Diversity in migratory patterns among Neotropical fishes in a highly regulated river basin

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Migratory behaviour of selected fish species is described in the Paraná River, Brazil–Argentina–Paraguay, to search for patterns relevant to tropical regulated river systems. In a 10 year mark–recapture study, spanning a 1425 km section of the river, 32 867 fishes composed of 18 species were released and 1083 fishes were recaptured. The fishes recaptured were at liberty an average 166 days (maximum 1548 days) and travelled an average 35 km (range 0–625 km). Cluster analysis applied to variables descriptive of movement behaviour identified four general movement patterns. Cluster 1 included species that moved long distances (mean 164 km) upstream (54%) and downstream (40%) the mainstem river and showed high incidence (27%) of passage through dams; cluster 2 also exhibited high rate of movement along the mainstem (49% upstream, 13% downstream), but moved small distances (mean 10 km); cluster 3 included the most fishes moving laterally into tributaries (45%) or not moving at all (25%), but little downstream movement (8%); fishes in cluster 4 exhibited little upstream movement (13%) and farthest downstream movements (mean 41 km). Whereas species could be numerically clustered with statistical models, a species ordination showed ample spread, suggesting that species exhibit diverse movement patterns that cannot be easily classified into just a few classes. The cluster and ordination procedures also showed that adults and juveniles of the same species exhibit similar movement patterns. Conventional concepts about Neotropical migratory fishes portray them as travelling long distances upstream. The present results broaden these concepts suggesting that migratory movements are more diverse, could be long, short or at times absent, upriver, downriver or lateral, and the diversity of movements can vary within and among species. The intense lateral migrations exhibited by a diversity of species, especially to and from large tributaries (above reservoirs) and reservoir tributaries, illustrate the importance of these habitats for the fish species life cycle. Considering that the Paraná River is highly impounded, special attention should be given to the few remaining low-impact habitats as they continue to be targets of hydropower development that will probably intensify the effects on migratory fish stocks. © 2012 The Authors

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INTRODUCTION

River–floodplain systems, especially in the tropics, support high biological diversity and important fisheries (Welcomme, 1985, 1990; Lowe-McConnell, 1987) often dependent on migratory fish species. Fish migrations are well-known seasonal occurrences in tropical rivers (Welcomme *et al*., 2006). Conventional concepts about Neotropical migratory fishes portray them as travelling long distances longitudinally during the reproductive season in search of habitats suitable for spawning. Longitudinal migrations represent migrations up and down the main river channel (Welcomme *et al*., 2006). The movements are seen as mostly upstream and coincidental with the wet season, when the hydrometric level is increasing, although adults are generally thought to drift or migrate back to their downstream habitats (Agostinho *et al*., 2003). Nevertheless, in large floodplain rivers, migrations can be complex, with fishes travelling not only longitudinally up and down the river mainstem but also in and out of the tributaries and floodplains. Migrations from the main river channel to and from tributaries and floodplain waterbodies, usually occur between breeding, feeding and refuge locations (Winemiller & Jepsen, 1998).

A general pattern for reproductive migrations in floodplain rivers is an upstream spawning movement followed by a downstream dispersion of eggs, larvae and spent adults into floodplain habitats (Carolsfeld *et al*., 2003). The passive downstream drift of larvae and juveniles is common to most migratory patterns in large South American rivers. Survival and life history are directly related to intact longitudinal pathways, including the possibility of lateral migration into tributaries that are often very important for reproduction and can serve as rearing areas for larvae and young fishes (Cowx & Welcomme, 1998). Connections between the river and floodplains or backwater habitats are essential in the life history of many migratory fishes that have evolved to take advantage of seasonal floods and utilize the inundated areas for spawning and feeding (Nakatani *et al*., 2004; Agostinho *et al*., 2007*a*). Although this pattern may be dominant in South America, there are several variations (Pompeu *et al*., 2012), including basins where migratory fishes complete their life cycles using in-river habitats because a floodplain is absent (Godinho & Kynard, 2009), such as in the Uruguay River (Zaniboni Filho & Schultz, 2003).

Neotropical rivers have become increasingly regulated by dams as a consequence of hydropower development, notably the Paraná River (Lucas & Baras, 2001). The large impoundments along the Paraná River, particularly on its upper reaches, have had major hydrological and ecological effects on the basin (Agostinho *et al*., 2003), including modification of the annual hydrograph, habitat alterations, loss of system continuity and disruption of fish migration routes affecting the sustainability of fisheries production (Hoeinghaus *et al*., 2009). In this region, 15 to 20 species are considered long-distance migrants and their populations have been reportedly reduced or decimated by the large number of dams built in the second half of the 20th century (Agostinho *et al*., 2007*a*). These species are potamodromous, locally known as 'piracema' fishes, which normally grow to a large size and represent the most important commercial and recreational fishes in Neotropical rivers (Godinho & Kynard, 2009).

