugivore species could have migrated to other areas. However a study of fruit phenology in the area would be necessary in order to make inferences on relationships between fruits production and frugivore fish abundance.

Detritivores was the second most abundant species guild in floating meadows, and was dominated by *P. rutiloides*. Detritivores fish such as curimatids and semaprochilodids gain energy mainly from phytoplankton (algae) present in the water column all over, while siluriform detritivores gain energy from other plant resources (e.g., tree leaves, tree seeds, wood, C<sub>3</sub> macrophytes and periphyton) (Araujo *et al.*, 1986b). This suggests that detritivores catfish would be more abundant in flooded forest than in floating meadows. In Caño Yarina, detritivores catfish were scarce in both habitats; however the abundance was slightly higher in floating meadows. Light penetration is the primary factor limiting algae production especially for sessile periphyton (Putz & Junk, 1997). These authors hypothesized that higher light interception by the canopy of flooded forest would be limiting periphyton growth and that the root bunches of floating meadows could be a more favorable area for periphyton. This mechanism could explain the higher abundance of detritivores found in the floating meadows of Caño Yarina.

### **Sampling Limitations**

Although there are limitations in sampling with gill nets (e.g., selectivity of body size (Jensen, 1986, 1990)), the method seems valid for comparing key assemblage characters between flooded forests and floating meadows habitats in a single floodplain. The use of a wider range of mesh size nets (e.g., 12 to 200 mm used by Saint-Paul *et al.* (2000)) in the future could yield a much more complete picture of the community. In order to increase the amount of research on fish community ecology in flooded forests, it is urgent to develop a reliable, inexpensive sampling technique for fishing in this habitat that can be easily adopted by local researchers. Such a method would yield a big amount

of information of fish assemblages from flooded forest as it has been produced from floating meadows.

### **Conclusion**

In conclusion, the fish assemblages found in the floodplain Caño Yarina were highly similar with subtle differences. Environmental factors explained part of the variation in fish assemblages. However, ecological processes such as competition and predation may also account for the observed variation in composition and abundance of species (*e.g.*, Layman & Winemiller, 2004). The fact that several species were shared between the two habitats suggests movement of species between the flooded forest and the floating meadows of Caño Yarina during the high waters season. The higher number of rare species caught in the flooded forest suggest that unique resources provided by flooded forests may be critical for sustaining populations of species only present in this habitat during the high-waters season.

APPENDIX  
SYSTEMATIC LIST OF SPECIES

Table 5. Systematic list of species organized by order, family, genus and species based on gill netting sampling of the Caño Yarina floodplain, Pacaya Samiria National Reserve (PSNR), during May 2003.

Taxon	Total FF	Total FM
Osteoglossiformes		
Arapaimidae	0	0
<i>Arapaima gigas</i> (Schinz, 1822)	1	0
Osteoglossidae	0	0
<i>Osteoglossum bicirrosom</i> (Cuvier, 1829)	6	7
Characiformes		
Anostomidae (3)		
<i>Leporinus trifasciatus</i> Steindachner, 1876	2	1
<i>Rhytiodus microlepis</i> Kner, 1858	1	4
<i>Schizodon fasciatus</i> Spix & Agassiz, 1829	4	4
Acestrorhynchidae (3)		
<i>Acestrorhynchus falcatus</i> (Bloch, 1794)	1	0
<i>Acestrorhynchus falcirostris</i> (Cuvier, 1819)	7	0
<i>Acestrorhynchus microlepis</i> (Schomburgk, 1841)	1	0
Characidae (17)		
<i>Astyanax bimaculatus</i> (Linnaeus, 1758)	1	2
<i>Brycon cephalus</i> (Gunther, 1869)	1	0
<i>Charax gibbosus</i> (Linnaeus, 1758)	1	2
<i>Colossoma macropomum</i> (Cuvier, 1818)	11	7
<i>Ctenobrycon spilurus</i> (Valenciennes, 1850)	75	25
<i>Cyphocharax cf. festivus</i>	1	0
<i>Gymnocorymbus thayeri</i> Eigenmann, 1908	14	6
<i>Moenkhausia cf. chrysagyrea</i>	2	0
<i>Mylossoma duriventre</i> (Cuvier, 1818)	0	2
<i>Pygocentrus nattereri</i> Kner, 1858	2	27
<i>Roeboides biserialis</i> (Garman, 1890)	1	0
<i>Serrasalmus rhombeus</i> (Linnaeus, 1766)	1	5
<i>Tetragonopterus argenteus</i> Cuvier, 1816	2	0
<i>Tetragonopterus chalceus</i> Spix & Agassiz, 1829	1	0
<i>Triportheus albus</i> Cope, 1872	2	6
<i>Triportheus angulatus</i> (Spix & Agassiz, 1829)	309	48
Curimatidae (8)		
<i>Curimata vittata</i> (Kner, 1858)	4	1
<i>Curimatella alburna</i> (Muller & Troschel, 1844)	20	6
<i>Curimatella meyeri</i> (Steindachner, 1882)	11	18
<i>Potamorhina altamazonica</i> (Cope, 1878)	33	22
<i>Potamorhina latior</i> (Spix & Agassiz, 1829)	3	18

