

A comparison of flooded forest and floating meadow fish assemblages in an upper Amazon floodplain

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Matched sets of gillnets of different mesh-sizes were used to evaluate the degree to which contiguous and connected flooded forest and floating meadow habitats are characterized by distinct fish faunas during the flooding season in the Peruvian Amazon. For fishes between 38–740 mm standard length (L_S) (the size range captured by the gear), an overriding pattern of faunal similarity emerged between these two habitats. The mean species richness, diversity, abundance, fish mass, mean and maximum L_S , and maximum mass did not differ significantly between flooded forest and floating meadows. Species abundances followed a log-normal distribution in which three species accounted for 60–70% of the total abundance in each habitat. Despite these similarities, multivariate analyses demonstrated subtle differences in species composition between flooded forest and adjacent floating macrophytes. In addition, the absolute number of species was higher in flooded forest, reflecting a higher percentage of rare species. The day–night species turnover was found to be greater in flooded forests than floating meadows. Further, nocturnal samples had higher abundances and greater species richness than diurnal samples in both habitats. Differences in habitat structural complexity between flooded forest and floating meadows may result in a higher abundance and species richness of day-active species in floating meadows.

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INTRODUCTION

In tropical floodplains, forests and savannas become flooded over large areas during the flooding season, producing enormous areas of seasonally available habitat for fishes. The annual cycle of flood disturbance is predictable in that

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it occurs annually or biannually, and at more or less the same time of the year. The onset of flooding and its magnitude and duration, however, vary regionally (Lowe-McConnell, 1987; Goulding *et al.*, 2003). The new habitat created by flooding and the movement of fishes into flooded habitat causes a dynamic seasonal rearrangement of fish communities. Clearly, regional species pools should influence local assemblage structure in the flooded habitats as well as the colonization dynamics following flooding (Arrington & Winemiller, 2006). Local assemblage structure is also influenced by biotic interactions such as predation (Rodriguez & Lewis, 1997; Layman & Winemiller, 2004) and competition (Jackson *et al.*, 2001) and physicochemical characters, such as dissolved oxygen (Junk *et al.*, 1983), transparency and water depth (Rodriguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998), water chemistry (Henderson & Crampton, 1997; Saint-Paul *et al.*, 2000) and structural complexity (Arrington *et al.*, 2005; Arrington & Winemiller, 2006). The continuity of habitats during the flooding season and the dramatic movement of fishes to and from flooded areas suggest a high level of interaction and mixing among floodplain habitats; yet, the unique elements of various habitats within the floodplain (*e.g.* inundated forest *v.* savannah) may foster diverse assemblages. In this study, a quantitative comparison of fish assemblage structure from flooded forests and floating meadows in the Peruvian Amazon is presented to evaluate the degree to which these contiguous, connected habitats are characterized by unique faunas during the flooding season.

The Amazon Basin is estimated to cover an area of *c.* 6.8 million km² (Goulding *et al.*, 2003). Within this system, floodplains that undergo an annual inundation regime are estimated to cover *c.* 570 000 km² (Goulding *et al.*, 2003). Amazonian floodplain habitats are highly connected during the high water period, and fishes are able to disperse within a mosaic of floating meadows (patches of aquatic macrophytes), flooded forests and main river channels. These habitats have different environmental characteristics and resources despite the high connectivity. Flooded forests are the source of a wide variety of allochthonous food resources, such as terrestrial herbaceous plants, leaves, flowers, seeds and fruits, periphyton and terrestrial invertebrates (Goulding, 1980), whereas floating meadows contain mostly autochthonous food resources, *e.g.* aquatic herbaceous plants, detritus and aquatic invertebrates (Junk *et al.*, 1997). Both habitat types have high structural complexity that provides shelter for fishes (*e.g.* submerged branches and roots), and the root mass of floating meadows is known to act as a nursery habitat for juveniles of many species (Saint-Paul & Bayley, 1979; Junk, 1984; Sánchez-Botero & Araujo-Lima, 2001; Carvalho de Lima & Araujo-Lima, 2004).

How fish species partition resources and microhabitats in the Amazonian floodplain is not well understood. Studies have tended to focus on specific habitat types within the floodplain, in particular floating meadows because these can be sampled using quantitative procedures (Araujo-Lima *et al.*, 1986; Henderson & Hamilton, 1995; Henderson & Crampton, 1997; Petry *et al.*, 2003). Studies of flooded forest communities are much more limited, mainly because of sampling difficulties, but have shown important associations between the fishes and forest resources (Goulding, 1980; Saint-Paul *et al.*, 2000). There are migrations of adults of many species moving directly between the river channel and

floodplain, and highly diverse communities have been documented (Goulding, 1980; Goulding *et al.*, 1988; Saint-Paul *et al.*, 2000).

The objective of this study was to provide the first direct quantitative comparison of fish assemblage structure from flooded forests and floating meadows from an upper Amazon floodplain. It evaluated the degree to which assemblage composition differs between habitats with dramatically different structural characters (trees and branches *v.* root systems), feeding resources (allochthonous *v.* autochthonous) and other environmental characters, and considered the relative importance of these habitats to patterns of richness and diversity within the floodplain ecosystem.