Understanding migratory behaviours, differences among species and requirements for critical spawning and nursery areas require additional attention in the Neotropical region (Agostinho *et al*., 2003). Pioneer studies in Brazil were conducted in the Mogi

Guaçu River, a tributary of the Paraná River (Godoy, 1957, 1967, 1972, 1985). Studies were also conducted in the lower and middle (Bonetto, 1963; Bonetto & Pignalberi, 1964; Bonetto *et al.*, 1971, 1981; Quiros & Vidal, 2000) and upper Paraná River (Agostinho *et al.*, 1993, 2003; Antonio *et al.*, 2007; Makrakis *et al.*, 2007*a*, *b*). A few selected Neotropical fish species have received research attention in the Amazon River basin (de Ribeiro & Petrere, 1990; Barthem *et al.*, 1991; Fernandes, 1997; Castello, 2008) and São Francisco River basin (Godinho & Kynard, 2006; Godinho *et al.*, 2007). Details about the migration patterns of most species, however, are still scant (Petrere, 1985; Carolsfeld *et al.*, 2003).

An understanding of migratory patterns is a basic requirement for successful management of fishes in regulated rivers, particularly because the decline in some fish species has been directly attributed to the construction of dams that can limit fish movements (Jungwirth *et al.*, 2000). Considering that the Paraná River system has a high diversity of migratory species and is highly modified with several dams (some of them with fish passes) and large reservoirs, the present study describes, categorizes and generalizes movement patterns of migratory species in the Paraná River to search for patterns relevant to tropical regulated river systems. It was predicted that a diversity of migratory patterns occurs and different fish species would react to migration obstacles differently. Advancing knowledge about the migratory fish fauna in this impacted river system may facilitate species protection, river management and mitigation of obstacles.

MATERIALS AND METHODS

STUDY REGION

The Paraná River flows through south-central Brazil, south-eastern Paraguay and northern Argentina before it joins the Plata River in central Argentina. With a length of 4695 km, it is the second longest river in South America, the tenth in the world. Its $2 \cdot 6 \times 10^6$ km^2 drainage area is the fourth largest in the world and includes most of south-central South America from the Andes to Serra do Mar mountains near the Atlantic Ocean (Agostinho *et al.*, 2003). The Paraná River is customarily divided into upper, middle and lower sections (Bonetto, 1989), each with distinctive geographical and biological characteristics. The upper stretches are characterized by high human occupation and intense anthropogenic activities, and few areas are still in pristine conditions (Agostinho *et al.*, 2007*b*). Besides extensive agriculture development, dams are the most common signs of human interference on the physiography of the region.

The study area included the upper and middle sections of the Paraná River, encompassing *c*. 1425 river km, and from upstream to downstream the Porto Primavera Reservoir (Brazil; 250 km long), the upper Paraná River floodplain (Brazil; 237 km long) above the Itaipu Reservoir and the Itaipu (Brazil and Paraguay; 170 km long) and Yacyreta (Paraguay and Argentina; 67 km long) reservoirs (Fig. 1). The upper Paraná River drains approximately the top third of the basin, extending 756 river km, and lies completely in Brazil, except for a stretch within the Itaipu Reservoir that borders Paraguay. Dams are present in all major tributaries and in the Paraná main channel above the Porto Primavera Reservoir.

The upper Paraná River floodplain (Fig. 1) stretches from the Porto Primavera Dam downstream to the upper reaches of the Itaipu Reservoir. This stretch is not impounded, spans as wide as 20 km, especially on the western margin (Agostinho *et al.*, 2003), and has large tributaries on the eastern margin. Flooded areas include active and semi-active channels, lagoons, elongated lowlands associated with paleochannels and lowlands associated with the flood basin (de Souza-Filho & Stevaux, 2004).

FIG. 1. Study area in the Paraná River along the borders of Argentina, Brazil and Paraguay. ──▶, principal displacements of the migratory fish species. ●, Porto Primavera Ladder; ◐, Canal da Piracema.

The Itaipu Dam separates the upper Paraná River from the middle Paraná River, just upriver of the confluence with the Iguassu River and the tri-national border of Brazil, Argentina and Paraguay (de Resende, 2003). The middle Paraná River flows 669 river km south-west and then west, forming the border between Paraguay and Argentina. Many tributaries to the middle Paraná River include natural falls near their confluence with the Paraná River, limiting fish passage upriver from the mainstem (Garcia, 1999).

Fish passage facilities are present at three locations. At Porto Primavera Dam, a fish elevator began to operate in November 1999, next to the central wall of the hydroelectric dam, where four pumps produce a flux into an attraction canal. The elevator raises the fishes 19 m and releases them into the reservoir (Companhia Energética de São Paulo, 2000). This dam also has a fish ladder next to the left border of the river, stretching 520 m to transcend the 19 m difference in elevations (Makrakis *et al.*, 2007*c*). At the Itaipu Dam, the recently constructed Piracema Canal utilizes a streambed, man-made canals, lagoons and fish ladders extending *c*. 10 km to overcome a 120 m difference in elevations and reach the Itaipu Reservoir (Makrakis *et al.*, 2007*d*). In addition, an experimental fish ladder (27 m high and

155 m long) devoted to research on fish pass operates next to the tailrace of one of the turbines (Fernandez *et al.*, 2004), but because it is experimental, the ladder does not reach the reservoir. Fish-pass facilities at the Yacyretá Dam consist of two elevators located in the main channel powerhouse (Oldani *et al.*, 2007) that raise fishes 23 m to release them into Yacyreta Reservoir (Garcia, 1999).

