

Movement patterns of armado, *Pterodoras granulosus*, in the Paraná River Basin

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Abstract – We studied the migratory behaviour of armado, *Pterodoras granulosus*, in the Paraná River Basin of Brazil, Paraguay and Argentina, during 1997–2005. This species invaded the Upper Paraná River after upstream dispersal was facilitated when Itaipu Reservoir inundated a natural barrier. Fish were tagged ($N = 8051$) in the mainstems of the Yacyreta and Itaipu reservoirs, bays of major tributaries, the Paraná River floodplain above Itaipu Reservoir, and below dams. In all, 420 fish were recaptured of which 61% moved away from the release area. Fish moved a maximum of 215 km (mean 42), and at a maximum rate of $9.4 \text{ km}\cdot\text{day}^{-1}$ (mean 0.6). Of the 256 armados that moved away from the release site, 145 moved upstream towards unimpounded stretches of the Paraná River and 111 moved downstream into the reservoir and bays of its tributaries (maximum 150 km). Based on the observed migratory movements, we suspect that most of the reproductive output originates in tributaries to the reservoirs. The ability of this species to expand its range presents a conundrum by pitting fishery management interests against conservation needs. Maintenance of the important armado fisheries depends on the ability of the species to migrate freely to use spawning and nursery areas in reservoir tributaries and floodplains. However, its ability to migrate long distances can allow this non-native species the opportunity to invade most of the Upper Paraná River.

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Introduction

The diversity of fish in the Paraná River is among the greatest in the world (Agostinho et al. 1994). However, impoundments have drastically modified the landscape, the hydrological and limnological features, and the distribution of aquatic habitats in the basin. Due to reduction in longitudinal and lateral connectivity, some species have almost disappeared from the basin's higher reaches, particularly species having long migrations at some stage of their life cycle. Nevertheless, impoundment of the river has also facilitated the spread of some species. For instance, the armored catfish *Pterodoras granulosus* (Valenciennes, 1833) (Siluriformes, Doradidae), popularly known as armado or abotoado, has expanded its

distribution after completion of Itaipu Reservoir. The armado was originally native to the Middle and Lower Paraná River, with its distribution into the Upper Paraná River restricted by a natural barrier, Sete Quedas Falls. However, these falls were flooded by Itaipu Reservoir, allowing armado and other species dispersal into the Upper Paraná River (Zawadzki et al. 1996).

The armado inhabits various environments including large rivers and lagoons, but avoids small streams (Agostinho et al. 2003). In the Upper Paraná River, it usually grows to 70 cm total length (Agostinho et al. 2003) by consuming filamentous algae, terrestrial macrophytes (including fruits, seeds and leaves), crustaceans, mollusks, insects and small fish (Hahn et al. 1992, 2004). Reportedly, this fish contributes to

dispersion of plant species (Stevaux et al. 1994; Pilati et al. 1999). Relative to other fish species in the Parana River, the armado has one of the most diverse diets; this flexibility has likely facilitated its increased population density in Itaipu Reservoir (Agostinho et al. 1994). Indeed, armado is presently the principal species in the commercial and artisanal fisheries of Itaipu Reservoir (Agostinho et al. 2003); 70% of the armado harvest is represented by juveniles, and overfishing has been reported (Agostinho & Gomes 2002).

The armado is considered a migratory species by most authors (Bonetto et al. 1971; Agostinho et al. 1994, 2003), but little is known about their migratory patterns. Females reach sexual maturity within 5 years (Feitoza et al. 2004) at about 36 cm total length (Agostinho et al. 1994). Mature fish are thought to make spawning migrations during the wet season between December and March (Suzuki et al. 2004) towards rivers and channels of the floodplain. Mark-recapture studies conducted by Bonetto et al. (1971) and Agostinho et al. (1994) provided only limited information about migratory behaviour. Therefore, we undertook a mark-recapture study to analyse the migratory behaviour of armado in the Parana River in terms of distance travelled, migration routes, seasonality and life stage. Our aim was to improve basic

knowledge about this little-known fish species and to help foresee the potential for this species to expand its range throughout the Upper Parana River.