MATERIALS AND METHODS

STUDY AREA

This study was conducted in the Caño (C.) Yarina, a small tributary (*c.* 100 m wide) of the Rio Pacaya in the Pacaya Samiria National Reserve (PSNR). This reserve is located at the confluence of the whitewater Marañon and Ucayali Rivers, in the Peruvian Amazon. Crampton *et al.* (2003) provide a map of the study site. The PSNR lies within the Ucamara Depression, a deposit of marine and continental sediments dating from the late Tertiary to the present (P. B. Bayley, F. Vázquez, P. Ghersi, P. Soini & M. Pinedo, unpubl. data). This area is inundated most of the year, with a short low water season from July to September (INRENA, 2000). In the PSNR, open water (rivers, drainage channels and lakes) constitute *c.* 1% of land area, whereas flooded forests constitute 85% (P. B. Bayley, F. Vázquez, P. Ghersi, P. Soini & M. Pinedo, unpubl. data). Approximately 40% of the open water is covered by rafts of floating macrophytes ('floating meadows') growing along the margins of lakes and channels (INRENA, 2000). Hence, within the PSNR, the area covered by flooded forest is *c.* 200 times [$85 / (1 \times 0.4)$] larger than the area occupied by floating meadows.

Physicochemical properties of the water in the Rio Pacaya and C. Yarina resemble that of other upper whitewater Amazonian floodplains (Henderson *et al.*, 1998). Conductivity varies from 100 to 200 $\mu\text{S cm}^{-1}$ and pH from 6.7 to 7.1. Dissolved oxygen is uniformly low during the flooding season (0–0.5 mg l^{-1}), except during the day within vegetation, and is usually relatively high during the low water season (1–4 mg l^{-1}). During the flood period, the waters are stained dark with vegetable matter, with transparency measured by Secchi disk having a mean \pm s.d. of 1.4 ± 0.4 m (range = 0.8–2.2 m) in flooded forest and 2.3 ± 0.7 m (range = 1.5–2.8 m) in the floating meadows. Mean \pm s.d. depth was 1.5 ± 0.6 m (range = 0.6–2.5 m) in the sampling sites in the flooded forest which grows on levees and 3.8 ± 0.7 m (range = 2.5–6.5 m) in the floating meadows, which grow on channel and lake surfaces.

Floating meadows in the study area are comprised of a mixture of plant species, primarily *Polygonium* sp., *Pistia stratiotes* (L.), *Eichhornia crassipes* Solms, *Paspalum* sp. and an unidentified legume species. Other plants include *Azolla* sp., *Neptunia* sp., *Ludvigia* sp., *Salvinia* sp., *Utricularia* sp. and *Echinochloeta* sp. Low-lying interlevees and the shallower margins of levees bordering the channel of C. Yarina support patches of 'pioneer' trees such as *Sena* sp., *Bactris* sp. and *Cecropia* sp. Mature seasonally flooded forest dominated by trees of 15–25 m tall grows on the levees.

DATA COLLECTION

Sampling was conducted over 10 consecutive days during the late flooding season (May, 2003). This time of year was selected because both habitat types (flooded forest and floating meadows) have been flooded and connected for several months, so fishes have opportunities for selection of these alternative habitat types. A systematic

sampling regime was used, which is useful for large heterogeneous areas and reduces clumping with smaller samples. Ten sites were sampled upstream and downstream from the second ranger headquarters of PSNR (5°20'57.5" S; 74°30'11.7" W). Sampling sites were situated along the main canal of C. Yarina, within two lakes, and along the canals that connected C. Yarina with those lakes. Sites were selected where patches of floating meadows were contiguous to flooded forests. Sites were 1 km apart, with the exception of sites 7 and 9 that were within 1 km of each other inside one of the lakes (Cocha Sapote). To account for variability within sites, cluster sampling was conducted deploying three sets of four gillnets (20 × 3.5–5.0 m) of different mesh-sizes (25, 40, 80 and 120 mm) at each site, with each set no further than 100 m apart. The total area of gillnet used per site, in each habitat, was 1000.23 m². In the flooded forest, the nets were located perpendicular to the shoreline, parallel to each other and with the largest mesh placed upstream [although currents were weak (<0.02 m s⁻¹)]. In patches of floating meadows, nets were positioned around the patch, along the edge with the open water and along natural canals running inside the patch. When a canal was not present, one was opened with a machete, from the canoe. The order of mesh-sizes was randomly assigned in order to locate every mesh-size at different positions along the patch of meadows (e.g. along the edge or inside the patch), and therefore to account for the different selectivity of each mesh-size. At each site, fishing was conducted for a period of 18 h from 1800 hours to the following noon (1200 hours) at each site, with nets checked every 6 h. The nets captured a broad size range of fishes between 38 and 740 mm *L_S*, though it is likely that they did not capture some very small species that may inhabit the area or larger individuals of large-bodied fishes. Specimens were euthanized by anaesthetic overdose in a 0.4 mg l⁻¹ solution of 2-phenoxyethanol, identified to species, and *L_S*, mass (*M*), time at capture and mesh-size were recorded. Vouchers of each species were deposited at the Florida Museum of Natural History.