FISH MARKING

Marking of 18 periodic fish species (Winemiller, 1992), many of them potentially migratory, occurred over 10 years beginning in 1997 and continuing until May 2006. In Porto Primavera Dam, fishes were caught in the ladder using cast nets and trawls, and downstream of the dam with hand lines and long lines. In the upper Paraná River floodplain, live fishes were purchased from commercial fishers. At the Itaipu Reservoir and its tributaries, fishes were collected with gillnets and long lines, and purchased from fishers. Also, fishes raised in cages [in particular piracanjuba *Brycon orbignyanus* (Valenciennes 1850), pacu *Piaractus mesopotamicus* (Holmberg 1887) and streaked prochilod *Prochilodus lineatus* (Valenciennes 1836)] within the Itaipu Reservoir (Borghetti & Canzi, 1993) and in nearby ponds were released in the main reservoir and its tributaries. Fishes rescued from turbines in the Itaipu Dam were released into the Itaipu Reservoir. At the Itaipu Dam, fishes were caught also in the experimental ladder using cast nets. In the Piracema Canal, fishes were collected with cast nets, long lines and gillnets. At the Yacyreta Reservoir, fishes collected in the elevators were released into the reservoir. All fishes were tagged and released near the location where they were caught.

Fishes were tagged with an external Lea tag (Fritz, 1959), which consists of a small plastic cylinder held by a polyester string inserted between the dorsal pterygiophores. To reduce stress and promote post-release survival, fishes were anaesthetized in a solution of clove oil (Griffiths, 2000) before tagging. Each tag was identified with a unique number and contained a message with information about the tagging programme and how to report the tag. The fishes tagged were measured for total length (L_T) before releasing them. The message asked fishers to provide information about capture date and location. Tagged fishes were released throughout all months of each study year.

The tagging programme and its purpose were advertised in fisher colonies and clubs, schools and churches and through radio and television stations to encourage tag returns. Additionally, leaflets, posters, T-shirts and hats were distributed as a promotion tool to encourage returns. Rewards for returns included raincoats, lanterns, thermal bottles and collaboration certificates.

DATA ANALYSIS

Movement patterns were analysed for species with at least 10 recaptures of individuals that had been at large for at least 10 days, to allow time for dispersal. Species were further grouped into juveniles and adults if there were at least 10 recaptures in each of these two life-stage groups. Selected descriptive statistics are reported according to species and life-stage group, and cluster analysis and ordination were used to identify general groups of migratory fishes. Descriptive statistics included means, maxima, 90% C.I. and percentage frequency distributions estimated for distance moved (shortest over-water distance between release and recapture site), rate of movement (ratio of distance moved to days between release and recapture) and direction (upstream on the mainstem Paraná River, downstream on the mainstem or laterally in and out of tributaries and floodplains). The 90% C.I. was estimated by bootstrapping (Efron & Tibshirani, 1993) to avoid parametric assumptions.

Cluster analysis grouped species with similar migratory patterns relative to 21 descriptors that described percentage of fishes that moved, direction of movement, distance moved, rate of movement and dam passage. A ln transformation had to be applied to some variables before normalizing them to compute a similarity matrix based on Manhattan distances. A hierarchical agglomerative clustering using the complete linkage method of joining species was applied to the similarity matrix. The resulting clusters identified groups of species and life stages that exhibited more similar migratory patterns than species assigned to different clusters. The

clusters were selected to be significantly different ($P < 0.05$) using the similarity profile test. Ordination with non-metric multidimensional scaling was applied to the similarity matrix to show the relationships between species in two-dimensional space and to verify patterns in species relationships identified by the clustering procedure. The PRIMER v.6 software package (Clarke & Gorley, 2006) was used to construct the clusters, conduct the similarity profile tests and perform the ordination.

RESULTS

During the study period, 32 867 fishes were marked and released, including 18 species of the families Ageneiosidae, Anostomidae, Characidae, Doradidae, Pimelodidae and Prochilodontidae presumed to be migratory (Table I). In general, 53% of the fishes were released within the main bodies of the Itaipu and Yacyreta reservoirs, 19% in the Itaipu Reservoir's tributaries, 17% in the upper Paraná River floodplain above Itaipu Reservoir, 11% below the Porto Primavera Reservoir's fish ladder and Itaipu Reservoir's migration canal and <1% in the Paraná River below the Itaipu Dam. At time of release, fish L_T ranged from 12 to 150 cm and averaged 41 cm (40–42 90% C.I.).

