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ORIGINAL PAPER

Migration and spawning of female surubim (*Pseudoplatystoma corruscans*, Pimelodidae) in the São Francisco river, Brazil

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Abstract Surubim, *Pseudoplatystoma corruscans*, is the most valuable commercial and recreational fish in the São Francisco River, but little is known about adult migration and spawning. Movements of 24 females (9.5–29.0 kg), which were radio-tagged just downstream of Três Marias Dam (TMD) at river kilometer 2,109 and at Pirapora Rapids (PR) 129 km downstream of TMD, suggest the following conceptual model of adult female migration and spawning. The tagged surubims used only 274 km of the main stem downstream of TMD and two tributaries, the Velhas and Abaeté rivers. Migration style was dualistic with non-migratory (resident) and migratory fish. Pre-spawning females swam at ground speeds of up to 31 km day^{-1} in late September–December to pre-spawning staging sites located 0–11 km from the spawning ground. In the spawning season (November–March), pre-spawning females migrated back and forth from nearby pre-spawning staging sites to PR for short visits to spawn, mostly during floods. Multiple visits to the spawning site suggest surubim is a multiple spawner. Most post-spawning surubims left the spawning ground to forage elsewhere, but some stayed at the spawning site until the next spawning season. Post-spawning migrants swam up or downstream at ground speeds up to 29 km day^{-1} during January–March. Construction of proposed dams in the main stem and tributaries downstream of TMD will greatly reduce surubim abundance by blocking migrations and changing the river into reservoirs that eliminate riverine spawning and non-spawning habitats, and possibly, cause extirpation of populations.

Keywords Life-history · Home range · Homing · Migratory fish · Fish conservation

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Introduction

The large piscivorous catfish, surubim, *Pseudoplatystoma corruscans*, occurs in the Paraná River

(Argentina, Brazil, Paraguay, and Uruguay) and São Francisco River (Brazil) (Lundberg and Littmann 2003). In the São Francisco River, it grows to 120 kg (Sato et al. 2003) and is one of the most important fisheries resources (Menezes 1956; Godinho et al. 1997; Godinho and Godinho 2003). Surubim is a major trophy for recreational anglers due to its large size and it is the most valuable fish for commercial fisheries because of its outstanding taste.

Surubim spawns in the rainy season, when females broadcast about 1.5 million, 1 mm diameter, non-adhesive eggs (Sato et al. 2003) during November–January (Godinho et al. 1997; Brito and Bazzoli 2003). The semi-buoyant eggs hatch in 20 h at 24°C (Sato et al. 2003) and eggs and larvae drift with the flow. Floodplain lakes downstream of spawning areas are likely the most important nursery grounds, but importance of the river channel as nursery habitat has not been evaluated. Surubim is a migratory species, however life history movements and spawning of adults are poorly known (Carolsfeld et al. 2003).

Surubim harvest in the São Francisco River has shown indications of collapse (Godinho and Godinho 2003). Reports in the first half of the 20th century, compiled by Menezes (1956), describe fisheries that do not occur anymore. For example, Menezes (1956) mentioned the capture of 6,000 surubims ranging from 5 to 50 kg in a floodplain lake in just one seine haul and in other seine hauls capturing 12,000 surubims. More recently, surubim catch in an important fishing area has declined from 10.3 kg fisher day^{-1} in 1987 to 0.8 kg fisher - day^{-1} in 1999 (Godinho et al. 1997; A. L. Godinho, unpublished data). Construction of any of the 16 proposed new dams on the main stem and tributaries is a major concern for the future of surubim and its fishery in the São Francisco River.

In the present study, we radio tracked 24 adult female surubims in the São Francisco River for as long as 32 months during 2000–2003 to investigated migrations, linear home ranges, homing, and to identify river reaches associated with spawning and non-spawning activities. We used this information to develop a conceptual model of migrations and spawning of females. The present study is one of the first to use biotelemetry to study migration and spawning of a widely ranging Neotropical freshwater fish species.

Materials and methods

Study site

The São Francisco River flows mostly northward 3,160 km in Eastern South America (Kohler 2003). The study area was the 1,047 km long section of the river downstream of Três Marias Dam (TMD), located at river km (rkm) 2,109. The stretch most intensively studied was the 274 km directly downstream of TMD (Fig. 1). The river from TMD to Pirapora Rapids (PR, rkm 1,980) has steep gradient, fast current, and rapids. The bottom is mostly rocky. The few narrow floodplains in this reach seldom flood because of the regulated flow from TMD. At PR, the river level descends 8 m within a distance of 1 km. Downstream of PR, the river has low gradient, slow current, no rapids, and mostly sandy bottom. Large floodplains, up to tens of km wide (Sato and Godinho 2003), are present downstream of the Paracatu River mouth at

