Habitat associations of exploited fish species in the Lower Amazon river–floodplain system

JOANA MARTELO*, KAI LORENZEN*, MARCELO CROSSA[†] AND DAVID G. MCGRATH[†]
Division of Biology, Imperial College London, Ascot, Berkshire, U.K.
[†]*IPAM, Santarém, Pará, Brazil*

SUMMARY

1. Modification of floodplain morphology and land use is widely recognized as a major threat to fish communities of river–floodplain systems. We assess habitat associations of major exploited fish species in the Lower Amazon, where modifications are more extensive than in the Central or Upper Amazon.
2. Habitat was characterized in terms of physical environment, vegetation cover, distance from river and mean depth. Habitat associations of late juvenile and adult fish of the 14 major exploited species were established by comparing the distribution of the habitat sampled with the distribution of the habitat sampled weighed by a fish abundance index (catch per unit of effort).
3. Eight species showed significant habitat associations, generally being most abundant in floodplain lakes. Five of these eight species were associated with open water. Of the three exceptions, two preferred flooded forest lakes and another macrophyte-dominated channels. The majority of those species with significant associations also preferred waters shallower than 7.25 m and relatively distant from the river mainstream.
4. While flooded forest is often assumed to be a key habitat for Amazon fish, only two of the main exploited species in the Lower Amazon had a significant association with this habitat. The majority of exploited species, including one that is associated with flooded forest in the central and upper Amazon, either showed no habitat associations or preferred open water lakes. The full range of pristine and modified floodplain habitats should be considered as important to fish conservation and fisheries productivity.

Keywords: Amazon floodplain, environmental variables, fisheries-dependent data, habitat-associations

Introduction

The Amazon, the world's largest river basin, supports a very high level of fish biodiversity and productivity. This forms the basis of diverse, subsistence and commercial fisheries that supply the bulk of animal protein and a significant share of income to the riparian population (Almeida, Lorenzen & McGrath, 2003). Fish assemblages and the fisheries they support are increasingly impacted by habitat modifications and fisheries exploitation. Habitat modifications are most extensive in the western and southern headwater regions of the basin and in the floodplains of the Lower Amazon, while the central basin remains largely pristine (Cardille, Foley & Heil Costa, 2002; Junk, Soares & Bayley, 2007). Geomorphology and vegetation cover of the Lower Amazon floodplain have been modified significantly over the recent past, and this trend is likely to intensify in the course of further economic development (Zarin *et al.*, 2001; Raffles & Winklerprins, 2003). Amazon fisheries on the whole are believed to be only moderately exploited, even though some of the largest species are probably overexploited (Neves, 1995; Isaac &

Correspondence: Kai Lorenzen, Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, U.K.
E-mail: k.lorenzen@imperial.ac.uk

Ruffino, 1996; Isaac, Ruffino & McGrath, 1998). Habitat modification as a result of land use and hydrological change is likely to pose the greatest long-term threat to Amazon fish and fisheries (Saint-Paul *et al.*, 2000). It is therefore important to understand and quantify the habitat preferences of Amazon fish in order to identify and protect key habitat.

The Lower Amazon river–floodplain system (*várzea*) offers a diversity of fish habitats. The geomorphological environments can be divided into five types: the main river (*rio*) itself, shallow lakes (*lagos*) bordered by natural levees (*restingas*), riverside channels (*paranás*) which connect the main river with other *várzea* systems, and deep forest channels (*igarapés*) (Smith, 1981; McGrath *et al.*, 1993). These environments may be covered by open water, or by various types of vegetation that can be broadly grouped into herbaceous macrophytes and flooded forest. Vegetation provides shelter for fish and their prey, and many fish species also consume detritus, seeds or fruit. Hence, vegetation cover is an important habitat variable and one that is particularly sensitive to land use change in the floodplain. The Amazon floodplain is characterized by a single annual flood with an amplitude of 4–6 m, driving great seasonal variation in the flooded area and associated biological production. During the flooded season or *Inverno* (December–July), all floodplain habitats become aquatic and connected while, during the dry season or *Verão* (August–November), only the main river and the deeper floodplain lakes are aquatic and many lakes become isolated. It is during the flooded season, therefore, that the greatest diversity of habitats is accessible to fish. The flooded season also is the main feeding/growth and spawning period for most floodplain species and thus plays a key role in fish production (Junk, Bayley & Sparks, 1989).

Geomorphology and vegetation cover of the Lower Amazon floodplain have been modified through river corridor engineering and land use change, as well as various interactions between them. River corridor engineering is practised at different scales and aims principally at improving navigation and expanding agricultural land (Raffles & Winklerprins, 2003). Land use change has involved removal of old-growth floodplain forest and conversion of land for cattle ranching and agriculture, but also re-growth of forest on abandoned farmland (Zarin *et al.*, 2001). There are multiple interactions between geomorphological and

land use change, such as deforestation in areas that become more accessible to navigation, or rapid erosion of deforested levees. Hence, floodplain habitats undergo many changes in their extent and characteristics which are poorly understood and quantified.