A total of 1083 fishes were recaptured and reported, representing a recapture rate of 3%. The species with the most recaptures were *Pterodoras granulosus* (Valenciennes 1821) ($n = 420$; 5% recapture rate) and *P. mesopotamicus* ($n = 376$; 11%) (Table I). Relative to season, 82% of the fishes were recaptured during the wet season (October to March). Relative to life stage, roughly 51% of the fish recaptured were juveniles and 49% were adults. Of the fishes recaptured, 130 were recaptured in <10 days after release and were excluded from analysis. Of those 953 fish remaining, 24% moved upstream, 11% moved downstream, 41% moved laterally and 24% stayed within their general release area. Some species moved mainly upstream or downstream. Most of the threespot leporinus *Leporinus friderici* (Bloch 1794) did not move, and many *Ageneiosus* sp., *B. orbignyanus*, *P. granulosus*, *Pimelodus maculatus* Lacépède 1803 and duckbill catfish *Sorubim lima* (Block & Schneider 1801) stayed near their release site; of those that moved, the majority travelled upstream or laterally. *Prochilodus lineatus*, however, exhibited balanced upstream, downstream and lateral movements.

Lateral movement was primarily to and from tributaries. Only 4% of the fishes recaptured and classified as moving laterally moved between the mainstem Paraná River and the floodplain and between the floodplain and the reservoir. Conversely, 23% moved from the reservoirs (Itaipu and Yacyreta) to their tributaries; 44% from tributaries of the Itaipu Reservoir into the Itaipu Reservoir and 20% from tributaries of the Itaipu Reservoir, through the reservoir, into other tributaries of the reservoir. The remaining 9% of the fishes exhibited various lateral movements including displacements between the Paraná River and its tributaries (*e.g.* Ivaí and Piquiri Rivers above the Itaipu Reservoir) and tributaries to the Itaipu Reservoir; from fish passages to tributaries of the unimpounded Paraná River below (*e.g.* Iguaçu River) and above (*e.g.* Ivaí River) Itaipu Reservoir and to tributaries of Yacyreta and Porto Primavera reservoirs; from tributaries to the Paraná River into reservoir tributaries; from Itaipu and Yacyreta reservoirs to tributaries to the Paraná River below (*e.g.* Guarupá, Iguaçu and Almada Rivers) and above (*e.g.* Paranapanema and Ivaí Rivers) the reservoirs and from tributaries of Itaipu Reservoir to tributaries of the Paraná River (*e.g.* Piquiri River).

TABLE I. Movement patterns of fish species in the Paraná River basin

Family and species	Life stage L_T (cm)*	Mean L_T (cm)	Number recaptured marked	Distance moved (km)†		Rate of movement (km day^{-1})†		Lon (%)	Up dams (%)‡
				Mean	Maximum	Mean	Maximum		
Ageneiosidae									
Ageneiosus sp.	19·2	31·1	7/71	56·2	150	1·5	3·3	0	0
Anostomidae									
Leporinus elongatus	26·0	40·6	21/597	195·9	565	2·1	6·2	93·3	53·3
Leporinus friderici	—	29·7	11/1297	3·5	5	0·2	0·2	50·0	0
Leporinus obtusidens	24·0	42·7	2/608	7·5	10	0·1	0·2	100	0
Schizodon borellii	—	35·0	12/1913	19·6	40	0·3	0·8	75·0	0
Characidae									
Brycon orbignyanus	29·4	35·7	34/196	7·5	20	0·2	0·6	83·3	0
Salminus brasiliensis	50·4	50·3	11/1111	27·5	86	1·4	7·2	66·7	0
Piaractus mesopotamicus	33·4	31·4	376/3550	42·7	625	0·8	26·4	49·3	0·3
Doradidae									
Oxydoras kneri	—	55·3	4/940	33·8	60	0·4	0·9	50·0	0
Pterodoras granulosus	35·4	39·7	420/8060	41·6	215	0·6	9·4	29·4	0
Pimelodidae									
Hemisorubim platyrhynchos	—	52·7	10/912	132·3	360	3·1	5·4	100	0
Pimelodus albicans	23·2	44·4	4/569	110·0	110	4·6	4·6	100	0
Pimelodus maculatus	11·8	34·7	29/4310	55·8	150	0·8	4·6	37·5	0
Pinirampus pirinampu	46·0	41·2	62/2656	44·7	225	1	4·6	40·4	0
Pseudoplatystoma corruscans	66·3	79·8	16/630	61·9	401	0·9	3·6	41·7	8·3
Sorubim lima	—	46·1	6/1122	13·0	25	0·02	0·03	100	0
Zungaro jahu	66·0	—	2/100	10·0	10	0·02	0·02	100	0
Prochilodontidae									
Prochilodus lineatus	27·4	48·7	57/4225	29·2	250	0·7	6·3	63·0	2·2

Lon, longitudinal movement on the mainstem river; lateral movement into tributaries would be 100 Lon. Up dams, recaptures following passage upstream of at least one dam.