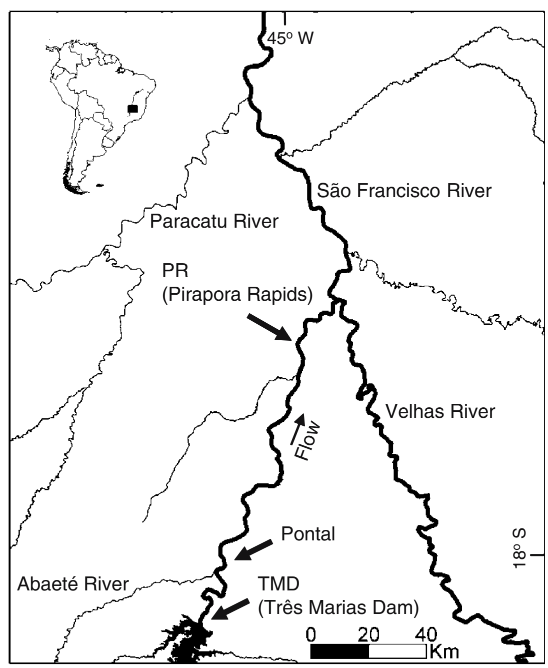

Fig. 1 Study area for female surubim in the São Francisco River Basin. *Arrows* show sites with data-logging receivers to automatically track fish: Três Marias Dam (*TMD*) at rkm 2,109, Pontal at rkm 2,077, and Pirapora Rapids (*PR*) at rkm 1,980. Only major tributaries are displayed

rkm 1,866. The rainy season is from October to March when rain storms supply 91% of the annual rainfall (1.13 m).

Fish tagging and tracking

We captured two females in the main stem within 3–7 km downstream of TMD and 22 females within 1 km downstream of PR. We tagged fish in December 2000, April–June 2001, December 2001, and March 2002. We captured fish mostly with 'tarrafão,' a specialized bottom drift net (Sato and Godinho 2003), and few were captured with cast or drift nets. We purchased one fish caught by harpoon from a commercial fisher.

We tagged and released most fish soon after capture, but we restrained some with a 5-m long rope tied around the mouth for several hours, and we kept one fish overnight in a 300 L tank. We immobilized fish for tagging in a tank filled with 150 L of river water that was frequently renewed or oxygenated. We immobilized fish in the tank using electronarcosis with non-pulsed 40–60 V DC (Kynard and Lonsdale 1975; Ross and Ross 1999), and then we reduced current to 25–40 V DC during tagging.

We inserted tags into the body cavity through an incision on the ventral middle line. The antenna extended posterior through the lateral body wall and outside the fish. We used Lotek© coded radio tags (frequency = 149.780 MHz, burst rate = 5 s, transmission life = 4 years). Tag weight in air (170 g) as a percent of fish weight was ≤1.8%. We determined sex and reproductive stage of fish during surgery using unaided visual observations of the ovaries through the incision. We classified reproductive stage of fish similar to Kynard and Kieffer (2002) as early-stage (ES, ovaries not containing maturing or mature eggs that could be spawned the present spawning season) or late-stage (LS, ripe ovaries). We added Stress Coat® or LabProtect® to the tank's water during surgery to aid fish recovery. We weighed and measured the standard length of each fish, and then released each tagged fish within 1–3 km of the capture site.

We manually tracked fish from December 2000 to July 2003 using a Lotek receiver. We located fish almost every month during the spawning season (November–January) and at least every other month during the non-spawning season. Most tracking used a boat, but we used a helicopter in July 2002 and July 2003. Most tracking was in the main stem within 274 km downstream of TMD; however, we tracked for fish in the main stem downstream to rkm 1,062 and tracked at least once in most major tributaries (Abaeté, Espírito Santo, Janeiro, Jequitaí, Pandeiros, Paracatu, Paraúnas, Preto, Sono, Urucuia, and Velhas rivers). We searched a total of ~7,500 km of river to locate tagged fish.

We also tracked fish using fixed-location, data-logging Lotek receivers at TMD, Pontal, and PR (Fig. 1). The TMD receiver had one antenna that surveyed for fish presence at the dam's stilling basin and in the downstream part of the tailrace. The Pontal receiver had two antennas that surveyed the mainstem (one surveyed downstream of the Abaeté River intersection and one surveyed upstream of the Abaeté River intersection) to determine up or downstream movement direction of fish and a third antenna surveyed the mouth of the Abaeté River to monitor fish movement in and out of the tributary. The PR receiver had two antennas (one antenna surveyed the rapids head and one antenna surveyed the rapids tail) to determine up or downstream movement direction of fish at the rapids. We eliminated false-positive records of codes logged by data-logging receivers using procedures described by Godinho and Kynard (2006).

We measured water temperature, turbidity, and discharge of the São Francisco River at PR. We determined daily mean water temperature from measurements taken every 3 h with an Onset StowAway® logger. Daily water turbidity was provided by SAAE (the Pirapora municipality water supply company, Brazil) and the mean daily discharge was provided by CEMIG (the Minas Gerais state power company, Brazil).

Data analyses

The PR receiver detected short-term movements (visits) of fish to PR. We determined duration of each visit during the rainy season using arrival and departure day and time. We also determined arrival and departure directions. We analyzed the frequency of visits for relationships with classes of water temperature, turbidity, and discharge at PR following methods described by Godinho and Kynard (2006). We tested frequency of fish visits for differences relative to classes of water temperature, turbidity, and discharge.

We classified migration as pre-spawning staging if it occurred before the spawning season (i.e., before late September), or if fish moved from a non-spawning site to a pre-spawning staging site in the spawning season. A spawning migration was a movement from a pre-spawning staging site to the spawning ground. We named a migration at the end or after the spawning season (February–March) a non-spawning migration (=post-spawning migration). We termed a migration a sprint migration when fish moved a distance >32 km at ground speed ≥1.9 km day^{-1}. We analyzed migrations for direction and type of migration.