Materials and methods

Study region

The Parana River flows through south-central Brazil, south-eastern Paraguay and northern Argentina before it joins the Plata River in central Argentina. It is the 10th longest river in the world (4695 km) and has a 2.6×10^6 km² drainage area that includes most of south-central South America. The Parana River is customarily divided into the Upper, Middle and Lower Parana River (Bonetto 1989), each with distinctive geographic and biologic characteristics. Next to the extensive agriculture development, dams are the most common signs of human interference on the physiography of the basin.

Our study area included the Upper and Middle Parana River, encompassing approximately 1425 river kilometres and from upstream to downstream the Porto Primavera Reservoir (Brazil), the Upper Parana River floodplain above Itaipu Reservoir and the Itaipu (Brazil/Paraguay) and Yacyreta (Paraguay/Argentina) reservoirs (Fig. 1). The Upper Parana River floodplain

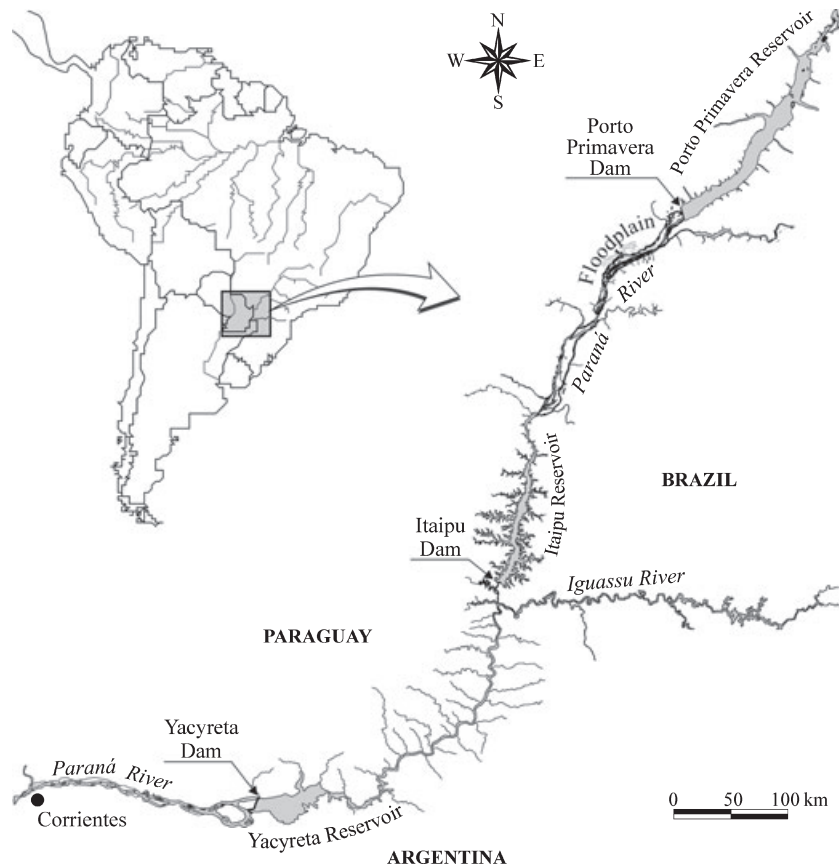


Fig. 1. Study area in the Parana River along the borders of Argentina, Brazil and Paraguay.

(Fig. 1) stretches from the Porto Primavera Dam downstream to the upper reaches of the Itaipu Reservoir. This 237-km stretch has no dams and may reach up to 20 km in width. The flooded areas include channels, lagoons and elongated lowlands (Souza-Filho & Stevaux 2004). 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-border of Brazil, Argentina and Paraguay. The Middle Paraná River flows 669 river kilometres south-west and then west, forming the border between Paraguay and Argentina, until the city of Corrientes, Argentina. Many tributaries to the Middle Paraná have falls near their confluence with the Paraná River, limiting fish passage upriver from the mainstem (Garcia 1999).