*Maximum total length (L_T) of juveniles.

†Excludes fishes recaptured in <10 days of release.

‡Excludes fishes that did not move.

Some fish species moved upstream through the fish passes installed at dams. *Leporinus elongatus* (Valenciennes 1850) appeared to be the most successful as 53% of fish of this species recaptured had passed through at least one fish pass (Table I). Single specimens of *L. elongatus* and *P. mesopotamicus* successfully ascended two fish passes, including the Piracema Canal at the Itaipu Dam and the fish ladder in the Porto Primavera Dam, 565 and 625 km upstream, respectively. Three specimens of *L. elongatus* and one of spotted surubim *P. corruscans* (Spix & Agassiz, 1829) moved upstream through the Piracema Canal reaching the floodplain above the Itaipu Reservoir. Similarly, two *P. lineatus* and two *L. elongatus* ascended the Piracema Canal into the Itaipu Reservoir and one *P. lineatus* and two *L. elongatus* moved upstream through the fish ladder at Porto Primavera Dam into the Porto Primavera Reservoir.

The mean length of time between release and recapture was 166 days (154–177 90% C.I.), with a maximum time at liberty of 1548 days (4·2 years). Fishes that moved upstream were at liberty an average 122 days (range 10–1363 days), those that moved downstream an average 98 days (10–825 days), those that moved laterally an average 152 days (10–1368 days) and those that did not move were at liberty an average 256 days (10–1548 days). The average distance travelled by all fishes that moved away from their release sites was 35 km (31–38 90% C.I.). The longest average movements for fish of a species were recorded for *Leporinus elongatus* Valenciennes 1850 and porthole shovelnose catfish *Hemisorubim platyrhynchos* (Valenciennes 1840), which as a species travelled distances averaging 196 and 132 km (Table I). The maximum distances moved were recorded for an adult *P. mesopotamicus* that displaced 625 km upstream, and for an adult *L. elongatus* that moved 565 km upstream in a lateral tributary. Conversely, individuals of some species moved long distances downstream, such as individuals representing *P. lineatus* and flatwhiskered catfish *Pinirampus pirinampu* (Spix & Agassiz, 1829) (250 and 210 km). Rate of movement averaged 0·6 km day^{-1} (0·5–0·7 km day^{-1} 90% C.I.). The highest mean species rates of movement were displayed by specimens of *Pimelodus albicans* (Valenciennes, 1840) and *H. platyrhynchos* (4·6 and 3·1 km day^{-1}, Table I), and a single specimen of *P. mesopotamicus* moved upstream faster than any other species (26·4 km day^{-1}). For fishes that moved downstream, average movements were fastest for specimens of dorado *Salminus brasiliensis* (Cuvier, 1816) and *P. lineatus* (7·2 and 6·1 km day^{-1}).

Classification and ordination was performed with 11 species that had at least 10 recaptures. Four of these 11 species were separated by life stage as at least 10 juveniles and 10 adults were recaptured. Four clusters were identified (Fig. 2). Cluster 1 included two species that moved primarily longitudinally in the Paraná River (Table II), including the highest percentage of fishes moving upstream (53·6%) or downstream (40·2%), with few fishes not moving (3·1%) or moving laterally (3·1%). Fishes in this cluster also moved the farthest (mean 164·1 km), farthest upstream (mean 245·8 km) and exhibited the greatest passage through dams (26·7%). Cluster 2 included two species, with one species separated into life stages. Fishes in cluster 2 had the second highest displacement upstream (49·3%), but generally moved only small distances (mean 10·0 km) and at slow rates (0·2 km day^{-1}) in any direction. None of the species in this cluster moved through dams. Cluster 3 included three species, two separated into life stages. Cluster 3 had the highest percentage of individuals moving through the tributaries (45·3%) or staying put (24·5%) and the fewest moving downstream (7·9%) in the Parana River. Cluster 4 included four
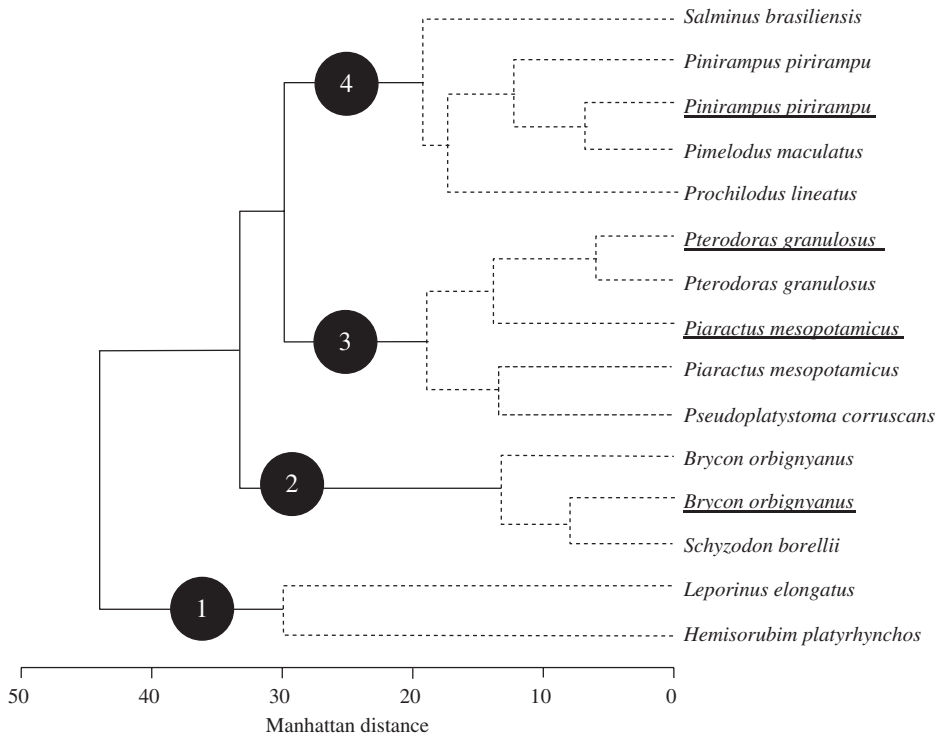
FIG. 2. Cluster analysis classification of 11 fish species in the impounded Paraná River basin. Underlined species indicate juvenile life stage, and circles indicate cluster numbers corresponding to cluster characteristics summarized in Table II.