We determined the total linear home range, i.e., the most upstream rkm minus the most downstream rkm each fish used (Young 1998), for all fish tracked during spawning and non-spawning seasons. We calculated the non-spawning linear home range, i.e., the most upstream rkm minus the most downstream rkm each fish used during the non-spawning season, using fish located at least twice during that season. We excluded the locations of fish during pre-spawning staging or non-spawning migrations from the calculation of non-spawning linear home range. If a fish used different river reaches in different non-spawning seasons, we estimated the non-spawning linear home range of the fish for each season. We tested total and non-spawning linear home ranges for relationships with fish body weight and Fulton condition factor. We tested mean body weight and Fulton condition factor for difference between resident fish (=total linear home range ≤2 km) and migratory fish (=total linear home range >32 km).

We used SAS for data analysis (SAS Institute 1999). We tested continuous variables for normality (Shapiro-Wilk test). We transformed non-normal variables (Sokal and Rohlf 1995) and tested again for normality. All non-normal variables achieved normality after transformation. Then, we used *t*-test for comparisons of data between two groups according to the homogeneity of variances (Sokal and Rohlf 1995), and we used Pearson correlation to test relationships between continuous variables. If we did not reject a null hypothesis, we determined the power of the test (Borenstein and Cohen 1988; Cohen 1988). We used chi-square to test frequency data among classes of environmental factors. We set the level of significance = 0.05 and power = 0.80.

Results

Characteristics of tracked surubims

We tagged 24 female surubims, 20 were LS fish (with ripe ovaries). Standard length of fish was 93–134 cm (range) and body weight was 9.5–29.0 kg (range). We tracked fish for 1–453 days (mean = 223 days) and the number of locations per fish ranged from 2 to 329 (mean = 61). Twenty-three fish provided tracking data. Thirteen tagged fish were harvested during the study. Fishers returned 12 tags and we found one tag at a house (fish harvested by a fisher). Two additional fish disappeared from the study area before the end of the study and perhaps were also harvested. Thus, 15 of 24 females (62.5%) were confirmed or suspected of being harvested by fishers.

Locations during spawning and non-spawning seasons

During the spawning season, we located tagged surubims most frequently at PR, followed by fish located downstream of PR, and finally, by fish located at Pontal (Fig. 2). Most surubims (n = 12) used a different river reach during the spawning and non-spawning seasons. After the spawning season, fish moved both up and downstream from the spawning reach.

Ten fish tagged at PR stayed at the rapids after release or moved downstream, and then, returned several days later. Two other fish (25 and 27) returned to PR during the spawning season after remaining downstream for 6–8 months (Fig. 2). Fish 27 returned to PR in November 2003 after the study period.

The PR receiver detected 43 visits by eight surubims during the three rainy seasons we

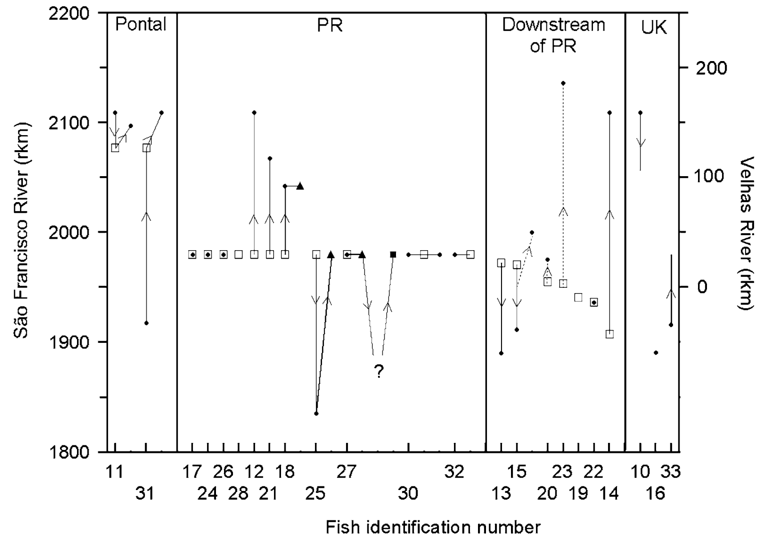

Fig. 2 Female surubim spawning and non-spawning locations and migrations in the São Francisco River study area. Fish are grouped into four clusters according to the river reach where they were located most frequently during the spawning season: Pontal, Pirapora Rapids (*PR*), downstream of PR, and unknown (UK). Within each cluster, fish with similar movements are grouped together. *Squares*, *triangles*, and *filled squares* indicate the most frequent location of fish during the spawning season. *Squares* = fish location during first spawning season, *triangles* = fish location during second spawning season, and *filled squares* = fish location during third spawning season. *Dots* mark the farthest up or downstream location of fish during the non-spawning season. *Question mark* = unknown destination. *Solid lines* = movements in the São Francisco River; *dotted lines* = movements in the Velhas River. *Arrows* show movement direction

tracked fish. Month and number of visits (in parenthesis) follow: December (8), January (15), February (8), and March (12). The number of visits per fish was 2–10. Duration of visits ranged from 1 to 6 days and 81% of visits lasted ≤2 days. The arrival time for 34 visits was during the day (06:38–18:04 h) for 82% of the visits.