Table 5. Continued

Taxon	Total FF	Total FM
<i>Psectrogaster amazonica</i> Eigenmann & Eigenmann, 1889	49	82
<i>Psectrogaster essequibensis</i> (Gunther, 1864)	9	3
<i>Psectrogaster rutiloides</i> (Kner, 1858)	202	209
Erythrinidae (3)	0	0
<i>Erythrinus erythrinus</i> (Bloch & Steindachner, 1801)	1	1
<i>Hoplerythrinus unitaeniatus</i> (Agassiz, 1829)	11	0
<i>Hoplías malabaricus</i> (Bloch, 1794)	6	32
Gasteropelecidae (1)	0	0
<i>Gasteropelecus sternicla</i> (Linnaeus, 1758)	1	1
Prochilodontidae (1)	0	0
<i>Prochilodus nigricans</i> Agassiz, 1829	9	7
Gymnotiformes		
Apteronotidae (1)		
<i>Adontosternarchus</i> sp. A	1	0
<i>Parapteronotus hasemani</i> (Ellis, 1913)	0	2
Electrophoridae (1)		
<i>Electrophorus electricus</i> (Linnaeus, 1766)	1	1
Gymnotidae (3)		
<i>Gymnotus carapo</i> Linnaeus, 1758	3	1
<i>Gymnotus ucamara</i> Crampton, Lovejoy & Albert, 2003	4	0
<i>Gymnotus varzea</i> Crampton, Thorsen & Albert, 2004	1	0
Sternopygidae (1)		
<i>Eigenmannia limbata</i> (Schreiner & Miranda Ribeiro, 1903)	0	1
Siluriformes		
Auchenipteridae (2)		
<i>Auchenipterichthys longimanus</i> (Gunther, 1864)	2	0
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	15	7
Callichthyidae (7)		
<i>Brochis splendens</i> (Castelnau, 1855)	2	19
<i>Callichthys callichthys</i> (Linnaeus, 1758)	5	1
<i>Dianema longibarbis</i> Cope, 1872	596	436
<i>Hoplosternum littorale</i> (Hancock, 1828)	19	11
<i>Lepthoplosternum</i> sp. PUA (black belly)	0	1
<i>Lepthoplosternum</i> sp. PUB (pepper belly)	1	0
<i>Megalechis thoracata</i> (Valenciennes, 1840)	26	6
Doradidae (5)		
<i>Agamyxis pectinifrons</i> (Cope, 1870)	1	1
<i>Anadoras grypus</i> (Cope, 1872)	9	2
<i>Doradidae</i> sp. PUA	2	3
<i>Doradidae</i> sp. PUB	0	1
<i>Pterodoras granulosus</i> (Valenciennes, 1821)	16	4
Loricariidae (11)		
<i>Ancistrus</i> sp. PUA	2	0
<i>Glyptoperichthys scrophus</i> (Cope, 1874)	1	0
<i>Hypoptopoma gulare</i> Cope, 1878	2	10
<i>Liposarcus pardalis</i> (Castelnau, 1855)	19	24
<i>Loricariichthys</i> cf. <i>acutus</i>	3	6