DATA ANALYSES

Assemblage characteristics were calculated per sampling site within each habitat; *i.e.* all fishes within the three sets of gillnets at each site were combined to produce site-specific values, with a sample size of 10 sites per major habitat type (flooded forest and floating meadows). Simpson's diversity index (Simpson, 1949), which describes the probability that two individuals drawn from a population belong to different species, and evenness (Hill, 1973) were calculated for each habitat. *t*-tests were conducted to test for differences in mean species richness (total number of species), diversity and evenness between flooded forest and floating meadow habitats. Species accumulation curves for each habitat were constructed based on number of species caught per site. Total species per habitat was estimated with a first and second order jackknife estimator (Heltshe & Forrester, 1983). Jackknife estimators are non-parametric resampling methods that can be used to estimate species richness derived from the number of species present in only one quadrant (first order) and the number of species present in exactly two quadrants (second order) (Heltshe & Forrester, 1983; Palmer, 1990). *t*-tests were used to test for between-habitat differences in abundance (total number of individuals), fish biomass (total mass of fishes captured), mean *L_S*, maximum *L_S*, mean *M* and maximum *M* of fishes. To compare the distribution of species abundance between flooded forest and floating meadows, all species in each habitat were ranked based on their abundance, and the ranks were plotted against number of individuals. The mean abundance of the 10 most common species was compared between flooded forest and floating meadow habitats using the non-parametric Mann–Whitney *U*-test.

The relative biomass captured per habitat was estimated by summing the total fish mass obtained in each site and expressing this value per total gillnet area (1000.23 m² per site). Body size distributions of fishes from flooded forest and floating meadows were compared using the Kolmogorov–Smirnov test for frequency distributions.

Diel variation was analysed with repeated measures ANOVA to test for effects of time of day, habitat and their interaction on abundance, fish mass and richness (log₁₀-transformed). Within-habitat contrasts were performed separately for each habitat

type to evaluate differences between specific sampling periods. A χ^2 test of independence was used to test the null hypothesis that the number of species caught per habitat is independent of the corresponding sampling period. A 3×2 contingency table of time v. habitat was analysed with three levels for time: species caught only at diurnal samples, species caught only at nocturnal samples (both early night and late night) and species caught at both diurnal and nocturnal samples. Additionally, a 2×2 contingency table was analysed with two levels of time (species caught only at nocturnal samples and species caught both at diurnal and nocturnal samples) and two levels of habitat. For the five most abundant species, 2×2 contingency tables were used to test the null hypothesis that number of individuals per habitat is independent of sampling time, with two levels of time (number of species caught only at nocturnal samples and species caught both at diurnal and nocturnal samples) and two levels of habitat.

In order to evaluate differences in species composition between habitats, non-metric multi-response permutation procedure (MRPP) and the indicator species analysis (ISA) were performed on a matrix of species abundance per site. Prior to the analyses, the 21 species that were present in only one site (5% of the sampling units) were deleted from the dataset as suggested by McCune & Grace (2002), and the resultant matrix was transformed [$y' = \log_{10}(y + 1)$] in order to reduce the variance and skewness of species abundance distributions. One site was identified as an outlier (*i.e.* site 5 of floating meadows; s.d. > 2; McCune & Grace, 2002), and it was deleted from the analysis. One additional site with extremely low capture (*i.e.* site 5 of flooded forest; s.d. = 1.77) was removed based on the fact that samples from this site, as well as the previous outlier site, were impacted by piranhas eating the catch, which reduced species richness and abundance. Three additional species were deleted from the matrix because they were present in only one site after removal of the two aforementioned sites.

The resulting matrix of 57 species and 18 sites of flooded forest and floating meadows was analysed with a MRPP. The MRPP (Mielke, 1984) is a non-parametric multivariate procedure to test for differences between *a priori* defined groups (*e.g.* habitats), and in this study it was used to test the null hypothesis of no difference in species composition between the two habitats. MRPP provides a measure of 'effect size' called *A* (ranging from 0 to 1), which describes within-group homogeneity, compared with the random (null) expectation. Indicator species analysis (ISA; Dufrêne & Legendre, 1997) is a method for identifying indicator species associated with different habitat types. This test is suggested to be used as a complement to MRPP to help describe how well each species separates among groups, in this case habitat types (McCune & Grace, 2002). ISA calculates an indicator value for each species in each group ranging from 0 (no indication) to 100 (perfect indication: always present in and exclusive of a group) and the highest indicator value ($I_{V_{max}}$) for a given species across groups is considered the indicator value for that species. The significance of indicator values was evaluated through a Monte-Carlo test (1000 permutations), which randomly reassigns sites to habitats 1000 times, calculating $I_{V_{max}}$ each time for each species. Species with significant indicator values ($P < 0.05$) are those which $I_{V_{max}}$ is higher than expected by chance (McCune & Grace, 2002). Statistical analyses were conducted using the software Species Diversity & Richness 3 (Henderson & Seaby, 2002), Statistica (Version 6.0, StatSoft, Tulsa, OK, U.S.A.), JPM (Version 5, SAS Institute Inc., Cary, NC, U.S.A.) and PC-ORD (McCune & Mefford, 1999).