Associations between habitat and fish assemblages in tropical and sub-tropical river–floodplain systems have been investigated at various levels. Indices of Biotic Integrity (IBIs) have been developed that relate structural attributes of fish assemblages to broad-scale conditions of the riverine landscape, effectively integrating the attributes of local aquatic and riparian habitats. IBI studies of tropical and sub-tropical rivers reveal a significant impact of catchment land use, in particular vegetation cover, on structural attributes of fish assemblages (Kamdem Toham & Teugels, 1999; Pinto, Araujo & Hughes, 2006). On smaller scales, fish species or assemblages are often associated with particular habitats or habitat attributes (Chapman & Chapman, 1993; Kamdem Toham & Teugels, 1997; Tejerina-Garro, Fortin & Rodrígues, 1998; Pouilly & Rodríguez, 2004).

In the Amazon basin, fish-habitat associations have been investigated mostly in relatively pristine riverine landscapes. Studies covering the full river–floodplain habitat continuum show influences of physical variables, vegetation cover, and habitat complexity on fish species assemblages (Saint-Paul *et al.*, 2000; Petry, Bayley & Markle, 2003). Detritivores are typically found in the interior floodplain and predators closer to the river, while omnivores show no preference in this regard (Petry *et al.*, 2003). Many species show associations with either herbaceous (rooted or floating) vegetation or with flooded forest. In the Central Amazon, many species are strongly associated with flooded forest and overall fish biomass has been estimated to be substantially higher in the flooded forest than in open water (Goulding, 1980; Saint-Paul *et al.*, 2000). This has contributed to a focus on deforestation as a major threat to aquatic resources in the Amazon. However, the floodplains of the Lower Amazon, where deforestation is fairly advanced, continue to support productive fisheries. A basin-wide bio-economic study found no evidence to suggest that the availability of fisheries resources was reduced in the lower basin as compared with the central and upper regions (Almeida *et al.*, 2003). No studies on fish-habitat associations in the Lower Amazon have been reported.

Despite of the studies discussed above, fish-habitat associations remain poorly quantified in tropical river–floodplain systems where research surveys have been very limited. One opportunity to gain further quantitative information on habitat preferences is the analysis of spatially related fisheries monitoring data as have been collected in many fisheries development and conservation projects. Here we analyse such a data set from the Lower Amazon fisheries. Fisheries-dependent data are available for many species, provide extensive spatial sampling and have been shown to yield distribution patterns similar to those of research surveys (Fox & Starr, 1996). However, sampling is influenced by fishing practices and the data may violate other assumptions of parametric statistics, such as normality and independence (National Research Council, 1998). These issues can be accounted for by using a method for identifying habitat associations from fisheries-dependent data, which uses a non-parametric test to compare cumulative distributions of habitat sampled and habitat sampled weighted by an index of abundance (Perry & Smith, 1994).

Here, we provide a first quantitative assessment of habitat associations of the main exploited fish species in the human-influenced riverine landscape of the Lower Amazon. The method mentioned above was applied to a fisheries-dependent data set, collected during 5 years of monitoring an artisanal (small-scale) fishery. We identify relations between the abundance of 14 species of fish and four environmental variables: geomorphological and covering environment, distance from the river and water mean depth. Management and conservation implications are discussed.

Methods

Study area

This study focuses on the regions of Tapará and Ituqui situated in the floodplain, or *várzea* of the Lower
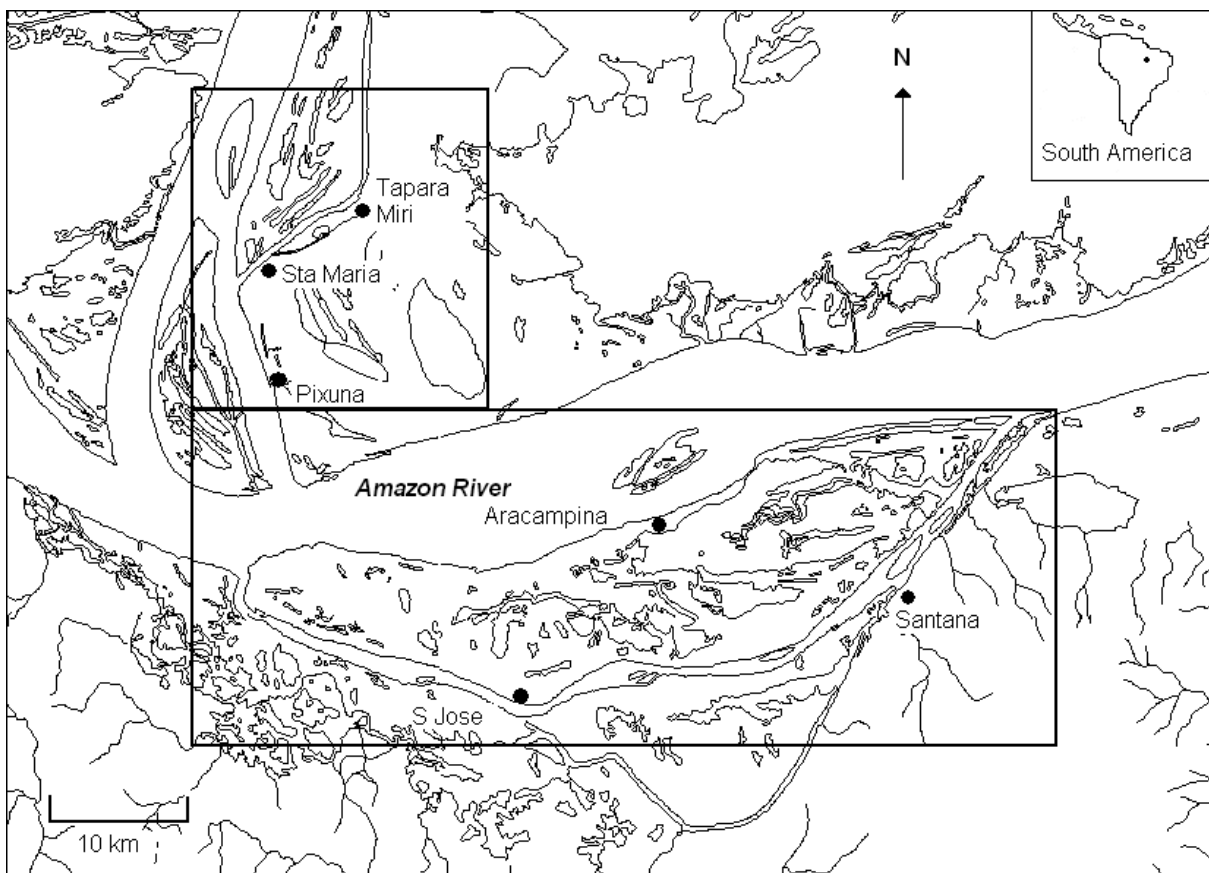