Fish passage facilities are provided at three locations. At Porto Primavera Dam, a fish elevator has been in operation since November 1999. The elevator raises the fish 19 m before releasing them into the reservoir (Companhia Energética de São Paulo 2000). This dam also has a fish ladder that stretches 520 m to transcend the 19 m difference in elevations (Companhia Energética de São Paulo 2002). At Itaipu Dam, the Canal da Piracema has allowed ascension of fish into Itaipu Reservoir and upstream reaches since December 2002. The Canal da Piracema partially utilises about 6 km of the Bela Vista River, in addition to man-made canals, lagoons and fish ladders, and extends close to 10 km in length, overcoming a 120-m difference in elevations (Fiorini et al. 2006). Moreover, an experimental fish ladder (27 m high and 155 m long) devoted to research on fish passage operates next to the tailrace of one of the turbines (Fernandez et al. 2004), but due to its experimental nature the ladder does not reach the reservoir. In addition to a navigation lock, the Yacyreta Dam was equipped with two fish elevators, one on each border, to allow fish passage (Garcia 1999). The elevators raise the fish 23 m to release them into Yacyreta Reservoir.

Fish marking

Marking was done in cooperation with hydroelectric companies including Companhia Energética de São Paulo, Itaipu Binacional (Brazil–Paraguay), and Entidade Binacional Yacyreta (Paraguay–Argentina). Marking and recapture of armado expanded over 9 years in 1997–2005. In Porto Primavera Dam, fish 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, fish were purchased from commercial fishermen. At the Itaipu Reservoir and bays of its tributaries, fish were collected with gill nets and long-lines, and purchased from fishers. Fish rescued from turbines in the Itaipu

Dam were tagged and released into the Itaipu Reservoir. At the Itaipu Dam, fish caught with cast nets in the experimental ladder were also tagged. In the Canal da Piracema, fish were collected with cast nets, long-lines and gill nets. At Yacyreta Reservoir, fish were caught in the elevators, tagged and released into the reservoir. All fish were released near the location where they were caught.

Before release, fish 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. Each tag contained a number and a message with information about the tagging programme and tag reporting. Fishers were asked to provide capture date and location. Tagged fish were released throughout the 9 years of study. Fish tagging and its purpose were advertised in fisher colonies and clubs, schools, churches, radio and television to stimulate tag returns. Additionally, we distributed leaflets, posters, T-shirts and caps to individuals and groups as a promotional tool. Rewards for returns included raincoats, lanterns, thermal bottles and collaboration certificates.

Data analysis

Data were analysed to estimate movements after pooling releases and recaptures over all study years. Although it is likely that annual differences could have existed, no attempt was made to sort them out because at this preliminary stage of inquiry they were not the focus of our study, and because our sample sizes were not large enough. Fish recaptured within 10 days of release were excluded from analyses of movements because they might not have had time to disperse, but were included in the determination of recapture rate.

Movement patterns were analysed through basic descriptive statistics and selected statistical comparisons. Descriptive statistics including means, maxima, standard deviations and percentage frequency distributions were estimated for distance moved (shortest over-water distance between release and recapture sites) and rate of movement (ratio of distance moved to days between release and recapture). A chi-squared test of homogeneity was used to test if fish were equally likely to move upstream, downstream or stay in place, relative to their release sites (bays of tributaries, main reservoirs, below dams and floodplain), to life stage (juvenile and adult) and to season (wet and dry). An analysis of variance was used to test if distance moved and rate of movement of the fraction of fish that moved away from the release sites to other regions of the river differed relative to direction moved (upstream or downstream), release time (wet or dry season), release site (bays of tributaries, main reservoirs, below dams and floodplain) and life stage (adult

or juvenile). For the wet versus dry season comparison, only fish that moved and that were released and recaptured during the same season (i.e., wet or dry) were included in the analyses, because otherwise our data would not allow us to discern in which season the movement occurred.