RESULTS

SPECIES RICHNESS AND ABUNDANCE

A total of 2701 individuals representing six orders, 20 families, 61 genera and 80 species of fishes were collected (Table I). Characiformes (36 species) was the most diverse taxon followed by Siluriformes (27 species), Perciformes (seven cichlid species), Gymnotiformes (seven species), Osteoglossiformes (two species) and Synbranchiformes (one species). Characiformes and Siluriformes accounted

TABLE I. Relative abundance (percentage over total number of individuals per habitat) of 80 species in flooded forests (FF) and floating meadow (FM) habitats. Number of species per family is given in parenthesis. Number of each species expressed as a percentage of the total number of individuals per habitat

Species	% FF	% FM
Arapaimidae (1)		
<i>Arapaima gigas</i>	0.063	0.000
Osteoglossidae (1)		
<i>Osteoglossum bicirrosom</i>	0.380	0.578
Anostomidae (3)		
<i>Leporinus trifasciatus</i>	0.127	0.083
<i>Rhytiodus microlepis</i>	0.063	0.330
<i>Schizodon fasciatus</i>	0.253	0.330
Acestrorhynchidae (3)		
<i>Acestrorhynchus falcatus</i>	0.063	0.000
<i>Acestrorhynchus falcirostris</i>	0.443	0.000
<i>Acestrorhynchus microlepis</i>	0.063	0.000
Characidae (17)		
<i>Astyanax bimaculatus</i>	0.063	0.165
<i>Brycon cephalus</i>	0.063	0.000
<i>Brycon pesu</i>	0.000	0.083
<i>Charax gibbosus</i>	0.063	0.165
<i>Colossoma macropomum</i>	0.697	0.578
<i>Ctenobrycon spilurus</i>	4.750	2.063
<i>Cyphocharax cf. festivus</i>	0.063	0.000
<i>Gymnocorymbus thayeri</i>	0.887	0.495
<i>Moenkhausia cf. chrysargyrea</i>	0.127	0.000
<i>Mylossoma duriventre</i>	0.000	0.165
<i>Pygocentrus nattereri</i>	0.127	2.228
<i>Roeboides biserialis</i>	0.063	0.000
<i>Serrasalmus rhombeus</i>	0.063	0.413
<i>Tetragonopterus argenteus</i>	0.127	0.000
<i>Tetragonopterus chalceus</i>	0.063	0.000
<i>Triportheus albus</i>	0.127	0.495
<i>Triportheus angulatus</i>	19.569	3.960
Curimatidae (8)		
<i>Curimata vittata</i>	0.253	0.083
<i>Curimatella alburna</i>	1.267	0.495
<i>Curimatella meyeri</i>	0.697	1.485
<i>Potamorhina altamazonica</i>	2.090	1.815
<i>Potamorhina latior</i>	0.190	1.485
<i>Psectrogaster amazonica</i>	3.103	6.766
<i>Psectrogaster essequibensis</i>	0.570	0.248
<i>Psectrogaster rutiloides</i>	12.793	17.244
Erythrinidae (3)		
<i>Erythrinus erythrinus</i>	0.063	0.083
<i>Hoplerythrinus unitaeniatus</i>	0.697	0.000
<i>Hoplias malabaricus</i>	0.380	2.640

TABLE I. Continued

Species	% FF	% FM
Gasteropelecidae (1)		
<i>Gasteropelecus sternicla</i>	0.063	0.083
Prochilodontidae (1)		
<i>Prochilodus nigricans</i>	0.570	0.578
Apteronotidae (2)		
<i>Adontosternarchus</i> sp. A	0.063	0.000
<i>Parapteronotus hasemani</i>	0.000	0.165
Electrophoridae (1)		
<i>Electrophorus electricus</i>	0.063	0.083
Gymnotidae (3)		
<i>Gymnotus carapo</i>	0.190	0.083
<i>Gymnotus ucumari</i>	0.253	0.000
<i>Gymnotus varzea</i>	0.063	0.000
Sternopygidae (1)		
<i>Eigenmannia limbata</i>	0.000	0.083
Auchenipteridae (2)		
<i>Auchenipterichthys longimanus</i>	0.127	0.000
<i>Trachelyopterus galeatus</i>	0.950	0.578
Callichthyidae (6)		
<i>Callichthys callichthys</i>	0.317	0.083
<i>Dianema longibarbis</i>	37.745	35.974
<i>Hoplosternum littorale</i>	1.203	0.908
<i>Lepthoplosternum altamazonicum</i>	0.000	0.083
<i>Lepthoplosternum ucumari</i>	0.063	0.000
<i>Megalechis thoracata</i>	1.647	0.495
Doradidae (6)		
<i>Agamyxis pectinifrons</i>	0.063	0.083
<i>Anadoras grypus</i>	0.570	0.165
<i>Brochis splendens</i>	0.127	1.568
<i>Doras</i> cf. <i>punctatus</i>	0.127	0.248
<i>Oxidoras</i> cf. <i>eigenmanni</i>	0.000	0.083
<i>Pterodoras granulosus</i>	1.013	0.330
Loricariidae (11)		
<i>Ancistrus</i> sp. A	0.127	0.000
<i>Hypoptopoma gulare</i>	0.127	0.825
<i>Hypoptopoma carinatum</i>	0.000	0.083
<i>Loricariichthys</i> cf. <i>acutus</i>	0.190	0.495
<i>Loricariichthys</i> cf. <i>maculatus</i>	0.443	0.248
<i>Loricariichthys</i> cf. <i>nudirostris</i>	0.127	0.413
<i>Loricariichthys</i> sp.1	0.190	0.165
<i>Loricariichthys</i> sp. 2 (may be a juvenile of <i>L. maculatus</i>)	0.190	2.228
Loricariinae sp. 1	0.063	0.000
<i>Pseudorinelepis genibarbis</i>	0.127	0.248
<i>Pterygoplichthys pardalis</i>	1.203	1.980
Pimelodidae (2)		
<i>Rhamdia quelen</i>	0.063	0.165
<i>Sorubim lima</i>	0.063	0.165