Table 5. Continued

Taxon	Total FF	Total FM
<i>Loricariichthys</i> cf. <i>maculatus</i>	7	3
<i>Loricariichthys</i> cf. <i>nudirostris</i>	2	5
<i>Loricariichthys</i> sp.1	3	2
<i>Loricariichthys</i> sp.2 (may be <i>L. maculatus</i> juvenile)	3	27
<i>Loricariinae</i> sp. Indeterminate TF03	1	0
<i>Pseudorinelepis genibarbis</i> (Valenciennes, 1840)	2	3
Pimelodidae (2)	0	0
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	1	2
<i>Sorubim lima</i> (Bloch & Schneider, 1801)	1	2
Perciformes		
Cichlidae (6)	0	0
<i>Cichlasoma amazonarum</i> Kullander, 1983	7	30
<i>Crenicichla proteus</i> Cope, 1872	1	18
<i>Heros appendiculatus</i> Heckel, 1840	1	1
<i>Hypselacara temporalis</i> (Gunther, 1862)	3	0
<i>Mesonauta mirificus</i> Kullander & Silfvergrip 1991	4	30
<i>Satanoperca jurupari</i> (Heckel, 1840)	5	4
Symbranchiformes		
Synbranchidae (1)		
<i>Synbranchus marmoratus</i> Bloch, 1795	1	0
Total number of individuals	1579	1210

Family followed by number of species in parenthesis. Total abundance for FF-flooded forest and FM-floating meadows is provided. Taxonomic nomenclature and authorities follows Reis *et al.* (2003)

## LIST OF REFERENCES

- Agudelo, E. (1994). Aspectos biológicos, composición y esfuerzo de las capturas de peces comerciales en el bajo Río Caquetá, (Amazonía Colombiana). Tesis Biología. Universidad del Valle, Cali. 129 p.
- Almeida, O.T., McGrath D.G., and Ruffino M.L. (2001). The commercial fisheries of the lower Amazon: an economic analysis. *Fisheries Management and Ecology* 8(3): 253-269.
- Anonymous (1981). Cultivo de peces tropicales en Pucalpa. Instituto Veterinario de Investigaciones Tropicales y de Altura, Convenio Universidad Nacional Mayor de San Marcos. Iquitos, Loreto, Organismo de Desarrollo de Loreto (Ivita-Crior).
- Araujo-Lima, C.A.R.M., Forsberg B., Victoria R., and Martinelli L. (1986a). Energy sources for detritivorous fishes in the Amazon. *Science* 234: 1256-1258.
- Araujo-Lima, C.A.R.M. and Oliveira E.C. (1998). Transport of larval fish in the Amazon. *J. Fish Biol.* 53: 297-306.
- Araujo-Lima, C.A.R.M., Portugal L.P.S., and Ferreira E.G. (1986b). Fish-macrophyte relationships in the Anavilhanas archipelago, a black water system in Central Amazonia. *J. Fish Biol.* 29: 1-11.
- Araujo-Lima, C.A.R.M., Savastano D., and Jordão L.C. (1994). Drift of *Colomesus asellus* (Teleostei: Tetraodontidae) larvae in the Amazon River. *Revue de Hydrobiologie Tropical* 27: 33-38.
- Arboleda, A.L. (1988). Determinación de las tallas de madurez para seis especies de bagres del Río Caquetá. *UB JTL-Bol. Fac. Biol. Mar.* 8: 3-7 p.
- Arrington, D.A. and Winemiller K.O. (2003). Diel changeover in sandbank fish assemblages in a Neotropical floodplain river. *J. Fish Biol.* 63(2): 442-459.
- Barthem, R. and Goulding M. (1997). *The Catfish Connection: Ecology, Migration and Conservation of Amazon Predators*. New York, Columbia University Press.
- Bayley, P.B. (1983). Central Amazon fish populations: biomass, production and some dynamic characteristics. Ph.D. Thesis, Dalhousie University, Halifax, Canada