Results

During the study period, we tagged and released 8051 armados in bays of major tributaries to the Itaipu Reservoir, in the main stems of the Yacyreta and Itaipu reservoirs, in the Paraná River below Porto Primavera Dam, and in floodplains above Itaipu Reservoir including those of large tributaries on the eastern margin. Relative to season, 89% of the fish was released during the wet season (October–March) and 11% during the dry season (April–September). Regarding life stages, 65% of the fish released were adults (i.e., ≥ 36 cm total length) and 35% juveniles, with total length ranging from 15.9 to 86.2 cm, and averaging 39.7 cm (SD 12.2).

Of 420 fish recaptured (5.2%), 27 were captured within 10 days of release and excluded from the analyses of movement patterns. Of the remaining 393 fish, 37% moved upstream, 24% moved downstream and 39% stayed within 1 km of the release area. There were no length differences between the fish that moved away from the release site and those that stayed in the area near the release site ($F = 1.21, P = 0.27$). Moreover, distance moved did not differ between juveniles and adults ($F = 0.09, P = 0.76$), or between fish released during the wet or dry seasons ($F = 0.18, P = 0.67$). However, there were differences between the percentage of fish that moved away from the release site (Table 1) relative to whether release occurred in bays of tributaries, main reservoirs, floodplain or below the dams ($\chi^2 = 41.4, P < 0.01$); between distance moved by fish that moved upstream (mean 50 km, maximum 215) compared with those that moved downstream (mean 27 km, maximum 150; $F = 6.73, P = 0.01$); and between fish released in the

main reservoirs (mean 67 km, maximum 215) compared with those released in the floodplain (mean 34 km, maximum 125) or Itaipu Reservoir’s tributaries (mean 32 km, maximum 160) ($F = 7.55, P < 0.01$).

Various movement patterns were observed. Nine armados released in tributaries to the Itaipu Reservoir moved downstream into the reservoir and then up the reservoir an average 65 km (maximum of 125 km) into the Paraná River, as far upstream as the floodplain, and one fish moved from Yacyreta Dam upstream into Yacyreta Reservoir 140 km. Some fish ($N = 65$) also moved downstream within the Itaipu Reservoir an average 19 km (maximum of 81 km), and some ($N = 20$) moved downstream an average 50 km (maximum of 150 km) and then entered one of the reservoir’s tributaries. However, one fish moved downstream past Itaipu Dam, and moved another 150 km downstream in the Paraná River. Similarly, two fish moved downstream pass Yacyreta Dam, an average 3 km below the dam. Fish released below dams only moved downstream, and no marked fish were detected to have moved upstream through the dams. Nevertheless, 2461 armados were collected for tagging in the Itaipu experimental ladder, Porto Primavera ladder, Canal da Piracema, and the Yacyreta Dam elevators, indicating that fish were at least attempting to use the fish passes.

The mean length of time between release and recapture was 216 days (SD 223), whereas the maximum time was 1363 days. Correspondingly, the average rate of movement was $0.6 \text{ km}\cdot\text{day}^{-1}$ (SD 1.3), whereas the maximum rate was $9.4 \text{ km}\cdot\text{day}^{-1}$. Rate of movement did not differ significantly between fish that moved upstream and those that moved downstream ($F = 2.90, P = 0.09$), between fish released at different sites ($F = 1.34, P = 0.23$), between juveniles and adults ($F = 0.30, P = 0.58$), or between fish released during the dry or wet seasons ($F = 2.39, P = 0.12$). Nevertheless, armados moved upstream (mean $1.2 \text{ km}\cdot\text{day}^{-1}$) faster than downstream (mean $0.5 \text{ km}\cdot\text{day}^{-1}$; $F = 7.07, P = 0.008$).