species, one separated into life stages. Species in cluster 4 had the lowest representation of fishes moving upstream (12·6%) through the Parana River, but the second highest representation of fishes moving downstream (31·0%) and laterally (39·4%). Also, this group exhibited the farthest (mean 41·1 km) and fastest (mean 1·2 km day^{-1}) displacements downstream in the Parana River.

Although the cluster analysis grouped species into four different clusters, the non-metric multidimensional scaling procedure showed ample spread among some species within groups (Fig. 3). This divergence suggests that while species can be numerically classified into groups with cluster analysis, migratory species exhibit unique movement patterns. Moreover, judging from the proximity in ordination space between juveniles and adults of the same species, the ordination suggested that no large differences in migratory patterns existed between life stages.

DISCUSSION

The present study depended on tag-recovery data that are commonly used to study movement patterns of fish populations, but suffer from a variety of biases (McGarvey & Feenstra, 2002; Miranda *et al*., 2002). Distance travelled considers only linear distance and ignores possible longer routes taken by the fishes. Moreover, time to

TABLE II. Movement characteristics of Paraná River basin fishes in four clusters

Movement variable	Cluster			
	1	2	3	4
No movement (%)	3·1	21·5	24·5	17·0
Upstream movement (%)	53·6	49·3	22·2	12·6
Downstream movement (%)	40·2	12·5	7·9	31·0
Lateral movement (%)	3·1	16·7	45·3	39·4
Mean distance (km)	164·1	10·0	45·6	40·2
Maximum distance (km)	462·5	23·3	366·6	158·2
Mean speed (km day^{-1})	2·6	0·2	0·7	0·9
Maximum speed (km day^{-1})	5·8	0·6	10·0	5·4
Mean distance upstream (km)	245·8	10·9	84·3	10·3
Maximum distance upstream (km)	390·0	20·0	359·6	17·8
Mean distance downstream (km)	24·5	6·2	17·6	41·1
Maximum distance downstream (km)	52·5	10·0	67·0	134·2
Mean distance lateral (km)	282·5	11·7	49·3	44·6
Maximum distance lateral (km)	282·5	17·0	242·4	130·4
Mean speed upstream (km day^{-1})	3·6	0·2	1·0	0·1
Maximum speed upstream (km day^{-1})	5·9	0·6	8·3	0·3
Mean speed downstream (km day^{-1})	1·0	0·1	0·3	1·2
Maximum speed downstream (km day^{-1})	2·2	0·2	1·0	4·0
Mean speed lateral (km day^{-1})	2·5	0·2	1·0	0·9
Maximum speed lateral (km day^{-1})	2·5	0·3	5·2	4·1
Upstream movement through dam (%)	26·7	0·0	1·7	0·4

complete the distance travelled is potentially an overestimate given that the fishes might have arrived at the capture site before it was recaptured. Therefore, distance travelled and speed of travel are probably underestimated, and underestimation may vary among species depending on species-specific meandering behaviours. Thus, these statistics are viewed only as coarse indicators. The low 3% recapture rate probably reflects other tag-recovery biases such as tag loss, non-reporting and post-release mortality. It may also reflect low fishing effort within this relatively remote region with low human population densities. Higher recapture rates occurred in the Itaipu Reservoir and tributaries that support more intensive fisheries for selected species. These biases probably distorted the movement statistics and cluster classification, but mostly for species classified into neighbouring clusters; less so for species classified into distant clusters. Obtaining information about fish movements using mark and recapture in this relatively remote region of South America is challenging. In the future, radio-tracking, transponder technology, satellite surveillance or forthcoming electronic surveillance tools will improve the ability to monitor movement patterns. Thus, the analyses should be viewed as tentative and as a starting point for more in-depth inquiry.