Fig. 1 Location of the study area, showing the communities where fishing activities were monitored. The top rectangle shows the Tapará region, the bottom rectangle Ituqui Island.

Amazon river (Fig. 1). Tapará and Ituqui show geomorphology and vegetation cover typical of the Lower Amazon floodplain. In the study area, the Amazon river begins to rise in December reaching its maximum height in May or June, then falls and reaches its minimum in October or November. Precipitation is approximately 2000 mm year^{-1}, and the average monthly air temperature 25–28 °C.

Habitat characterization

Aquatic habitats in the study area were delineated according to the topography recognized and used by local fishers when describing fishing locations. All identified habitats were surveyed in July 2006, and characterized in terms of physical environment and vegetation cover. Physical environment was classified as: (i) river (*rio*); (ii) lake (*lago*s); (iii) deep forest channel (*igarapé*); (iv) riverside channel (*paranás*); and (v) natural levee (*restinga*). All sites were also classified according to vegetation cover as: (i) open water of floodplain; (ii) open water of floodplain with macrophytes; (iii) open water of floodplain with flooded forest; and (iv) open water of river. Volume, area and mean distance from the river of all aquatic habitats were measured using satellite images and GPS-referenced echosounder depth readings using AUTOCAD software 16.1 (Autodesk Inc., San Rafael, CA, U.S.A.).

Fisheries data

Detailed data on catches and fishing effort were collected from 2000 to 2005 in the communities of Aracampina, Santana and São José in Ituqui, and Pixuna, Santa Maria and Tapará-Miri in Tapará (Fig. 1). Data were recorded on a fishing trip basis and included the gear used, time spent fishing, fishing location and its vegetation cover, and catch in weight by species. Interviews were held in the last week of each month and covered 14 fishermen per community, resulting in a total of 13 904 fishing trip records. Because our study focused on the use of floodplain habitats, we analysed only the data for the flood season (March–July, 4413 records). Fishing during the flood season was carried out primarily by gill nets, and only gill net catches were analysed for habitat associations to avoid problems of standardizing catch per unit of effort (CPUE) across gear types.

Analysis of habitat associations

We used an adaptation of the method proposed by Perry & Smith (1994) and Reynolds (2003) for characterizing habitat associations based on commercial fisheries data. The method accounts for the fact that fishing is often targeted and does not sample habitat representatively. Following Perry & Smith (1994), cumulative density functions of sampled habitat and sampled habitat weighed by an index of abundance were compared using a Kolmogorov–Smirnov test, under the null hypothesis of fish being randomly distributed among habitats. An empirical cumulative distribution function (cdf) was created for each habitat variable to express the range of conditions sampled by fishers. The probability of each sample within a fishing site is $1/n_h$, where n is the total number of times fishers go fishing in sample site h (Chambers & Dunstan, 1986), and the cdf for the habitat sampled is

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi}, t) \tag{1}$$

where $I(x_{hi}, t)$ is an indicator function with the values

$$I(x_{hi}, t) = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases} \tag{2}$$

The variable t is a sequence of values ranging from the lowest to the highest of the continuous habitat variables (distance from river and water mean

Table 1 Distribution of available habitat volume by physical environment and vegetation cover

Physical environment		Vegetation cover	
Level	Proportion (%)	Level	Proportion (%)
River (*rio*)	80.5	Open water of floodplain	10.3
Lake (*lago*)	14.4	Open water with macrophytes	4.3
Deep forest channel (*igarapé*)	0.8	Open water with flooded forest	4.9
Riverside channel (*paraná*)	4.1	Open water of river	80.5
Natural levee (*restinga*)	0.2		

depth). For the categorical variables (physical environment and vegetation cover), t is the number assigned to each of their levels. W_h is the proportional volume of each sample site within the study area. Eqn 1 was calculated for all values of t. Secondly, another empirical cumulative distribution function, $g(t)$, was completed to compare the distribution of sampled habitat with the distribution weighted by CPUE. The cdf $g(t)$ ilustrates the range of conditions at which the species occurred, and is expressed as

$$g(t) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{\bar{y}_{st}} I(x_{hi}, t) \quad (3)$$

where y_{hi} is the CPUE. The variable $\bar{y}_{st}$ is the estimated stratified mean abundance of fish:

$$\bar{y}_{st} = \sum_{h=1}^{L} W_h \left(\sum_{i=1}^{n_h} \frac{y_{hi}}{n_h} \right) \quad (4)$$