There was a significant association between the frequency of visits by fish and river discharge ($\chi^2 = 28.5$, $df = 4$, $p < 0.0001$), turbidity ($\chi^2 = 14.6$, $df = 4$, $P = 0.006$), and water temperature ($\chi^2 = 11.8$, $df = 3$, $P = 0.008$). Visits occurred more frequently during discharge peaks (49%), turbidity peaks (42%), and temperature troughs (47%, Fig. 3).

We manually located for 21 times six pre-spawning staging fish that visited PR during a rainy season. These fish staged 0.4–10.6 km downstream of PR, but they were no farther than 2 km from PR most (76%) of the locations.

Female surubims migrated to Pontal just before or during the spawning season. Fish 31 migrated to Pontal 2 weeks before the spawning season and stayed there the entire season (Fig. 4). The fish captured by harpoon (fish 11) moved downstream from TMD to Pontal during the spawning season (Fig. 4). While at Pontal, these fish stayed in the main stem, but each made several trips of short duration (usually <2 days) into the Abaeté River. These movements were likely short spawning migrations.

The spatial distributional of female surubims was greater during the non-spawning season than during the spawning season (Fig. 5). The greatest numbers of females were at PR. Most fish used the main stem, and a few used the Velhas River. Three fish migrated 12–47 km upstream in the Velhas River and we found one tag on land near the riverbank at rkm 183 in the Velhas River. This fish was harvested and the tag discarded.

Five surubims (fishes 10, 11, 12, 14, and 31) were at TMD for 8–211 days (Fig. 4). Only fish 14 was located in the TMD tailrace, where it was manually tracked, and then was harvested 5 days after being tracked. Most locations of fish at TMD were detected by the data-logging receiver, which tracked fish in the dam's stilling basin and the lower part of the tailrace. However, fish were not

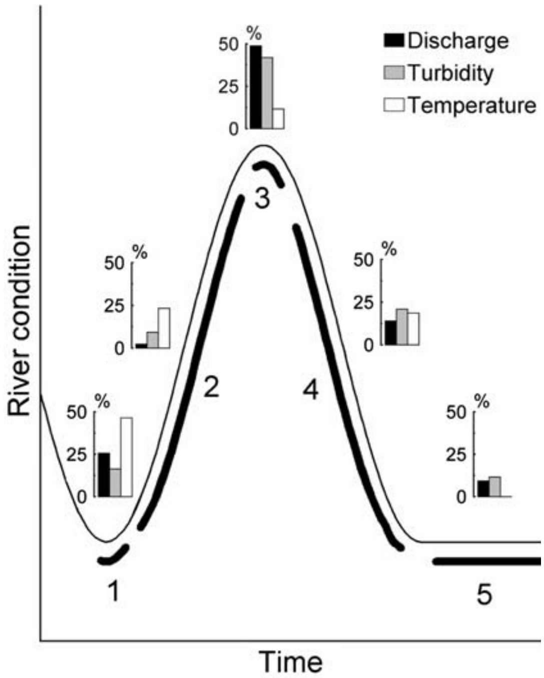

Fig. 3 Frequency of visits of female surubims to Pirapora Rapids during various classes of river condition in the São Francisco River. The *thin line* represents the theoretical variation of the river condition (*discharge*, *temperature*, or *turbidity*) through time as determined by periodic function. The *thick lines* define timing of the following classes of river condition: trough (1), increasing (2), peak (3), decreasing (4), and stable (5). The relative frequency of visits by female surubims for each river class condition is shown in the histograms

within the short range of the TMD antenna all of the time they were at TMD. It is likely that other tagged females (more than fish 14) moved to the upstream part of the tailrace or remained in the tailrace, just out of the range of the antenna.

Two female surubims returned to the same pre-spawning site they used previously. Fish 12 moved from a pre-spawning staging site at rkm 1,969 to PR and then returned to the same pre-spawning site (Fig. 4). Fish 24 returned three times to the same pre-spawning staging site at rkm 1,977–1,978 after visiting PR.

Linear home range

We tracked 18 fish during the spawning and non-spawning seasons. Total linear home range for the 18 fish was 87 ± 70 km (mean ± SD) and ranged from 1 to 210 km. Total linear home range was ≤2 km for four fish, 32–145 km for 11 fish, and >191 km for three fish. Total linear home range did not have a significant correlation with the number of days that fish were tracked (r = -0.29, P = 0.27, power = 0.22), body weight (r = -0.16, P = 0.53, power = 0.09), or Fulton condition factor (r = 0.19, P = 0.45, power = 0.12). No difference in body weight (t = 0.22, df = 16, P = 0.83, power = 0.04) or Fulton condition factor (t = -1.34, df = 16, P = 0.20, power = 0.23) was found between resident and migratory fish.

Non-spawning linear home range for 17 fish was 0–145 km. Ten fish had non-spawning linear home range <5 km and five fish had a non-spawning linear home range >60 km. We tracked two surubims (11 and 31) for two non-spawning seasons: one used almost the same reach both years and the other fish used very different reaches each year (Fig. 4). Non-spawning linear home range had no significant correlation with body weight (r = –0.10, P = 0.69, power = 0.06) or Fulton condition factor (r = –0.23, P = 0.38, power = 0.15).

Timing of migration and sprint migration

Four females provided data on timing of the pre-spawning staging migration and six females provided data on timing of the non-spawning migration. Pre-spawning staging migrations occurred from late September to December. Non-spawning migrations, all by post-spawning fish, occurred from January to March.