TABLE I. Continued

Species	% FF	% FM
Cichlidae (7)		
<i>Cichlasoma amazonarum</i>	0.443	2.475
<i>Crenicichla proteus</i>	0.063	1.485
<i>Heros efasciatus</i>	0.063	0.083
<i>Hypselaacara temporalis</i>	0.190	0.000
<i>Mesonauta mirificus</i>	0.253	2.475
<i>Pterophyllus scalare</i>	0.063	0.000
<i>Satanoperca jurupari</i>	0.317	0.330
Synbranchidae (1)		
<i>Synbranchus marmoratus</i>	0.063	0.000

for 79% of the total number of species. A total of 73 species were caught in flooded forest, with 21 exclusive to this habitat, and 59 species were caught in floating meadows, with seven species exclusive (Table I). Species richness per site ranged from nine to 33 species in flooded forest and from 14 to 30 species in floating meadows; mean species richness, Simpson's diversity index and evenness were similar between habitats (Table II).

Species accumulation curves for each habitat were constructed based on number of species captured per site. For both habitats, species richness seemed to achieve an approximate asymptote at an effort of approximately eight sites (Fig. 1). Total species richness per habitat was estimated with a first- and second-order jackknife estimator (Heltshe & Forrester, 1983). Total species richness estimates were 102 and 117 for flooded forest, and 74 and 79 for floating meadows from first- and second-order jackknife, respectively. In flooded forest, 32 species (44%) occurred in only one site while in floating meadows, 19 species (33%) occurred in only one site.

Abundance (number of individuals), fish biomass, L_S , maximum L_S , M and maximum M , averaged across sites, were similar between flooded forest and

TABLE II. Mean \pm S.D. values (10 sites) of different assemblage characteristics for flooded forest (FF) and floating meadows (FM) habitats. Differences in fish assemblage characters between habitats were detected with t -tests (P -values)

	FF	FM	P
Abundance (number of individuals per site)	158 \pm 128	121 \pm 56	0.42
Biomass [sum of fish mass (kg) per site]	7.1 \pm 4.5	5.0 \pm 4.5	0.31
Richness (number of species per site)	19.3 \pm 7.6	19.0 \pm 5.1	0.92
Simpson's diversity index	3.26	3.36	0.40
Evenness	0.38	0.40	0.31
Mean L_S (mm)	98 \pm 15	95 \pm 15	0.65
Maximum L_S (mm)	528 \pm 164	366 \pm 196	0.08
Mean mass (kg)	0.07 \pm 0.05	0.05 \pm 0.05	0.44
Maximum mass (kg)	1.7 \pm 1.2	1.2 \pm 1.2	0.33

L_S , standard length.

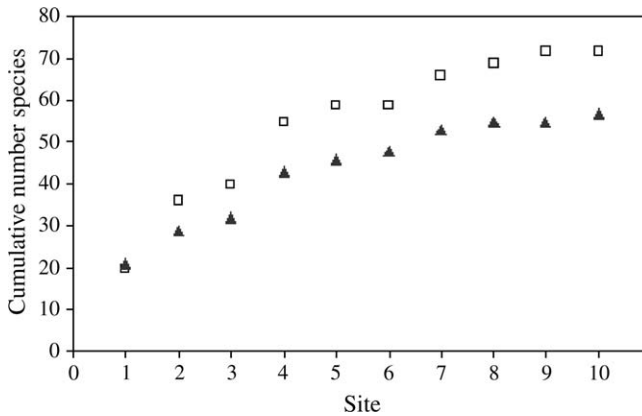


FIG. 1. Rank ordered abundances (absolute number of individuals per species) of 78 species of fish captured in flooded forest (\square , FF; 72 species) and floating meadows (\blacktriangle , FM; 57 species). Mean species richness among sites was not significantly different in the two habitats (t -test, $P > 0.05$). Note the hollow curve (log-normal distribution, both FF and FM; $P < 0.001$) where only three species account for 70 and 60% of the total abundance in FF and FM, respectively.