- Bayley, P.B. (1989). Aquatic environments in the Amazon basin, with an analysis of carbon sources, fish production and yield, *In*: Dodge, D.P. (ed). Proceedings of the international large river symposium. Spec. Publ. Can. J. Fish. Aquat. Sci. 106: 399-408.
- Bayley, P.B. (1995). Sustainability in tropical inland fisheries: the manager's dilemma and a proposed solution. Defining and measuring sustainability: the biogeographical foundations. M. Munasinghe and W. Shearer. Washington D.C., The World Bank.
- Bayley, P.B. (1996). Status of fisheries, fisheries information, and management options in the Marmirauá Reserve for Sustainable Development (ODA Consultancy Report). London, ODA.
- Bayley, P.B. and Petreire M. (1989). Amazon fisheries: assessment methods, current status and management options. Spec. Publ. Can. J. Fish. Aquat. Sci. 106: 385-398.
- Bayley, P.B., Vázquez F., Ghersi P., Soini P., and Pinedo M. (1992). Environmental review of the Pacaya-Samiria National Reserve in Peru and assessment of project (527-0341). Report to the Nature Conservancy. Washington DC. July 1992.
- Begon, M., Harper J.L., and Townsend C.R. (1996). Ecology. Individuals, Populations and Communities. Liverpool, Blackwell Science.
- Benedito-Cecilio, E., Araujo-Lima C.A.R.M., Forsberg B.R., Bittencourt M.M., and Martinelli, L.C. (2000). Carbon sources of Amazonian fisheries. Fisheries Management and Ecology 7(4): 305-314.
- Boujard, T., Pascal M., Meunier J.F., and Le Bail P.Y. (1997). Poissons de Guyane. Guide écologique de l'Approuague et de la Réserve des Nouragues. Paris, Institut National de la Recherche Agronomique.
- Burgess, W.E. (1989). An Atlas of Freshwater and Marine Catfishes: a Preliminary Survey of the Siluriformes. Neptune City, New Jersey, T.F.H. Publications.
- Cala, P., González E., and Varona M. P. (1996). Aspectos biológicos y taxonómicos del tucunare, *Cichla monoculus* (Pisces:Cichlidae). Dahlia 1: 23-37 p.
- Carvalho de Lima, A. and Araujo-Lima C.A.R.M. (2004). The distributions of larval and juvenile fishes in Amazonian rivers of different nutrient status. Freshwater Biology 49(6): 787-800.
- Celis, J. (1994). Aspectos sobre la biología pesquera del dorado (*Brachyplatystoma flavicans*, Castelnau, 1985) Pisces: Pimelodidae en el bajo Río Caquetá, Amazonía Colombiana. Facultad de Ciencias. B.Sc. Thesis, Universidad del Valle, Cali, Colombia.

- Clarke, K.R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18(1): 117-143.
- Correa, S.B. (1999). Estudio ecológico preliminar de asociaciones de peces en el Lago Taraira, Amazonía Colombiana. Facultad de Ciencias. B.Sc. Thesis, Universidad del Valle, Cali, Colombia.
- Crampton, W.G.R. (1996). Gymnotiform fish: an important component of Amazonian flood plain fish communities. *J. Fish Biol.* 48: 298-301.
- Crampton, W.G.R., Castello L., and Viana J.P. (2004). Fisheries in the Amazon Várzea: Historical trends, current status, and factors affecting sustainability. Pp. 76-98. *In: People and Nature: K. Silvinus, R. Bodmer, and J. Fragoso (eds.) Wildlife Conservation in South and Central America.* New York, Columbia University Press.
- Crampton, W.G.R., Lovejoy N.R., and Albert J.S. (2003). *Gymnotus ucamara*: a new species of Neotropical electric fish from the Peruvian Amazon (Ostariophysi: Gymnotidae), with notes on ecology and electric organ discharges. *Zootaxa* 277: 1-18.
- Forsberg, B.R., Araujo-Lima C.A.R.M., Martinelli L.A., Victoria R.L., and Bonassi J.A. (1993). Autotrophic Carbon-Sources for Fish of the Central Amazon. *Ecology* 74(3): 643-652.
- Gopal, B. and Junk, W.J. (2000) Biodiversity in Wetlands: an Introduction. Pp. 1-10. *In: B. Gopal, W.J. Junk, and J.A. Davis (eds), Biodiversity in Wetlands: Assessment, Function and Conservation.* Volume 1, Leiden, Backhuys Publishers.
- Goulding, M. (1980). *The Fishes and the Forest: Explorations in the Amazonian Natural History*, Berkeley, University of California Press.
- Goulding, M. (1981). Man and Fisheries on an Amazon Frontier. *In: H.J. Dumont (ed.). Developments in Hydrobiology*, v. 4. The Hague, Dr. W. Junk Publishers.
- Goulding, M. and Carvalho M.L. (1982) Life history and management of the tambaqui (*Colossoma macropomum*, Characidae): an important Amazonian food fish. *Rev. Bras. Zool.* S. Paulo 1: 107-133.
- Goulding, M., Carvalho M.L., and Ferreira E.G. (1988). *Rio Negro, Rich Life in Poor Water.* The Hague, SPB Academic Publishing.
- Goulding, M., Barthem R., and Ferreira E. (2003). *The Smithsonian Atlas of the Amazon.* Smithsonian Institution. Hong Kong, Oakwood Arts.
- Groombridge, B. and Jenkins M. (Ed) (1998) *Freshwater Biodiversity: A Preliminary Global Assessment.* WCMC Biodiversity Series 8, World Conservation Press.