Five fishes (10, 12, 14, 18, and 31) made a sprint migration that was detected by two or more data-logging stations (Table 1). The migrations of four fish were upstream and the migration of one fish (fish 10) was downstream (Fig. 4). Two fish made sprint migrations during pre-spawning staging migrations and four fish made sprint migrations during non-spawning migrations. Ground speeds of upstream sprint migration ranged from 1.9 to 29.1 km day^{-1}. For fish that migrated from PR to TMD (fishes 12 and 14), the first leg (PR to Pontal) was 1.7–2.9 times faster than the second leg (Pontal to TMD).

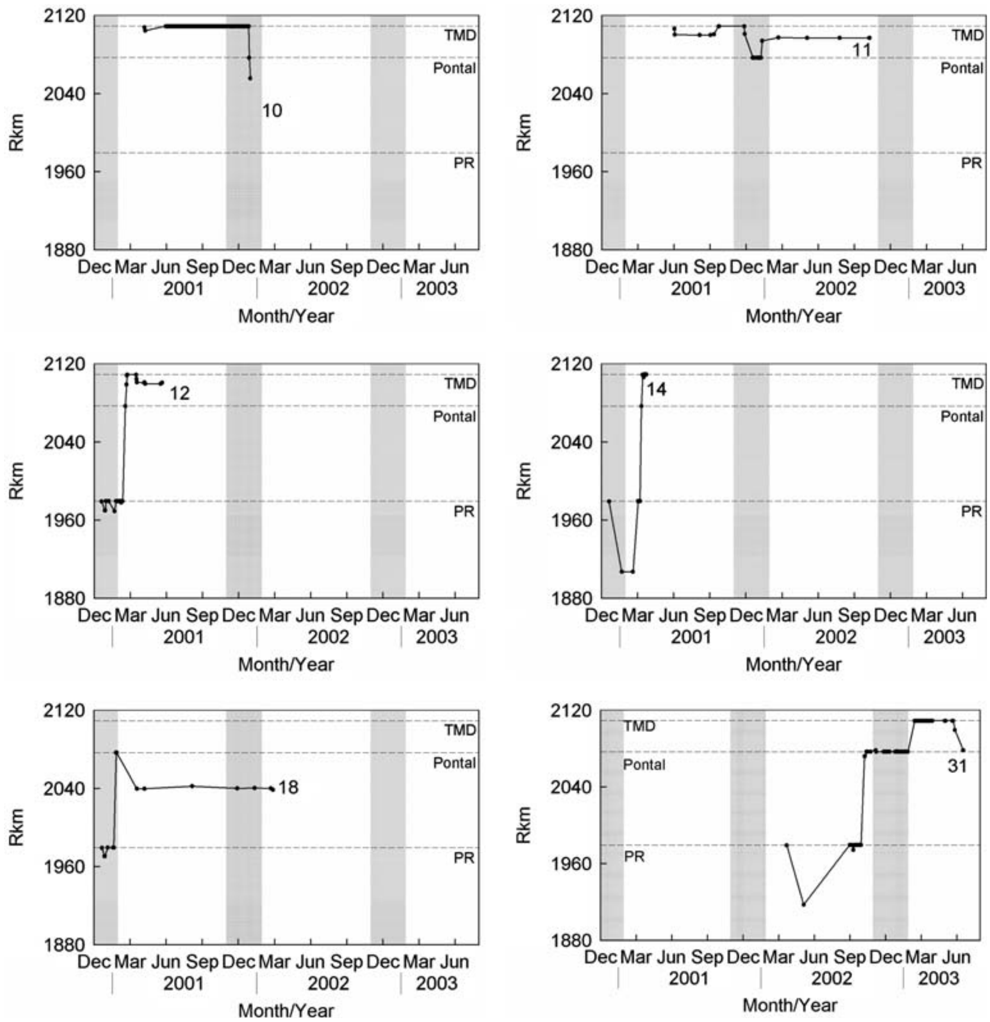

Fig. 4 Migrations of six female surubims (fishes 10, 11, 12, 14, 18, and 31) during tracking in the São Francisco River. *Gray vertical bars* represent the spawning season and *unshaded areas* show non-spawning seasons. *Horizontal dashed lines* show the location of data-logging receivers at Três Marias Dam (*TMD*), Pontal, and Pirapora Rapids (*PR*)

Discussion

Female surubims migrated among pre-spawning staging, spawning, and non-spawning sites. Spawning sites were discrete areas that females visited multiple times from nearby pre-spawning staging sites. After spawning, most fish left the spawning site and migrated to non-spawning sites.