floating meadows (Table II). The distribution of species abundances in each habitat followed a very steep concave distribution (log-normal distribution, both $P < 0.001$) with few very abundant species and many species represented by few individuals. In flooded forest, three species accounted for 70% of the total abundance in the habitat [*Dianema longibarbis* Cope, *Psectrogaster rutiloides* (Kner) and *Triporthesus angulatus* (Spix & Agassiz)], and 25 species were captured only once. In floating meadows, 60% of the total abundance was accounted for by three species (*D. longibarbis*, *P. rutiloides* and *Psectrogaster amazonica* Eigenmann & Eigenmann), and 12 species occurred only once. Among the 10 most abundant species, only *T. angulatus* was more abundant in flooded forest (Mann-Whitney U -test, d.f. = 18, $P < 0.001$; flooded forest 30.9 ± 19.0 ; floating meadows 4.8 ± 3.4), whereas *Hoplias malabaricus* (Bloch) (Mann-Whitney U -test, d.f. = 18, $P < 0.01$; flooded forest 0.6 ± 1.1 ; floating meadows 3.2 ± 2.7), *Cichlasoma amazonarum* Kullander (Mann-Whitney U -test, d.f. = 18, $P < 0.05$; flooded forest 0.7 ± 1.6 ; floating meadows 3.0 ± 2.8) and *Mesonauta mirificus* Kullander & Silfvergrip (Mann-Whitney U -test, d.f. = 18, $P < 0.05$; flooded forest 0.4 ± 0.7 ; floating meadows 3.0 ± 2.8) were more abundant in floating meadows.

The relative biomass caught per area of gillnet was 7.10 g m^{-2} in flooded forest and 4.99 g m^{-2} in floating meadows. The L_S ranged from 38 to 740 mm and the frequency distributions did not differ statistically between the two habitats (Kolmogorov-Smirnov, d.f. = 2, $P > 0.05$) (Fig. 2).

DIEL CHANGES

There was temporal variation in abundance and species richness of active fishes (*i.e.* fishes that were actively swimming during the sampling period and therefore captured by stationary nets) (Fig. 3). The variation in abundance

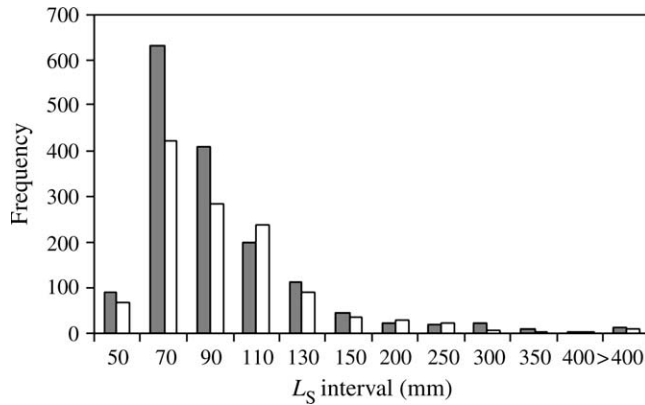


FIG. 2. Standard length (L_S) frequency distributions of fishes captured in floating forest (■) and floating meadows (□).

(means \pm s.d.; repeated measures ANOVA, d.f. = 2,36, $P < 0.001$, 1800–2400 hours: 72.2 ± 54.0 , 2400–0600 hours: 44.7 ± 41.1 , 0600–1200 hours: 18.2 ± 17.4) was also related to habitat type. In flooded forest, abundance was highest in early night samples (1800–2400 hours: 87.4 ± 71.9) and lowest in the diurnal samples (0600–1200 hours: 9.2 ± 6.5 ; contrast analysis for: 1800–2400 v. 0600–1200 hours, d.f. = 1, $P < 0.001$; 2400–0600 v. 0600–1200 hours, d.f. = 1, $P < 0.01$). In floating meadows, abundance was also highest in early night samples (1800–2400 hours: 56.9 ± 21.9), but did not differ between the late night (2400–0600 hours: 30.4 ± 16.4) and day samples (0600–1200 hours: 27.1 ± 20.5 ; contrast analysis for: 1800–2400 v. 0600–1200 hours, d.f. = 1, $P < 0.01$;

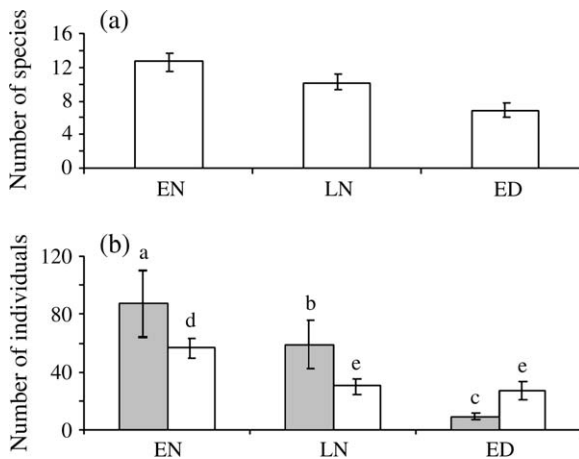


FIG. 3. Diel variation in mean \pm s.e. species richness and abundance of active fishes among habitats in three sampling periods (EN, early night: 18:00–24:00 hours; LN, late night: 24:00–06:00 hours; ED, early day: 06:00–12:00 hours): (a) combined means for the two habitats and (b) means for floating forest (■) and floating meadows (□). Means marked with the same lower case letter are not statistically different ($P > 0.05$).

2400–0600 v. 0600–1200 hours, d.f. = 1, $P = 0.56$). The temporal variation in species richness (means \pm s.d.; repeated measures ANOVA, d.f. = 2,36, $P < 0.001$, 1800–2400 hours: 12.7 ± 4.8 , 2400–0600 hours: 10.2 ± 4.3 , 0600–1200 hours: 6.9 ± 3.8) was not related to habitat type (repeated measures ANOVA, d.f. = 2,36, $P > 0.05$). Fish biomass was similar in diurnal and nocturnal samples (repeated measures ANOVA, d.f. = 2,36, $P > 0.05$; 1800–2400 hours: 2.1 ± 1.6 , 2400–0600 hours: 1.8 ± 2.1 , 0600–1200 hours: 2.2 ± 3.2).