- Heltsh, J.F. and Forrester N.E. (1983). Estimating species richness using the jackknife procedure. *Biometrics* 39: 1-11.
- Henderson, P.A. and Crampton W.G.R. (1997) A comparison of fish diversity and abundance between nutrient-rich and nutrient-poor lakes in the Upper Amazon. *J. Trop. Ecol.* 13: 175-198.
- Henderson, P.A. and Hamilton H.F. (1995) Standing crop and distribution of fish drifting and attached floating meadow within an Upper Amazonian várzea lake. *J. Fish Biol.* 47: 266-276.
- Henderson, P.A., Hamilton W.D., and Crampton W.G.R. (1998). Evolution and diversity in Amazonian floodplain communities. Pp. 385-419. *In:* D.M. Newbery, H.H.T. Prins, and N.D. Brown (Eds). *Dynamics of Tropical Communities*. Oxford, Blackwell Science.
- Henderson, P.A. and Robertson B.A. (1999). On structural complexity and fish diversity in an Amazonian floodplain. Pp. 45-58. *In:* C. Padoch, J.M. Ayres, M. Pinedo-Vasquez, and A. Henderson (Eds). *Várzea: Diversity, Development and Conservation of Amazonia's Whitewater Floodplains*. New York, New York Botanical Garden Press
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. New Jersey, Princeton University Press.
- Hurtado, J. (1999). Consideraciones biológico-pesquera de *Arapaima gigas* en el sistema de várzea (Lagos de Tarapoto y el Correo) Municipio de Puerto Nariño. Amazonía-Colombiana. Facultad de Ciencias, B.Sc. Thesis, Universidad del Valle, Cali, Colombia.
- INRENA (2000). Plan Maestro para la conservación de la diversidad biológica y el desarrollo sostenible de la Reserva Nacional Pacaya-Samiria y su zona de amortiguamiento. Iquitos, Instituto Nacional de Recursos Naturales.
- Jensen, J.W. (1990). Comparing fish catches taken with gill nets of different combination of mesh sizes. *J. Fish Biol.* 37: 99-104.
- Junk, J. (1984). Ecology, Fisheries and Fish culture in Amazonia. Pp. 443-476. *In:* H. Sioli (ed) *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and its Basin*. Dordrecht, Dr. W. Junk Publishers.
- Junk, W.J. (1997) General Aspects of Floodplain Ecology with Special Reference to Amazonian Floodplains. Pp. 3-20. *In:* W.J. Junk (ed) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Ecological studies Vol. 126, Berlin, Springer.

- Junk, W.J. and Howard-Williams, C. (1984). Ecology of Aquatic Macrophytes in the Amazonia. Pp. 269-293. *In*: H. Sioli (ed) The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dordrecht, Dr. W. Junk Publishers.
- Junk, W.J., Soares M.G.M., and Carvalho F.M. (1983). Distribution of fish species in a lake of the Amazon River floodplain near Manaus (Lago Camaleão) with special reference to extreme oxygen conditions. *Amazoniana* 7(4): 397-431.
- Junk, W.J., Soares M.G.M., and Saint-Paul U. (1997) The Fish. Pp 385-408. *In*: W.J. Junk (ed) The Central Amazon Floodplain: Ecology of a Pulsing System. Ecological studies Vol. 126, Berlin, Springer.
- Keith, P., Le Bail O.-Y., and Planquette P. (2000). Atlas des Poissons d' Eau Douce de Guyane (tome 2, fascicule I). Paris, Publications scientifiques du M.N.H.N.
- Kruskal, J.B. (1964). Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.
- Kubitzki, K. (1989). The Ecogeographical differentiation of Amazonian inundation forests. *Plant Syst. Evol.* 162(1-4): 285-304.
- Kubitzki, K. and Ziburski A. (1994). Seed Dispersal in Flood-Plain Forests of Amazonia. *Biotropica* 26(1): 30-43.
- Kullander, S.O. (1986). The Cichlid Fishes of the Amazon River Drainage of Peru. Stockholm, Swedish Museum of Natural History.
- Layman, C.A. and Winemiller K.O. (2004). Size-based responses of prey to piscivore exclusion in a species-rich neotropical river. *Ecology* 85(5): 1311-1320.
- Le Bail, P.-Y., Keith P., and Planquette P. (2000). Atlas des Poissons d' Eau Douce de Guyane (tome 2, fascicule II). Paris, Publications scientifiques du M.N.H.N.
- Leenheer, J.A. (1980). Origin and nature of humic substances in the waters of the Amazon River. *Acta Amazonica* 10(3): 513-526.
- Leite, R. G., Araujo-Lima C.A.R.M., Victoria R.L., and Martinelli, L. A. (2002). Stable isotope analysis of energy sources for larvae of eight fish species from the Amazon floodplain. *Ecology of Freshwater Fish* 11(1): 56-63.
- Magurran, A. E. and Henderson P. A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature* 422(6933): 714-716.
- Manheimer, S., Bevilacqua G., Camaraschi E.P., and Rubio F.S. (2003). Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. *J. Trop. Ecol.* 19: 215-218.