Table 1. Movements of armado in the Paraná River Basin during 1997–2005.

Release environment	Number tagged	Captured away from release site (%)	Mean distance travelled (km)		Maximum distance travelled (km)	
			Upstream	Downstream	Upstream	Downstream
Floodplain	1157	2.3	35 (51)	29 (17)	125	60
Main reservoir	2436	2.6	81 (57)	38 (58)	215	150
Bays of tributaries†	3601	9.0	36 (45)	26 (39)	160	150
Below dam‡	857	0.5		28 (35)		80
All	8051	5.2	50 (53)	27 (37)	215	150

Standard deviations are given in parentheses.

†Fish released in bays of tributaries only in Itaipu Reservoir.

‡Fish released in the experimental ladder below Itaipu Dam.

Moreover, fish released in the mainstem of reservoirs moved faster (mean $1.3 \text{ km}\cdot\text{day}^{-1}$) than those released in bays of tributaries (mean $0.5 \text{ km}\cdot\text{day}^{-1}$), but as fast as those released in the floodplain or below the dams (mean $0.8 \text{ km}\cdot\text{day}^{-1}$; $F = 5.52$, $P = 0.001$).

Discussion

The 5.2% recapture rate observed in our study was small but similar to that reported by Bonetto et al. (1981) in the Middle Paraná River in Argentina (4.5%), and by Okada et al. (1989) in Itaipu Reservoir (3.9%). These recapture rates reflect fishing intensity that is likely biased low due to errors associated with tag loss, nonreporting and possibly handling-induced mortality. Obtaining information about fish movements using mark and recapture in this relatively remote region of South America is challenging; we suspect that in the future, radio-tracking or related electronic surveillance technologies will improve our ability to monitor movement patterns.

The movement patterns of the armado, with most moving away from the main reservoir towards the unimpounded stretches of the Paraná River above Yacyreta and Itaipu reservoirs, evidence the migratory behaviour of the species. The observed movements during the wet season were apparently for reproduction, with fish moving upstream fast and downstream at a slower rate. Agostinho et al. (2003) commented that the species uses the upstream area of the Itaipu Reservoir and probably large tributaries to reproduce, spawning repeatedly during the spawning season (December–March), which occurs later than that of other migratory species in the basin. Similar to our findings, Okada et al. (1989) reported maximum movement distances near 200–220 km for armado released in Itaipu Reservoir, but Bonetto et al. (1981) reported longer displacements (308 km) for fish released in the Middle Paraná River, Argentina. Much longer distances are covered by the large pimelodid catfishes of the Amazon River, which descend the Amazon as eggs, larvae and juveniles, and ascend it as large juveniles or adults, a lifetime journey of 7000–8000 km (Barthem & Goulding 1997), occurring over several years. However, armado's upstream movements are evidently limited by dams without locks or fish passages as the species has not been reported upstream of the Jupia Reservoir (Paraná River) with its distribution upstream apparently limited by the Ilha Solteira Dam (Paraná River), or upstream of the Capivara Dam in the Parapanema River. In spite of high concentrations below ladders and in the initial sections of the ladders (Fernandez et al. 2004; Makrakis et al. 2005), few armados reach the upper sections of ladders. Fish ladders usually are turbulent environments that increase drag forces on fish

swimming and may also cause difficulties in orientation for some fish species, inhibiting upstream progress through them (Lucas & Baras 2001).