In general, in the flooded forest, 59% of the species (44 out of 73 species in this habitat) were only caught in nocturnal samples, whereas 8% of the species (six species) were only caught in diurnal samples. In floating meadows, 41% of the species (24 out of 59 species in this habitat) were only caught in nocturnal samples, whereas 10% of the species (six species) were only caught in diurnal samples. Interestingly, a higher percentage of fishes that were active both diurnally and nocturnally were caught in the floating meadows (49%, 29 species) than in the flooded forest (31.5%, 23 species). The proportion of species in a habitat was marginally dependent on the sampling period, when analysing the three sampling periods v. habitat type (χ^2 , d.f. = 2, $P > 0.05$), and it was significantly dependent when analysing two levels of time v. habitat type (χ^2 , d.f. = 1, $P < 0.05$). At the species level, four out of the five most common species were more abundant in nocturnal samples (1800–2400 and 2400–0600 hours combined) in both habitats (*D. longibarbis*: χ^2 , d.f. = 1, $P < 0.001$; *P. rutiloides*, χ^2 , d.f. = 1, $P < 0.001$; *T. angulatus*, χ^2 , d.f. = 1, $P < 0.001$; *P. amazonica*, χ^2 , d.f. = 1, $P < 0.01$).

PATTERNS OF SPECIES DISTRIBUTION

There was a significant difference in species composition between flooded forest and floating meadows (MRPP, $A = 0.15$, $P < 0.001$). Although the A value was small, it was significantly different from zero and indicates that the homogeneity within groups is higher than expected by chance (McCune & Grace, 2002). This provides evidence for a subtly different assemblage in each habitat type. Out of the 57 species analysed, only five had significant indicator values (Table III), four species associated with floating meadows (*C. amazonarum*, *Crenicichla proteus* Cope, *M. mirificus* and *H. malabaricus*), and one species associated with flooded forest (*T. angulatus*). Thus, these species have a different likelihood of being found in one habitat although they are present

TABLE III. Indicator species and their indicator values ($I_{V_{\max}}$) as defined by the indicator species analysis for flooded forest (FF) and floating meadows (FM) habitats. P -values resulted from 1000 permutations in a Monte-Carlo test

Species	FF	FM	P -value
<i>Cichlasoma amazonarum</i>		60	0.03
<i>Crenicichla proteus</i>		50	0.04
<i>Mesonauta mirificus</i>		58	0.02
<i>Hoplias malabaricus</i>		75	0.01
<i>Triportheus angulatus</i>	68		0.001

in both habitats. The remaining 52 species had the same likelihood of being found in one or the other habitat type and are thus not indicator species in the sense of the ISA test.

DISCUSSION

The predictable and frequent disturbance (*i.e.* changes in water level) that affects Amazonian floodplains imposes unique challenges to fishes; for instance, resource availability fluctuates highly, with a 'bonanza' in seasonally flooded forests. During the flood, predator densities are low, food is abundant, but dissolved oxygen is low. At low water, food becomes scarce, predators are dense, but oxygen is generally not limiting. Floating meadows represent important shelter, spawning and feeding sites. Because they float, they are found for much of the year (although at low water they are drastically reduced in extent as large mats become stranded). At high water, fishes have the possibility to move freely through the floodplain among flooded forests, floating meadows and river channels, allowing the opportunity for seasonal rearrangements of fish assemblage structure.

Fish assemblages in flooded forest and floating meadows of C. Yarina were similar in many assemblage characters (mean abundance, mean species richness, mean diversity and mean fish mass). These similarities are not surprising since the habitats are adjacent, and therefore, fishes can swim freely between them. If the percentage of area covered by each habitat type is accounted for, flooded forests may have a greater amount of fishes in total during the flood season. Within the PSNR, flooded forest is *c.* 200 times larger than the area occupied by floating meadows. Additionally, the fact that three times more rare (uncommon) species were caught in the flooded forests suggests that there is a differential use of the available habitats during the flooding season. This highlights the importance of flooded forests as seasonally available habitat.

Species abundance distributions in both animal and plant communities are commonly skewed having very few highly abundant species and many rare (uncommon) species (Magurran & Henderson, 2003), and species-rich assemblages tend to have more rare species than species-poor assemblages (Hubbell, 2001). Data on Amazonian floodplain fish communities provide support for both these patterns (the present study; Henderson & Crampton, 1997). Both the higher absolute species richness and higher number of rare species observed in flooded forests are expected from the absolutely larger aerial extent of this habitat as compared with floating meadows. Indeed, if these two habitats were distinct and disjunct from each other (completely unconnected and species saturated) one would expect *c.* 15 times ($\sqrt{200}$) more species in flooded forests (Hubbell, 2001), with a correspondingly higher number of rare species in samples.