- Mather, P.M. (1976). *Computational Methods of Multivariate Analysis in Physical Geography*. London, J. Wiley & Sons.
- McCune, B. and Grace J.B. (2002). *Analysis of Ecological Communities*. MjM Software. Gleneden Beach.
- McCune, B. and Mefford M.J. (1999). *PC-ORD. Multivariate Analysis of Ecological Data*. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.
- McCune, B., Rosentreter R., Ponzetti J.M., and Shaw D.C. (2000). Epiphyte habitats in an old conifer forest in western Washington, U.S.A. *The Briologist* 103(3): 417-427.
- Merona, B. de (1990). Amazon fisheries: general characteristics based on two case studies. *Interciencia* 15: 461-468.
- Mielke, P.W. Jr. (1984). Meteorological Applications of Permutation Techniques Based on Distance Functions. Pp. 813-830. *In*: P.R. Krishnaiah and P.K. Sen (Eds) *Handbook of Statistics*, Vol. 4. Elsevier Science Publishers.
- Mills, D. and Vevers G. (1989). *The Tetra Encyclopedia of Freshwater Tropical Aquarium Fishes*. New Jersey, Tetra Press.
- Mittelbach, G.G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62(5): 1370-1386
- Mittelbach, G.G. (1984). Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* 65(2): 499-513
- Mol, J.H. (1995). Ontogenetic diet shifts and diet overlap among three closely related Neotropical armored catfishes. *J. Fish Biol.* 47: 788-807.
- Palmer, M.W. (1990). The estimation of species richness by extrapolation. *Ecology* 72: 1512-1513.
- Palmer, M.W. (1991). Estimating species richness: the second-order Jackknife reconsidered. *Ecology* 72: 1512-1513.
- Peterson, E.B. and McCune B. (2001). Diversity and succession of epiphytic macro-lichen communities in low-elevation managed conifer forest in western Oregon. *Journal of Vegetation Science* 12: 511-524.
- Petry, P., Bayley P.B., and Markle D.F. (2003). Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *J. Fish Biol.* 63(3): 547-579.
- Pianka, E.R. (1970). On r- and K- selection. *Am. Nat.* 100: 592-597.