where L is the number of sample sites in the study area. Finally, the degree to which the cdfs $f(t)$ and $g(t)$ (Eqns 1 and 3) differed was assessed by calculating the maximum absolute difference between them. This approach is similar to that used for comparing empirical cdfs in Kolmogorov–Smirnov non-parametric tests (Perry & Smith, 1994). D gives the maximum absolute difference between $f(t)$ and $g(t)$:

$$D = \max_{\forall t} |g(t) - f(t)|$$
$$= \max_{\forall t} \left| \sum_h \sum_i \left(\frac{W_h}{n_h} \right) \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{hi}, t) \right| \quad (5)$$
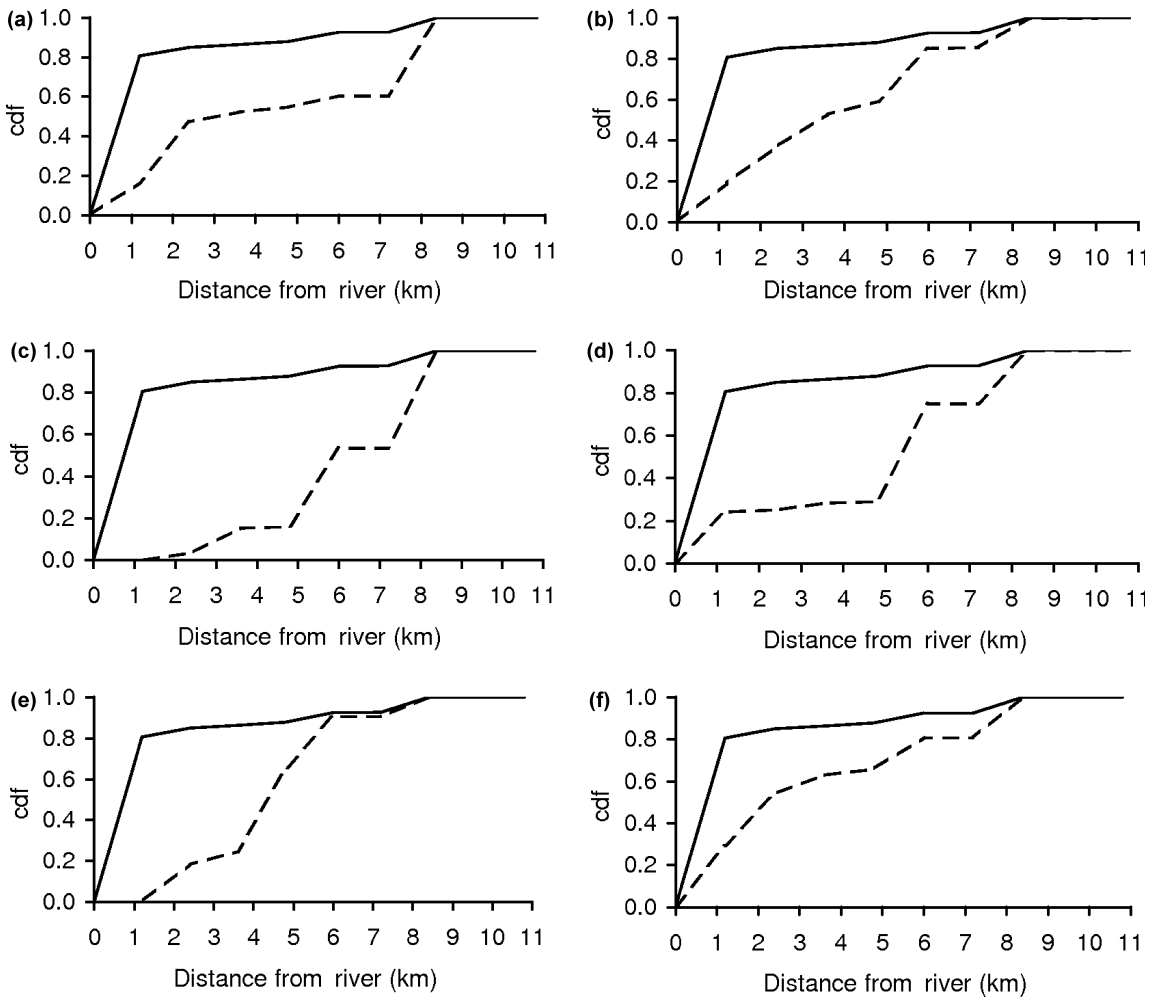

Fig. 2 Cumulative distribution functions (cdf) for the sampled distance from river, $f(t)$ (continuous line), and sampled distance from river weighted by abundance, $g(t)$ (dashed line): (a) *Colossoma macropomum*; (b) *Astronotus crassipinis*; (c) *Hypophthalmus* spp.; (d) *Pimelodina flavipinnis*; (e) *Pterygoplichthys pardalis*; (f) *Cichla* spp.