Spawning grounds and spawning season

Tagged female surubims likely used only two spawning sites, i.e., the PR in the main stem and the Abaeté River. The sympatric zulega *Prochilodus argenteus* (Prochilodontidae) also spawns at PR (A. L. Godinho, personal observation). There was synchronization between visits of ripe female surubims to PR and occurrence of main stem floods, strongly suggesting that the visits were to spawn, because floods trigger the spawning of broadcast spawners in the São Francisco River (Godinho and Kynard 2006; Godinho et al. in press). Also, fishers reported seeing the spawning behavior of surubim at PR during floods, i.e., females lying abdomen side up at the water's surface while releasing eggs that are fertilized by males (Sato and Godinho 2003). Tracking and visual observations suggest spawning at PR occurs

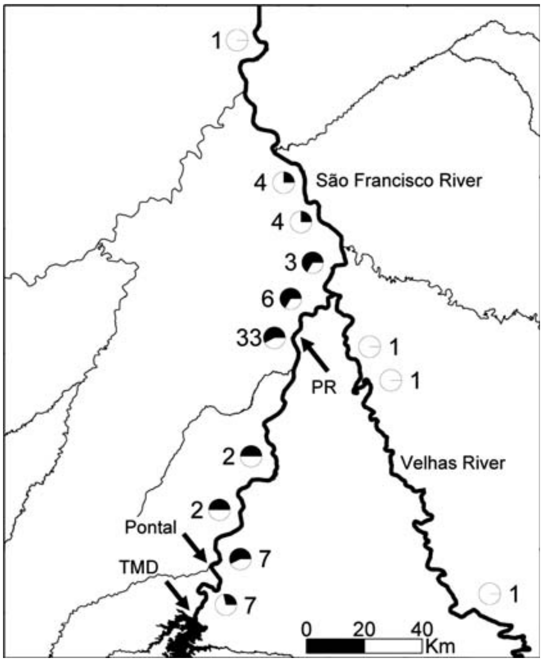

Fig. 5 Frequency of occurrence of tracked surubims in 20-km long segments of the São Francisco and Velhas rivers. *Numbers* represent the total number of fish located in each segment. *Pie chart* shows percentage of fish located during the spawning (*black*) and non-spawning (*white*) seasons. Location of data-logging receivers was at Três Marias Dam (*TMD*), Pontal, and Pirapora Rapids (*PR*)

in a small stretch (several hundred meters) at the end of the rapids. Movements into the Abaeté River of two females during flooding suggested this tributary was another spawning ground. The exact location of spawning in the Abaeté River was not determined; however, we believe spawning likely occurs near the mouth because most surubim may staged nearby the spawning ground as they did in the case of PR spawning ground.

Surubim at PR spawn until January according to Brito and Bazzoli (2003). Our data suggest that the spawning period is much longer extending throughout March. Three of five fish we tagged in late March at PR had late-stage eggs, which suggests that spawning should occur soon. Also, the second highest number of surubims visited PR in March.

Multiple visits and pre-spawning staging sites

Pre-spawning female surubims migrated from late September to December to stage at or near PR. From pre-spawning staging sites, females made short distance movements (spawning migrations) to PR. After these visits, fish returned to the pre-spawning staging site or moved to a non-spawning site (post-spawning or non-spawning migration).

We found eight females that moved repeatedly back and forth from a pre-spawning staging site to the PR spawning site. We considered the repeated return of ripe females to the same spawning ground to be homing, i.e., the returning to a place formerly occupied instead of going to other equally probable places (Gerking 1959). In South America, homing of fish was first found in *Prochilodus lineatus* for adults returning to a spawning ground (Godoy 1959, 1975), and recently, homing was discovered in another *Prochilodus* (zulega) for adults returning to

Table 1 Sprint migrations of five surubims during pre-spawning and non-spawning (=post-spawning) migrations in the São Francisco River

Fish	Leg	Distance (km)	Time (h:min)	Ground speed (km day^{-1})	Migration type
31	PR-near Pontal[a]	92.8	189:42	11.7	Pre-spawning staging
31	Pontal-TMD	32.2	411:42	1.9	Non-spawning
10	TMD-Pontal	32.2	24:45	31.2	Pre-spawning staging
12	PR-Pontal	97.3	162:42	14.4	Non-spawning
12	Pontal-TMD	32.2	92:24	8.4	Non-spawning
14	PR-Pontal	97.3	80:15	29.1	Non-spawning
14	Pontal-TMD	32.2	75:48	10.2	Non-spawning
18	PR-Pontal	97.3	153:03	15.3	Non-spawning

For the two fish (12 and 14) that went from Pirapora Rapids (*PR*) to Três Marias Dam (*TMD*), the PR-Pontal and Pontal-TMD legs are shown separately. Sprint migration of all fish was upstream except for fish 10

[a] Fish moved upstream to 4.5 km of Pontal in 189 h; then, it spent 104 h moving the 4.5 km to Pontal. This final movement was not included in calculation of ground speed to Pontal

pre-spawning staging sites, spawning sites, and non-spawning sites in the São Francisco River (Godinho and Kynard 2006). Homing may be a widespread behavior among migratory South American fishes.

Female surubims are believed to be single spawners (Bazzoli 2003; Sato and Godinho 2003). However, the repeated visits to PR by several ripe females suggest that they spawned multiple times. Also, the ovaries of post-spawned surubims had post-ovulatory follicles, oocytes with intact yolk globules, and oocytes with cortical vesicles (Godinho et al. 1997), which are structures that are used by many researchers to characterize multiple-spawning fish species (e.g., Lamas and Godinho 1996; Rinchard and Kestemont 1996; Msiska and Costa-Pierce 1999; Sivakumaran et al. 2003).

Staging at or close to the spawning ground provides quick, low-energy access of multiple spawning fish that need to move back and forth between staging and spawning areas. Most surubims did not stage at PR, perhaps because intense fisheries since the 16th century (Silva et al. 2000) may have selected against phenotypes that stage there. Pre-spawning staging sites within a few kilometers of the spawning ground has also been found in other North and South American riverine species (Kynard 1997; Pegg et al. 1997; Paragamian and Kruse 2001; Godinho and Kynard 2006; Kieffer and Kynard in press).