Conventional concepts about Neotropical migratory fishes portray them as travelling long distances during the reproductive season in search of habitats suitable for spawning (Carolsfeld *et al.*, 2003). The movement is seen as mostly upstream coinciding with the wet season, when the hydrometric level is increasing. After spawning, adults are generally thought to drift or migrate back to their downstream habitats. The present results broaden these concepts and steers future investigations
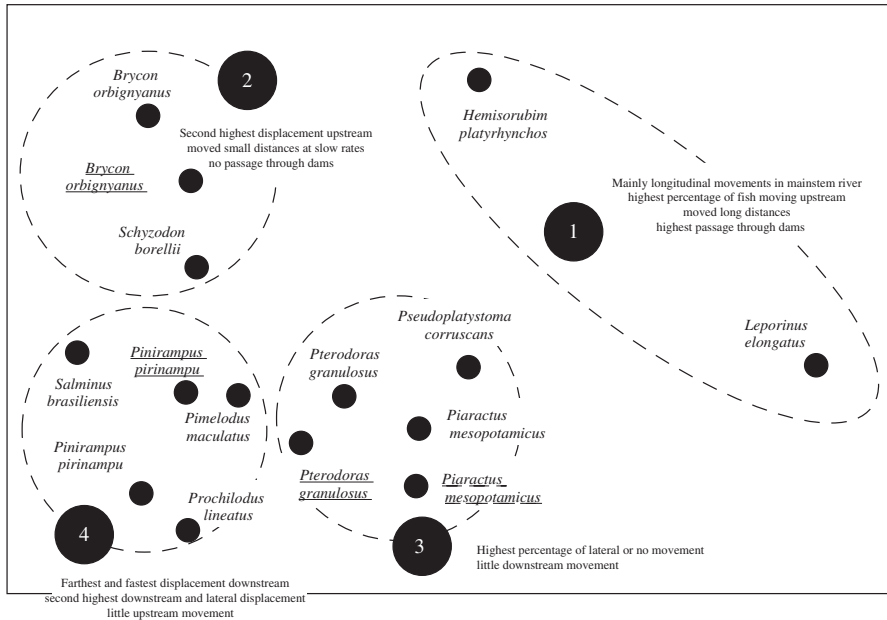
Fig. 3. Non-metric multidimensional scaling ordination of 11 fish species in the impounded Paraná River basin. Underlined species indicate juvenile life stage and circles indicate cluster numbers corresponding to cluster characteristics summarized in Table II.

by suggesting that migratory movements are more diverse; could be long, short, or at times absent; upriver, downriver, or lateral into tributaries and the diversity of movements varies within and among species.

This diversity in migratory patterns was illustrated by the four clusters identified by the analysis and by the ordination of species relative to movement characteristics. Cluster 1 included two species that followed those traditionally considered migratory species as they moved long distances along the mainstem river. The other three clusters departed from the traditional model in that some migrated only short distances (cluster 2), some migrated mainly in tributaries moderately long distances (cluster 3) and some migrated moderately long distances downstream (cluster 4). These results suggest that species have either evolved a wide spectrum of migratory patterns that is similar for adults and juveniles of the same species, adjust their migratory patterns to best utilize local conditions, or both.

The long-distance upstream spawning migrations into running water reportedly provide adequate distance for eggs to develop and hatch, and allow young to be carried into suitable nursery habitat as they drift downstream (Lucas & Baras, 2001). Upstream migrations have been reported for many species including *Prochilodus* spp., *P. corruscans*, *P. granulosus*, *S. brasiliensis* and *P. mesopotamicus* (Bonetto *et al*., 1981; Okada *et al*., 1989; Agostinho *et al*., 1993; Antonio *et al*., 2007; Makrakis *et al*., 2007*a,b*). This resilience is largely due to lotic environments in some large tributaries of the Paraná River, and the extensive backwaters that serve as nursery areas in the remaining floodplain above the Itaipu Reservoir (Nakatani *et al*., 2004; Sanches *et al*., 2006). Moreover, reservoir tributaries (*e.g.* Porto Primavera

Reservoir tributaries) have provided critical habitats (reproduction and nursery) for many migratory fish species (Silva *et al.*, 2011).