The downstream movements registered for 24% of the armados recaptured later than 10 days after release, especially in Itaipu Reservoir and in bays of its tributaries (maximum of 150 km), suggest migrations toward feeding habitats; after spawning, the parental stock apparently returns downstream, more slowly, restoring energy lost in the upstream migration. A maximum downstream distance movement of 1054 km was registered to one individual released in the Middle Paraná River, Argentina (Bonetto et al. 1981), below Yacyreta Dam. Similar behaviour was reported for various characin and pimelodid species, migrating back downstream over hundreds of kilometres to find feeding areas (Godoy 1972; Bayley 1973; Bonetto et al. 1981; Agostinho et al. 1993). Armados passed downstream over the Itaipu and Yacereta dams, probably through turbines and spillways given that at the time of passage the Canal da Piracema next to Itaipu Dam was not operational.

Swimming speed limits the places to which, and times of the year when a fish can travel. Considering the rates of movement in our study and those reported for armado by Bonetto et al. (1981) and by Okada et al. (1989), we speculate that armados moving upstream through these long reservoirs would require weeks to reach the river above Yacyreta Dam or the floodplain above Itaipu Dam, although potentially some individuals might traverse the reservoirs faster. Because of this limitation, we suspect that much of the reproductive output for this species originates in tributaries to the reservoirs. From a fishery management perspective it would make sense to protect potential spawning sites in the tributaries and fish migrating into the tributaries during this spawning period.

The minimum stretch of unimpounded river required by migratory fish to complete their life history varies according to species and regional characteristics of the waterscape, and may even vary among members of the same species (Agostinho et al. 2003). Conceivably, armados recaptured at or near release sites, especially those released in the Itaipu Reservoir's tributaries, might have moved away but returned to the area of release. Also some may not have had a chance to move before they were taken by fishing; the armado fishery is more intense in the Itaipu's tributaries. Alternatively, some members of a population may not conduct annual migrations or may not migrate at all, depending on the distribution of feeding and spawning areas in a river system (Lucas & Baras 2001). Bonetto et al. (1981) reported that many marked migratory characids stayed near the release sites or moved only short distances, but that these subpopulations spawned and supported their population.

Most seasonal strategists in tropical rivers spawn at the onset of the wet season, or under maximum floods, and some of them start upstream migrations during the late dry season. Considering that armados spawn during the maximum flood period (December–March), its slow average migration rate suggests it might be an early migrant. Moreover, our data suggest that juveniles accompany adults during upstream migrations. For riverine species, rheotaxis and information transfer should probably be invoked for homing mechanisms. Reportedly, for some migratory species, juveniles accompanying adults during the spawning runs, and their return to previously occupied feeding and resting habitats, intimately rely on the possibility of memorising characteristic features of the home area (Lucas & Baras 2001).

The migrations of armados present a conundrum by pitting fishery management interests against conservation needs. On one hand, this species is currently the most important in the commercial and artisanal fisheries of Itaipu Reservoir (Agostinho et al. 2003) and can potentially become as important in other reservoirs of the Upper Paraná River. Maintenance of these fisheries depends on the effective management of the spawning and nursery areas in reservoir tributaries and floodplains, and on the ability of fish to migrate freely to use these habitats. On the other hand, the species is exotic to the Upper Paraná River, and due to its ability to migrate long distances, is capable of invading most of the upper basin. There is currently no information available to assess the magnitude of potential effects of expansion into reservoirs or into lotic environments that retain riverine communities, so we assume that extension of their range is detrimental to the health of the fish community of the upper basin. From a practical perspective, it is questionable whether the eradication of armado from Upper Paraná River is feasible in view of the lack of technology to achieve this end, or desirable in view of the fishery benefits. Given the limited existing information, we suspect that any ecological effects armados may have in the basin may be reversed when society no longer has a need for artificial reservoirs if native fish communities are maintained in unimpounded sections of the basin. Nevertheless, it is vital to implement efforts to control expansion of this species. Such strategies might include management of fish passes to preclude spreading, but research is needed to identify passage requirements. Education efforts are needed to alert the public about the exotic status of the species to avoid transplantations into regions where passage is precluded by natural or anthropogenic obstacles. Lastly, environmental impact studies should be required prior to construction of diversions, canals, or additional dams which could permit range expansion.

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