Typically, looking at the standard tables for the Kolmogorov–Smirnov test would assess the significance of D. However, because sampling among sites was unequal, a randomization procedure was applied to evaluate the significance of the test statistic. Monte Carlo simulation was used to model the distribution of D under the null hypothesis of random association between fish abundance and the habitat variable. In order to do this, 1000 random pairings of $(W_h/n_h)[(y_{hi} - y_{st})/y_{st}]$ and x_{hi} were generated for all fishing trips and sample sites and D recalculated for each realization to generate a pseudo population of D'. Percentiles (95% and 90%) of the pseudo-population of D' provide critical values. If D was greater than the
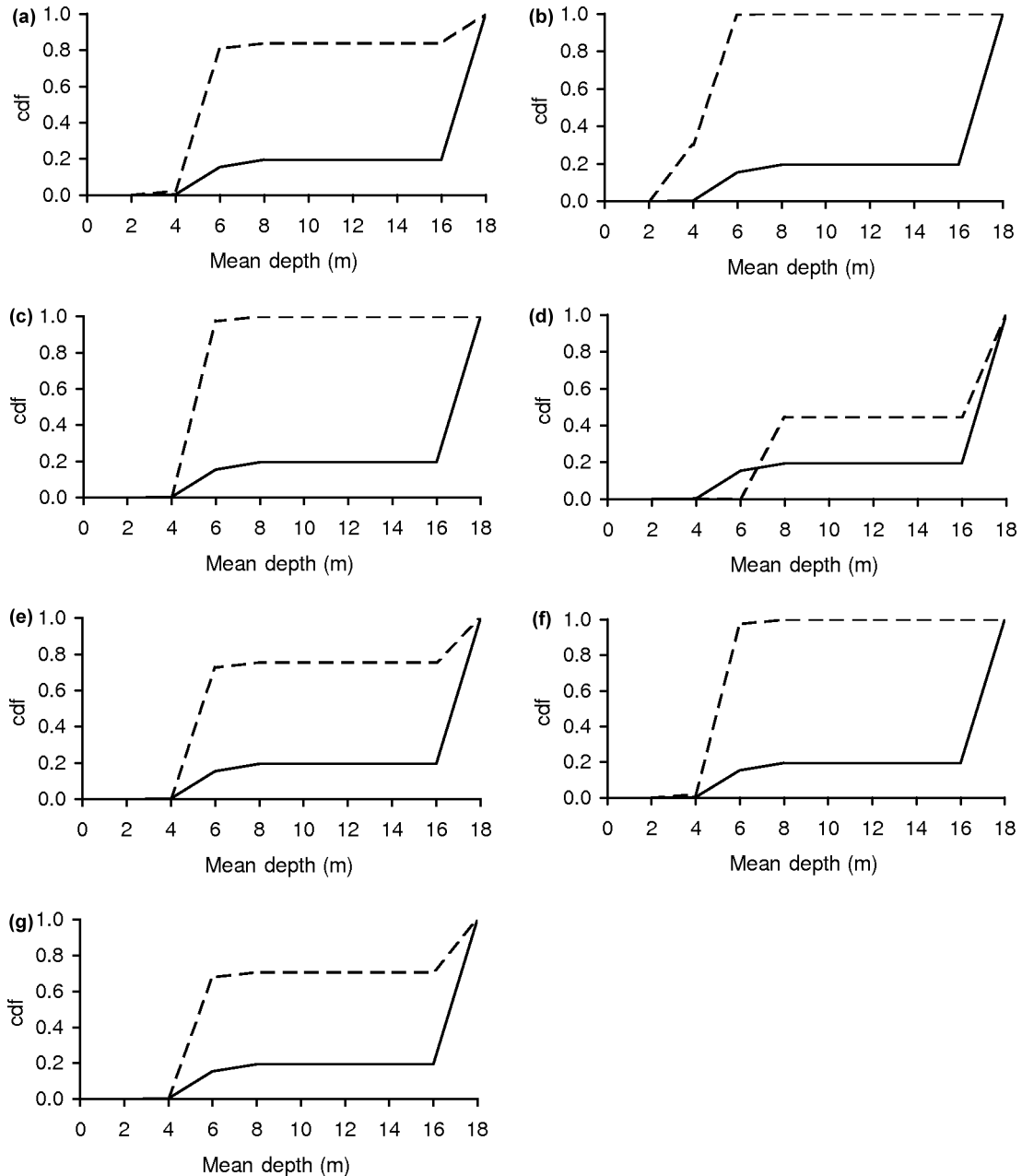

Fig. 3 Cumulative distribution functions (cdf) for observed water mean depth, $f(t)$ (continuous line), and water mean depth weighted by abundance, $g(t)$ (dashed line): (a) *Colossoma macropomum*; (b) *Astronotus crassipinis*; (c) *Hypophthalmus* spp.; (d) *Semaprochilodus taeniurus*; (e) *Pimelodina flavipinnis*; (f) *Pterygoplichthys pardalis* (g) *Cichla* spp.

critical values of D', the null hypothesis was rejected; thus, fish abundance was associated with habitat. A permutation-invariant test statistic was used for the categorical variables (Pettitt & Stephens 1977).

To identify the level of a categorical variable with which fish abundance was most strongly associated, the differences between the frequencies associated with each category was calculated:

$$J(t_a) = (g(t_{a+1}) - g(t_a)) - (f(t_{a+1}) - f(t_a)) \qquad (6)$$

The highest $J(t_a)$ corresponds to the category with which fish were most strongly associated. All calculations and statistical test were conducted in Excel, Visual Basic and R 2.3.1.

Results

Habitat availability and distribution

Physical environment and vegetation cover, distance from river and mean depth were the explanatory variables used in the analysis of fish habitat associations. The physical environment was dominated by the riverine habitat, followed by lakes and with only a small proportion of other types. Vegetation cover was dominated by open water of river and floodplain, with macrophyte and forest cover accounting for just under 5% each (Table 1). Of the continuous habitat variables, distance from river was dominated by the river itself, but distances of up to about 9 km were well represented (Fig. 2). The distribution of depth was essentially bi-modal, with floodplain habitats ranging from 4 to 8 m and the river exceeding 16 m depth (Fig. 3).