Although many similarities in fish communities between the flooded forest and floating meadow habitat were found, evidence for subtle differences in assemblage structure was also found. The differences in the species composition, as reflected in the MRPP analysis, may indicate both the structural and biotic characteristics of the habitats, as well as the physicochemical environment. Despite the fact that flooded forest and floating meadows habitats in C. Yarina lie in close proximity, the floating meadows were characterized by

deeper and more transparent waters than the flooded forest. Water depth and transparency were the best predictors of fish assemblage structure in Orinoco and Amazon lakes (Rodriguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998). Flooded forest and floating meadows also differ in other environmental characteristics, such as vegetation cover and structural complexity of the submerged portion of the vegetation. The habitat of floating meadows is a dense tangled underwater root mat, while flooded forests comprise a more open substratum of submerged branches and leaves (Henderson & Crampton, 1997; Junk, 1997). These structural and environmental characteristics may contribute to the subtle differences in species composition between floating meadow and flooded forest habitats.

Shifts in the abundance and number of active species between day and night were observed. Since gillnets capture fishes that are actively moving, the diel differences observed in floating meadows and flooded forests of C. Yarina are likely to reflect primarily changes in fish activity rather than changes in the abundance of fishes in the habitat, unless fishes move to or from the area covered by the net design. Diel changeover in fish assemblage structure has been reported for other Neotropical freshwater fishes (Lowe-McConnell, 1964; Arrington & Winemiller, 2003). In a study in the Cinaruco River, Orinoco Basin, Arrington & Winemiller (2003) found more species and greater abundances in nocturnal samples. Similarly, in C. Yarina, species richness and abundance were higher in nocturnal samples. In addition, samples from floating meadows contained more species that were active both during diurnal and nocturnal periods, than samples from flooded forest. In other words, the day–night species turnover is greater in flooded forest. Differences in habitat structural complexity between flooded forest and floating meadows could provide a mechanism allowing higher abundance and species richness of day-active species in floating meadows. The submerged portions of floating meadows constitute a very dense matrix of stems and roots that may not only limit light penetration during the day but also act as barriers for larger-bodied predators. Fishes are able to assess predation risk and modify their foraging behaviour through foraging rate/mortality risk trade-off mechanisms (Mittelbach, 1981, 1984; Werner *et al.*, 1983), and thus limit use of resource-rich habitats as part of predation avoidance behaviours (Werner *et al.*, 1983). This could explain the lower species richness and abundance of active fishes observed in flooded forest during the day. The similarity in fish biomass of active fishes among diurnal and nocturnal samples, despite the higher abundance in nocturnal samples, may be explained by a few large individuals caught during the day in both habitats. For instance, in flooded forest, just 21 individuals (23% of the total abundance) accounted for 85% of the fish biomass obtained in day samples. In floating meadows, 20 individuals (7% of the total abundance) accounted for 75% of the fish biomass obtained in day samples.

The mesh-size of the gillnets used in the present study yielded a sample of fishes with a relatively broad size range from 38 to 740 mm L_S , and the size distributions (within this range) were similar among the two habitats. The technique provided a direct comparison of the fish assemblage (within this size range) between flooded forest and floating meadows. It should be noted, however, that these gillnets do exclude juveniles and small-bodied fishes. Small

fishes have in earlier studies been noted as especially abundant among the roots of floating meadows (Saint-Paul & Bayley, 1979; Junk, 1984; Sánchez-Botero & Araujo-Lima, 2001; Carvalho de Lima & Araujo-Lima, 2004). These studies, however, have focused on seine samples that are particularly effective at sampling small fishes. Unfortunately, seines cannot be used effectively within flooded forests because of the numerous obstacles (*e.g.* branches, trees and large roots). It is thus important to recognize that the sampling effort of this study focused on juveniles and adults within a broad, but not all inclusive size range. In floating meadows of Marchantaria Island, on the confluence of the Solimões and Rio Negro, Petry *et al.* (2003) found species richness ranging from one to 35 species per sampled patch. This richness per patch is similar to C. Yarina where species richness per site ranged from 14 to 30 species in floating meadows, although the total number of species found in C. Yarina was much lower (59 *v.* 139 species). Petry *et al.* (2003) conducted their sampling with seines, and a large proportion of the total number of species could be represented by juveniles and small-bodied species. In flooded forests, Saint-Paul *et al.* (2000) found 73 to 113 species per sampling period (2 days) in white water, and between 83 and 109 species in black waters. Goulding *et al.* (1988) found 140 species in a survey of black-water forests where multiple fishing gears were used. In C. Yarina, 73 species were caught in the forest sites. It is clear that these habitats are speciose, but absolute richness reported may relate, in part, to sampling gears used and season of sampling.

In summary, a quantitative comparison of fish assemblage structure in flooded forest and floating meadows indicates that these seasonally connected habitats exhibit a high degree of similarity in aspects of fish community structure during the flooded season. The high proportion of species that are shared by both habitats coupled with behavioural observations indicate that many fishes are clearly moving between these habitats. Three times more rare species, however, were found in the flooded forest than in the floating meadows, and species richness estimators predicted a larger number of species in flooded forests, suggesting that the particular characteristics of flooded forests are influencing the occurrence of a suite of species that prefers this habitat during the high water season. These results confirm the important role of this seasonally available habitat in the maintenance of fish diversity in Amazon floodplains.

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