- Planquette, P., Keith P., and Le Bail P.-Y. (1996). Atlas des Poissons d' Eau Douce de Guyane (tome 1). Collection du Patrimoine Naturel, vol. 22. Paris, IEGB-M.N.H.N., INRA, CSP, Min. Env.
- Prance, G.T. (1979). Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 31:26-38.
- Prance, G.T. (1980). A terminologia dos tipos de florestas amazonicas sujeitas a inundação. *Acta Amazonica* 10(3): 495-504.
- Putz R. and Junk, W. (1997). Phytoplankton and primary production Pp. 207-222. *In:* W.J. Junk (ed) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Ecological studies Vol. 126, Berlin, Springer.
- Reis, R.E., Kullander S.O., and Ferraris C.J. Jr. Eds. (2003). Check List of the Freshwater Fishes of South and Central America (CLOFFSCA). Porto Alegre, Brazil, Edipucrs.
- Riehl, R. and Baensch H.A. (1991). *Aquarien Atlas*. Band. 1. Melle: Mergus, Verlag für Natur- und Heimtierkunde, Germany.
- Rodriguez, C.A. (1991). Bagre Malleros y Cuerderos en el Bajo Río Caquetá. Tropenbos, Colombia.
- Rodriguez, M.A. and Lewis J.W.M. (1997). Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecol. Monogr.* 67(1): 109-128.
- Saint-Paul, U. and Bayley P. (1979). A situação da pesca na Amazonia Central. *Acta Amazonica* 9: 109-114.
- Saint-Paul, U., Zuanon J., Villacorta M.A., Garcia M., Fabr e N.N., Berger U., and Junk W.J. (2000) Fish communities in central Amazonian white- and blackwater floodplains. *Env. Biol. Fish.* 57: 235-250
- Sanch ez-Botero, J. I. and Araujo- Lima C. A. R. M. (2001). As macr ofitas aqu ticas como berc rio para a ictiofauna da v rzea do rio Amazonas. *Acta Amazonica* 31: 437-447.
- Sazima, I. and Machado F.A. (1990). Underwater observations of piranhas in western Brazil. *Env. Biol. Fish.* 28: 17-31.
- Silvano, R.A.M., Oyakawa O.T., do Amaral B.D., and Begossi A. (2001). Peixes do Alto Rio Juru  (Amazonas, Brasil). Editora da Universidade de S o Paulo, Brazil.

- Sioli, H. (1984). The Amazon and its Main Affluents: Hydrography, Morphology of the River Courses, and River Types. Pp. 127-165. *In*: H. Sioli (ed) The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dordrecht, Dr. W. Junk Publishers.
- Soares, M.G.M., Almeida R.G., and Junk W. (1986). The trophic status of the fish fauna in Lago Camaleao, a macrophyte dominated floodplain lake in the middle Amazon. *Amazoniana* 9(4): 511-526.
- Stawikowski, R. and Werner U. (1998). Die Buntbarsche Amerikas, Band 1. Stuttgart, Germany, Verlag Eugen Ulmer.
- Tejerina-Garro, F.L., Rejean F., and Rodríguez M.A. (1998). Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon basin. *Env. Biol. Fish.* 51: 399-410.
- Val, A.L. and de Almeida-Val V.M.F. (1995). Fishes of the Amazon and their Environment: Physiological and Biochemical Aspect. Berlin, Springer-Verlag.
- Val, A.L., Schwantes A. R., and de Almeida Val V.M.F. (1986). Biological aspects of Amazonian fishes. VI. Hemoglobins and whole blood properties of *Semaprochilodus* species (Prochilodontidae) at two phases of migration. *Comp. Biochem. Physiol.* 83 B: 659 - 667.
- Vazzoler, A.E.A.M. and Menezes, N.A. (1992). Reproductive behaviour of South America Characiformes (Teleostei, Ostariophysi): a review. *Rev. Bras. Biol.* 52: 627-640.
- Werner E.E., Gilliam J.F., Hall D.J., and Mittelbach G.G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64(6):1540-1448.
- Winemiller, K.O. (1989). Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan Llanos. *Env. Biol. Fish.* 26: 177-199.
- Winemiller, K.O. (1996). Dynamic diversity in fish assemblages of tropical rivers. Pp. 99-132. *In*: Cody M.L. & Smallwood J.A. (eds.), Long-term Studies of Vertebrate Communities, Orlando, Academic Press.
- Yossa, M.I. and Araujo-Lima C.A.R.M. (1998). Detritivory in two Amazonian fish species. *J. Fish Biol.* 52: 1141-1153.

## BIOGRAPHICAL SKETCH

Sandra Bibiana Correa was born on November 11<sup>th</sup>, 1974, in Popayán, Cauca, Colombia. She is one of two children of Jose Alvaro Correa and Rosalba Valencia. She followed her passion for marine life and enrolled at the Universidad del Valle, where she earned her bachelor's degree in biology with emphasis in marine biology. During the course of her career she found an opportunity to do research in Amazon fish ecology. Since then, she has devoted her studies to fish communities in different Amazonian locations. After graduating, she worked for several organizations to gain experience in tropical forest ecology. In 2002 she was accepted into the graduate program at the Department of Zoology at the University of Florida where was awarded a Master of Science degree in May 2005. She is still exploring and enjoying the magic of Amazonian ecosystems.