Fishery catches

A total of 38 fish species were recorded over the study period, but 14 species from nine families accounted for 96.6% of the catches (Table 2). Catches of these 14 species were analysed for habitat associations.

Habitat associations

The distribution of eight species (*Astronotus crassipinnis*, *Cichla* spp., *C. macropomum*, *Hypophthalmus* spp., *Pimelodina flavipinnis*, *Pterygoplichthys pardalis*, *Semaprochilodus taeniurus* and *Serrasalmus* spp.) was

Table 2 Taxonomic and life history information on the main fish species caught in the study area and included in the habitat association study

Order	Family	Species	Local name(s)	Feeding habit	Migratory	Catch (%)
Characiformes	Anostomidae	*Leporinus trifasciatus* (Steindachner, 1867)	Aracu	Omnivore	Yes	6.2
Characiformes	Prochilodontidae	*Prochilodus nigricans* (Agassiz, 1829)	Curimata	Detritivore	Yes	8.0
Characiformes	Prochilodontidae	*Semaprochilodus taeniurus* (Steindachner, 1882)	Jaraquí	Detritivore	Yes	8.8
Characiformes	Characidae	*Mylossoma* spp.	Pacu	Omnivore	Yes	3.5
Characiformes	Characidae	*Serrasalmus* spp.	Piranha	Piscivore	Yes	1.7
Characiformes	Characidae	*Piaractus brachypomus* (Eigenmann, 1903)	Pirapitinga	Herbivore	Yes	1.8
Characiformes	Characidae	*Colossoma macropomum* (Cuvier, 1817)	Tambaqui	Omnivore/frugivore	Yes	14.8
Lamniformes	Clupeidae	*Pellona castelnaeana* (Valenciennes, 1847)	Apapa	Piscivore	No	1.4
Perciformes	Cichlidae	*Astronotus crassipinnis* (Heckel, 1840)	Acará-açu	Omnivore/frugivore	No	1.9
Perciformes	Sciaenidae	*Plagioscion* spp.	Pescada	Piscivore	No	11.5
Perciformes	Cichlidae	*Cichla* spp.	Tucunaré	Piscivore	No	1.5
Siluriformes	Loricariidae	*Pterygoplichthys pardalis* (Castelnau, 1855)	Acari	Omnivore	No	22.1
Siluriformes	Pimelodidae	*Pimelodina flavipinnis* (Steindachner, 1876)	Fura Calça	Piscivore	No	5.8
Siluriformes	Hypophthalmidae	*Hypophthalmus* spp.	Mapará	Planktivore	Yes	7.7
Total						96.7

Table 3 Associations of fish species with physical environments and vegetation cover

| Species | Physical environment | | | | Vegetation cover | | | |
| | *D* | Critical *D'* | | Habitat associated | *D* | Critical *D'* | | Habitat associated |
		P = 0.05	*P* = 0.1			*P* = 0.05	*P* = 0.1	
Astronotus crassipinnis	0.81**	0.15	0.12	Lake $J(t_2)' = 0.73$	0.81**	0.17	0.14	Open water $J(t_1)' = 0.43$
Cichla spp.	0.52**	0.23	0.19	Lake $J(t_2)' = 0.48$	0.51**	0.28	0.25	Open water with flooded forest $J(t_3)' = 0.25$
Colossoma macropomum	0.60**	0.22	0.2	Lake $J(t_2)' = 0.63$	0.64**	0.26	0.23	Open water $J(t_1)' = 0.37$
Hypophthalmus spp.	0.81**	0.16	0.14	Lake $J(t_2)' = 0.82$	0.81**	0.18	0.16	Open water $J(t_1)' = 0.42$
Leporinus trifasciatus	0.09	0.29	0.26	–	0.07	0.34	0.31	–
Mylossoma sp.	0.10	0.32	0.29	–	0.06	0.38	0.36	–
Pellona castelnaeana	0.03	0.29	0.27	–	0.04	0.35	0.32	–
Piaractus brachypomus	0.01	0.31	0.28	–	0.02	0.36	0.34	–
Pimelodina flavipinnis	0.56**	0.21	0.18	Lake $J(t_2)' = 0.55$	0.56**	0.23	0.2	Open water $J(t_1)' = 0.37$
Plagioscion spp.	0.04	0.3	0.28	–	0.05	0.36	0.32	–
Prochilodus nigricans	0.07	0.29	0.26	–	0.06	0.33	0.31	–
Pterygoplichthys pardalis	0.81**	0.14	0.11	Lake $J(t_2)' = 0.75$	0.80**	0.16	0.13	Open water $J(t_1)' = 0.36$
Semaprochilodus taeniurus	0.40**	0.25	0.21	Riverside channel $J(t_4)' = 0.40$	0.35**	0.27	0.24	Open water with macrophytes $J(t_1)' = 0.27$
Serrasalmus spp.	0.31**	0.28	0.24	Lake $J(t_2)' = 0.28$	0.29*	0.3	0.28	Open water with flooded forest $J(t_3)' = 0.22$

Maximum difference *D* between the cumulative density functions *g(t)* and *f(t)*.
Significance of *D*: **$P < 0.05$; *$P < 0.1$.
The corresponding critical values of *D'* are also shown.