Northcote (1978) proposed a general model of freshwater fish migration that was republished with slight modifications by Lucas and Baras (2001). In both publications, migration is among only three habitats: spawning, feeding, and refuge. The pre-spawning staging habitat was not mentioned, but this habitat has been found for diverse fish species. Therefore, pre-spawning staging behavior may be more widespread and important than is presently recognized. A model that includes pre-spawning staging habitat is presented in Fig. 6.

Non-spawning grounds

Feeding and refuge are the two types of non-spawning sites identified for fishes by Lucas and Baras (2001). We used the term non-spawning site for female surubims tracked outside the spawning season because we collected no data to indicate if fish were foraging or seeking refuge. We are unaware of any extreme river condition, like for temperature or dissolved oxygen, that exist and would cause fish to seek refuge. Thus, we suspect that all non-spawning grounds of female surubims were foraging sites.

The non-spawning ground of female surubims was the 274 km directly downstream of TMD and almost 200 km of the lower Velhas River. Post-spawning females left the spawning ground and migrated up and downstream in the main stem and migrated upstream many kilometers in the Velhas River. Females were scattered along the main stem with the greatest number of fish either upstream of Pontal or far downstream of Pontal near PR. Upstream of Pontal was an important foraging habitat likely because of abundant prey, particularly *Prochilodus* (A. L. Godinho, personal observation), which is the main surubim prey elsewhere (Marques 1993; Resende 2003).

Sprint migration

Ground speed during sprint migrations was highly variable partly because of the heterogeneous river geomorphology. The main stem between PR and Pontal has some small rapids, but the river upstream of Pontal has at least one large steep rapid that might delay fish. The movement of post-spawning fish that swam the same leg at fairly different speeds suggests that migration drive may also be different among fish. The upstream ground speed of female surubim is among the fastest for any tropical seasonal fish listed by Lucas and Baras (2001).

Dualistic migration and home range

Animal populations with migratory and resident individuals have been termed partial migratory (Jonsson and Jonsson 1993). Partial migratory populations of fishes often show polymorphism with dwarf residents, mostly males, and large migrants, mostly females (Jonsson and Jonsson 1993; Klemetsen et al. 2003). Migratory and resident female surubims were similar-sized fish. Moreover, one surubim was migratory 1 year and resident another year. Thus, the migration style of

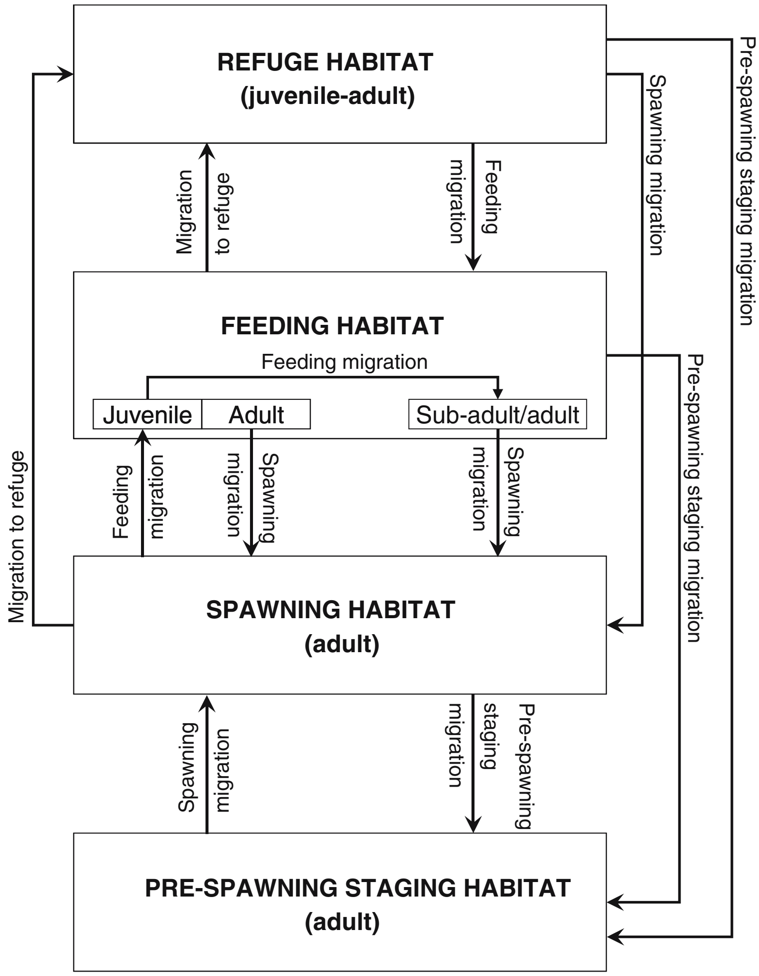

Fig. 6 Generalized model of fish migration (Lucas and Baras 2001) modified to include pre-spawning staging habitat

female surubims does not fit the partial migration concept. Thus, we used the term dualistic migration for the dichotomous migration style of surubim. A dualistic migration style has also been found between similar-size yearling shortnose sturgeon, *Acipenser brevirostrum* (Kynard et al. in press) and zulega (Godinho and Kynard 2006).