If desired habitats exist in downstream reaches, however, the migration pattern might be reversed. Such behaviour was reported for *Prochilodus* spp. and *Semaprochilodus* spp. in the Madeira River in the central Amazon region (Goulding, 1980; de Ribeiro & Petrere, 1990). Similarly, in the Mamore River, Bolivia, black prochilodus *Prochilodus nigricans* Agassiz 1829 migrated relatively short distances because adequate habitats existed in close proximity (Loubens & Panfilli, 1995). Thus, short distances (<100 km) travelled upstream by some species included in the present study and classified as long-distance migrants by Agostinho *et al.* (2003, 2007a), may be due to the availability of spawning and feeding areas close by [*e.g.* *B. orbignyanus*, *Leporinus obtusidens* (Valenciennes, 1836), *S. brasiliensis* and *Zungaro jahu* (Ihering 1898)]. Neotropical fishes in the study area exhibited diverse movement patterns that varied among species as well as among individuals within the same species. These species might travel hundreds of kilometres, but may not always travel long distances, and sometimes short migrations may be essential.

The present results indicate that upstream spawning migration may not be essential, and some individuals and species display no upstream or downstream migration, even though they might do so in other parts of their natural range. According to Lucas & Baras (2001), whether fish migrate depends on the distribution of feeding and spawning areas in the river system. Moreover, the minimum stretch required by migratory fishes to complete their life history varies according to species and regional characteristics of the waterscape and may even vary among individuals of the same species (Agostinho *et al.*, 2003). Many fishes recaptured at or near release sites, especially those released in the Itaipu Reservoir's tributaries, might have moved away but returned to the general area of release. Some fishes may not have had a chance to displace before they were taken by fishing; the fishery is more intense in the Itaipu Reservoir's tributaries where *B. orbignyanus* is an important target species. It is also likely that some members of the population may not migrate annually or at all. Migratory patterns may change both within and among species due to changes in environmental biotic and abiotic conditions; environmental conditions may induce alterations in the timing of the start and finish of migration and in migratory patterns. Bonetto *et al.* (1981) reported that many tagged characids such as *S. brasiliensis* and *P. lineatus* stayed near their release sites or moved only short distances. These passive-migratory subpopulations may spawn and support their populations in smaller home ranges. This behaviour, however, may lead to loss of genetic variability. Hatanaka *et al.* (2006) reported that populations of zulega *Prochilodus argenteus* Spix & Agassiz 1829 in the upper São Francisco River (Minas Gerais State, Brazil) immediately below Três Marias Dam showed lower heterozygosity in relation to populations further downstream that were able to migrate to locations with more favourable environmental conditions for reproduction.

Although various facilities have been constructed to aid passage of migratory fishes through dams in the Paraná River, the capacity of many fish species to swim upstream through fish passes (*e.g.* the existing Piracema Canal at the Itaipu Reservoir and ladder at the Porto Primavera Reservoir) might be limited. Four fish species (*L. elongatus*, *P. mesopotamicus*, *P. corruscans* and *P. lineatus*) were documented to ascend fish passes and continue upstream migrations. *Pimelodus maculatus* was not included in the analyses but it has often been reported to transcend fish ladders

(Borghetti *et al*., 1994; Fernandez *et al*., 2004, 2007). Fish passage facilities in the Paraná River appear to be highly selective and favouring passage of few species and not always the target ones (Agostinho *et al*., 2007c; Fernandez *et al*., 2007; Makrakis *et al*., 2007c, d; Oldani *et al*., 2007; Makrakis *et al*., 2011) and may require additional attention if their aim is to re-establish the longitudinal connectivity required by all or most of the species in the native fish assemblage.

The downstream long and slow displacements exhibited by many species (*i.e. P. lineatus*, *P. granulosus*, *P. maculatus* and *P. pirinampu*), most of them into the Itaipu Reservoir and its tributaries, may denote movements into feeding areas. Some characins and pimelodids exhibit large upstream longitudinal migrations for spawning and then migrate back downstream over hundreds of kilometres to feeding grounds that are often near river confluences or in floodplain lakes (Bonetto *et al*., 1981; Agostinho *et al*., 1993; Antonio *et al*., 2007). Factors responsible for the downstream migration of adults may include environmental harshness and excessive water velocity for efficient feeding, especially for those species having little or no adaptation to fast current (Lucas & Baras, 2001). Also, some fishes passed downstream over the Itaipu Dam, probably through turbines or spillway or through the Piracema Canal. Similar downstream movement over the dam was observed at the Yacyreta Dam.

Although less studied than longitudinal migrations in tropical river floodplain systems (Osório *et al*., 2011), lateral migrations are at least as important as long-distance longitudinal migrations in terms of fish production. In the Amazon floodplain, the lateral migration of the pirarucu *Arapaima gigas* (Schinz 1822) is reportedly a very cost-effective strategy for optimizing the spatial and temporal heterogeneity of resources of the várzea (Castello, 2008). The intense lateral migrations exhibited by a diversity of species in this study, especially to and from tributaries, illustrate the importance of these habitats for fish species' life cycles. The lateral movements focused not only on large tributaries (located above reservoirs) but also reservoir tributaries. Considering that the Paraná River is highly impounded, special attention should be given to the few remaining low-impact habitats as they continue to be targets of hydropower development that will probably intensify pressures on migratory fish stocks.

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