significantly related to one or more habitat variables (Table 3). Seven of the species were associated with lakes, while the jaraqui *S. taeniurus* was associated with channels. Five of the species were associated with open waters, while tucunaré *Cichla* spp. and piranha *serrasalmus* spp. were associated with flooded forest and jaraqui *S. taeniurus* with macrophytes. Consistent with their preference for floodplain rather

Table 4 Associations of fish species with distance from river and mean depth

| Species | Distance from river (km) | | | | Mean depth (m) | | | |
| | *D* | Critical *D'* | | Association | *D* | Critical *D'* | | Association |
		P = 0.05	*P* = 0.1			*P* = 0.05	*P* = 0.01	
Astronotus crassipinnis	0.61**	0.18	0.16	>1.2 km	0.85**	0.12	0.1	<6.5 m
Cichla spp.	0.51**	0.33	0.28	>1.2 km	0.41**	0.35	0.31	<4.25 m
Colossoma macropomum	0.60**	0.33	0.29	>1.2 km	0.61**	0.27	0.22	<6.5 m
Hypophthalmus spp.	0.81**	0.22	0.18	>2.4 km	0.81**	0.14	0.11	<6.5 m
Leporinus trifasciatus	0.07	0.53	0.5		0.05	0.51	0.47	
Mylossoma sp.	0.06	0.64	0.6		0.11	0.75	0.71	
Pellona castelnaeana	0.04	0.47	0.4		0.07	0.27	0.25	
Piaractus brachypomus	0.05	0.57	0.51		0.04	0.53	0.5	
Pimelodina flavipinnis	0.60**	0.28	0.25	>2.4 km	0.33**	0.26	0.22	<4.25 m
Plagioscion spp.	0.05	0.5	0.45		0.09	0.5	0.46	
Prochilodus nigricans	0.06	0.49	0.42		0.03	0.4	0.37	
Pterygoplichthys pardalis	0.80**	0.16	0.13	>1.2 km	0.82**	0.11	0.09	<6.5 m
Semaprochilodus taeniurus	0.25	0.33	0.28		0.20*	0.24	0.17	<7.25 m
Serrasalmus spp.	0.27	0.48	0.44		0.21	0.57	0.53	

Maximum difference *D* between the cumulative density functions *g(t)* and *f(t)*.
Significance of *D*: **$P < 0.05$; *$P < 0.1$.
The corresponding critical values of *D'* are also shown.

than river habitat, six of the eight species with significant physical habitat associations also preferred habitats at a distance of over 1 km from the river (Table 4; Fig. 2). Two of these species, the catfishes mapará *Hypophthalmus* spp. and fura-calça *P. flavipinnis*, were associated with floodplain habitat far from the river mainstream. All species preferred habitat of <8 m depth, most of <6.5 m (Table 4; Fig. 3). Six species (*Leporinus trifasciatus*, *Pellona castelnaeana*, *Prochilodus nigricans*, *Piaractus brachypomus*, *Mylossoma* spp. and *Plagioscion* spp.) showed no significant associations with any habitat variable.

Discussion

Our study is the first to quantify habitat associations of tropical freshwater fish from artisanal fisheries monitoring data, using a rigorous and robust statistical methodology. It demonstrates that artisanal fisheries monitoring data can be used to derive information on basic ecological requirements of exploited freshwater species, and thus fills an important gap in our understanding of tropical freshwater systems. Naturally, this approach provides information on exploited species only, and on the exploited stages of their life cycle. Other species that are present but not exploited may have different habitat associations and the same may be the case for juvenile stages of the exploited species. Hence, the associations established here need not be representative of the fish assemblage as a whole. The analysis is based on the use of fisheries CPUE as a measure of relative abundance, and it implicitly assumes that the catching efficiency (catchability) of fishing gear does not differ systematically between habitat types. This assumption has not been tested explicitly, but it underlies all catch-based assessments of habitat use and community composition including those informed by research netting surveys (e.g. Saint-Paul *et al.*, 2000; Layman & Winemiller, 2005). Gill nets have been used extensively in all available habitats, i.e. no habitat type has remained un-sampled by the fishery.

Eight out of 14 species showed significant habitat associations. Five of these were associated with open water lakes in the Lower Amazon: *A. crassipinnis*, *C. macropomum*, *Hypophthalmus* spp., *P. flavipinnis*, and *P. pardalis*. It is noteworthy that *Hypophthalmus* spp. is typically associated with flooded forest in the Central Amazon (Saint-Paul *et al.*, 2000). This may indicate a degree of plasticity in habitat associations, i.e. the species may occur in flooded forest where that habitat type is dominant in the floodplain, but associates with open water habitats where forest is scarce. Only three species included in our study were strongly associated with vegetation: *Cichla* spp. and *Serrasalmus* spp. (with flooded forest) and *S. taeniurus* (with macrophyte-dominated channels). There was no consistent relationship between trophic guild and habitat association.

Our results suggest that the full range of floodplain habitats is important in maintaining exploited fish populations and fisheries production in the Lower Amazon. The most abundant habitat type, open water lakes, is also particularly important to the majority of exploited species. While it is possible that juvenile stages of the same species are more strongly associated with vegetation, it nonetheless is apparent that open water floodplain lakes play a key role as wet season habitat of exploited stages and thus, the production of biomass supporting fisheries. Efforts at conserving aquatic habitats in the Lower Amazon, therefore, should embrace the full range of habitats and their connectivity, rather than focusing on flooded forests (see also Ward, Tockner & Schiemer, 1999).