A dualistic migration of female surubims also occurred during the non-spawning season. Most females used less than several km of river during the non-spawning season so most fish found food in a small area, including the PR spawning site. Total linear home range of female surubims is, together with total linear home range of zulega (Godinho and Kynard 2006), the smallest described so far for any large South American migratory fish species (Petrere 1985; Lucas and Baras 2001; Carolsfeld et al. 2003).

Conceptual model of migration and spawning

The present study suggests the following conceptual model for migrations and spawning of female surubims in the São Francisco River. They are dualistic migrants, multiple spawners that spawn from November to March. Pre-spawning staging migration occurs from late September to December and post-spawning migrations occur from January to March. Sprint migration is used for both pre- and post-spawning migrations. Spawning grounds are located in the main stem just downstream of a large rapids (but not below all rapids) and in a select tributary (but not all tributaries). In the non-spawning season, female surubims tend to use a short reach of river and to be widely distributed.

Female surubims make multiple short distance spawning migrations, which usually occur in the day and during flooding. The spawning migration originates at a pre-spawning staging site and spawning occurs during a short visit. Some females repeatedly return to the same pre-spawning staging site. Most post-spawning females leave the spawning site moving up or downstream to non-spawning grounds, but some fish stay at the spawning site until the next spawning season. Some spawning females return to the same spawning ground in successive years.

The sympatric surubim and zulega (Godinho and Kynard 2006) share many common migration and spawning traits, i.e., selection of the same spawning grounds, spawning at the same time during floods; using pre-spawning staging sites near the spawning site; homing to spawning sites; using non-spawning sites that are both up and downstream from spawning sites; and a dualistic migratory pattern. These similarities suggest that the same selective forces in the São Francisco River have shaped the life history migrations and spawning of both species.

With the exception of the present study of surubim, a conceptual model for spawning and migrations of large South American catfish exists only for the piscivorous piramutaba, *Brachyplatystoma vaillanti*, and dourada, *Brachyplatystoma rousseauxii*, in the Amazon Basin (Barthem and Goulding 1997). Piramutabas make round trip migrations of 6,600 km from the feeding site in the estuary to spawning sites in the upper basin. Douradas also migrate from the estuary to the upper basin, but they leave the estuary as pre-adults and do not return. Offspring of both species migrate downstream to the estuarine nursery site. Piramutaba and dourada are potamodromous fishes that do not enter brackish water in the estuary (Barthem and Goulding 1997).

The migration style of piramutaba differs in a major way from the migration style of surubim. Piramutaba has evolved a unidirectional, long distance, aggregative post-spawning migration. This migration style suggests that there is only one adaptive post-spawning migration, perhaps to exploit abundant food resources at the estuary (Barthem and Goulding 1997) or to obtain essential resource(s) found only there. Conversely, the present study shows surubim has evolved short, multi-directional, non-aggregative post-spawning migrations. The widely spaced distribution of female surubims during the non-spawning season suggests intraspecific competition for food is keen.

Another major difference among the Amazon River catfishes and the São Francisco River surubim is the nursery habitat used by young fish. Surubim is the only one of the three species that extensively uses floodplain lakes for rearing. Barthem and Goulding (1997) suggested that low dissolved oxygen, competition, predation, disease, and/or predation in the floodplains are the proximate causes for the use of the river channel as nursery habitat by dourada and piramutaba. We think that this strategy could also had evolved if one or more essential resources are only found in the river channel or at the estuary.

Conservation and management

Construction of dams planned for the São Francisco, Velhas, and Abaeté rivers will greatly reduce surubim abundance, and possibly, cause extirpation of the population(s). The dam planned for just upstream of PR will change quality and quantity of water and disrupt spawning at PR, one of the most important surubim spawning habitats in the entire basin. This dam will also block up and downstream migratory routes, flood the Pontal spawning ground, and change lotic non-spawning grounds into lentic habitat. Any reservoir built on the main stem will block the downstream migration of offspring to nursery grounds resulting in the death of drifting early-life stages. Also, some nursery grounds will be impounded. Dams built on the Velhas River will block fish access to non-spawning grounds. Those built on the Abaeté River will destroy the Pontal spawning ground.

Surubims that live just downstream of TMD may attempt to pass around the dam during the non-spawning season; however, no fish passage is available at TMD. An upstream fish passage might allow surubim to pass upstream, but the available technology has been inefficient for passing bottom-orientated catfishes because fishway entrances are usually located at the surface (Oldani and Baigún 2002). Even if this problem was solved, surubims passed upstream would eventually try to return downstream to their spawning grounds. However, TMD does not have a passage facility or protection for downstream migrant fishes. Downstream passage needs to be solved before (or during) any attempt to pass surubim upstream of TMD.

This study provides insight that is helpful for solving a serious long-term conflict between law enforcement and illegal fisheries at PR. The PR rapids have been a major fishing spot since the 16th century (Silva et al. 2000), but since 1967, fishing has been forbidden by a federal law. Although prohibited, 50–100 fishers still fish at PR. Surubims are present at PR all months of the year, but landings increase dramatically during floods because fish concentrate there to spawn. A change in regulation so that fishing at PR was only prohibited during floods could help reduce the conflict, maximize the cost-benefit of law enforcement, and contribute to surubim conservation by allowing fish to spawn without disturbance.

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