References

Almeida O.T., Lorenzen K. & McGrath D.G. (2003) Commercial fishing in the Brazilian Amazon: regional differentiation in fleet characteristics and efficiency. *Fisheries Management and Ecology*, **10**, 109–115.

Cardille J.A., Foley J.A. & Heil Costa M. (2002) Characterizing patterns of agricultural land use in Amazonia by merging satellite classifications and census data. *Global Biogeochemical Cycles*, **16**, 18-1–81-4.

Chambers R.L. & Dunstan R. (1986) Estimating distribution functions from survey data. *Biometrika*, **73**, 597–604.

Chapman L.J. & Chapman C.A. (1993) Fish populations in tropical floodplain pools: a re-evaluation of Holden's data on the river Sokoto. *Ecology of Freshwater Fish*, **2**, 23–30.

Fox D.S. & Starr R.M. (1996) Comparison of commercial fishery and research catch data. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1694–2681.

Goulding M. (1980) *The Fishes and the Forest*. University of California Press, Berkeley, CA.

Isaac V.J. & Ruffino M.L. (1996) Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the Lower Amazon – Brazil. *Fisheries Management and Ecology*, **3**, 315–333.

Isaac V.J., Ruffino M.L. & McGrath D. (1998). In search of a new approach to fisheries management in the middle Amazon. in: *Fisheries Stock Assessment Models for the 21st Century* (Eds F. Funk, J. Heifetz, J. Power, T. Quinn, J. Schweigert, F. P. Sullivan & C.I. Zhang), pp. 889–902. Alaska Sea Grant College Program, Anchorage, AK.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river–floodplain systems. *Canadian Special Publications in Fisheries and Aquatic Sciences*, **106**, 110–127.

Junk W.J., Soares M.G.M. & Bayley P.B. (2007) Freshwater fishes of the Amazon River basin: their biodiversity, fisheries, and habitats. *Aquatic Ecosystem Health & Management*, **10**, 153–173.

Kamdem Toham A. & Teugels G.G. (1997) Patterns of microhabitat use among fourteen abundant fishes of the lower Ntem River basin (Cameroon). *Aquatic Living Resources*, **10**, 289–298.

Kamdem Toham A. & Teugels G.G. (1999) First data on an index of biotic integrity (IBI) based on fish assemblages for the assessment of the impact of deforestation in a tropical West African river system. *Hydrobiologia*, **397**, 29–38.

Layman C.A. & Winemiller K.O. (2005) Patterns of habitat segregation among large fishes in a Venezuelan floodplain river. *Neotropical Ichthyology*, **3**, 103–109.

McGrath D.G., Castro F., Futemma C., de Amaral B.D. & Calabria J. (1993) Fisheries and the evolution of resource management on the Lower Amazon floodplain. *Human Ecology*, **21**, 167–195.

National Research Council (1998) *Improving Fish Stocks Assessments*. National Academy Press, Washington, DC.

Neves A.M.B. (1995) Conhecimento atual sobre o pirarucu *Arapaima gigas* (Cuvier 1817). *Boletim Museu Paraense Emílio Goeldi. Série Zoológica*, **11**, 1.

Perry R.I. & Smith S.J. (1994) Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 589–602.

Pettitt A.N. & Stephens M.A. (1977) The Kolmogorov-Smirnov goodness-of-fit statistic with discrete and grouped data. *Technometrics*, **19**, 205–210.

Petry P., Bayley P.B. & Markle D.F. (2003) Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, **63**, 547–579.

Pinto B.C.T., Araujo F.G. & Hughes R.M. (2006) Effects of landscape and riparian condition on a fish index of biotic integrity in a large southeastern Brazil river. *Hydrobiologia*, **556**, 69–83.

Pouilly M. & Rodríguez M.A. (2004) Determinism of fish assemblage structure in neotropical floodplain lakes: influence of internal and landscape lake conditions. In: *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries (LARS2)*Vol. II (Eds R. Welcomme & T.T. Petr), pp. 243–265. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand.

Raffles H. & Winklerprins M.G.A. (2003) Further reflections on Amazonian environmental history: transformations of rivers and streams. *Latin American Research Review*, **38**, 165–187.

Reynolds J.A. (2003) Quantifying habitat associations in marine fisheries: a generalization of the Kolmogorov–Smirnov statistic using commercial logbook records linked to archived environmental data. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 370–378.

Saint-Paul U., Zuanon J., Villacorta M.A., García M., Fabré N.N., Berger U. & Junk W.J. (2000) Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes*, **57**, 235–250.

Smith N.J.H. (1981) *Man, Fishes, and the Amazon*. Columbia University Press, New York, NY.

Tejerina-Garro F.L., Fortin R. & Rodrígues M.A. (1998) Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon basin. *Environmental Biology of Fishes*, **51**, 399–410.

Ward J.V., Tockner K. & Schiemer F. (1999) Biodiversity of floodplain river ecossystems: ecotones and connectivity. *Regulated Rivers: Research & Management*, **5**, 125–139.

Zarin D.J., Pereira V.F.G., Raffles H., Rabelo F.G., Pinedo-Vasquez M. & Congalton R.G. (2001) Landscape change in tidal floodplains near the mouth of the Amazon River. *Forest Ecology and Management*, **154**, 383–393.