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[Article]

Migration and Spawning of Radio-Tagged Zulega *Prochilodus argenteus* in a Dammed Brazilian River

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Abstract.—It is difficult for agencies to evaluate the impacts of the many planned dams on São Francisco River, Brazil, migratory fishes because fish migrations are poorly known. We conducted a study on zulega *Prochilodus argenteus*, an important commercial and recreational fish in the São Francisco River, to identify migrations and spawning areas and to determine linear home range. During two spawning seasons (2001–2003), we radio-tagged fish in three main-stem reaches downstream of Três Marias Dam (TMD), located at river kilometer (rkm) 2,109. We tagged 10 fish at Três Marias (TM), which is 5 km downstream of TMD; 12 fish at Pontal, which is 28 km downstream of TMD and which includes the mouth of the Abaeté River; and 10 fish at Cilga, which is 45 km downstream of TMD. Late-stage (ripe) adults tagged in each area during the spawning season remained at or near the tagging site, except for four Cilga fish that went to Pontal and probably spawned. The Pontal area at the Abaeté River mouth was the most important spawning site we found. Prespawning fish moved back and forth between main-stem staging areas upstream of the Abaeté River mouth and Pontal for short visits. These multiple visits were probably needed as ripe fish waited for spawning cues from a flooding Abaeté River. Some fish homed to prespawning staging areas, spawning areas, and nonspawning areas. The migratory style of zulega was dualistic, with resident and migratory fish. Total linear home range was also dualistic, with small (<26-km) and large (53–127-km) ranges. The locations of spawning areas and home ranges suggest that the Pontal group (which includes Cilga fish) is one population that occupies about 110 km. The Pontal population overlaps a short distance with a population located downstream of Cilga. Movements of late-stage TM adults suggest that the TM group is a separate population, possibly with connections to populations upstream of TMD.

Fishes of the genus *Prochilodus* forage on detritus and periphyton and inhabit many South American rivers, where they are an important fisheries resource (Castro and Vari 2003). Zulega *Prochilodus argenteus* is endemic to the São Francisco River, a large basin southeast of the Amazon River. Zulegas grow to a maximum body weight of 15 kg (Sato et al. 1996) and are one of the most important recreational and commercial fish in the basin (Franco de Camargo and Petrere 2001; Godinho et al. 2003). Despite the importance of zulegas, most aspects of their life history (especially migrations, home range, and spawning locations) are not known. This information is urgently needed to evaluate the environmental impacts of the many large dams and reservoirs planned for the main stem and tributaries.

The only available conceptual model of adult *Prochilodus* spp. migration and total linear home range is from mark–recapture studies on *P. lineatus* (=*P. scrofa* and *P. platensis*) during the 1950s–1960s (Godoy 1959; Godoy 1962; Bonetto 1963; Bonetto and Pignalberi 1964; Bonetto et al. 1971; Godoy 1975). *P. lineatus*, which is found in a neighboring basin of the São Francisco River, migrates a maximum round trip distance of 1,300 km between feeding grounds in the main stem and spawning grounds in a tributary (Godoy 1975; Toledo et al. 1986). Spawning occurs during river flooding (Schubart 1954). In the São Francisco River, two mark–recapture studies on zulega provided some information on total linear home range. Fish, presumed to be adults, from different reaches had different total linear home ranges, i.e., 1,100 km maximum displacement for fish tagged in the lower region (Sato and Godinho 2003) and 250 km for fish tagged in the upper region (Paiva and Bastos 1982).

Some information on spawning and early life history of zulega is available. During spawning, a female broadcasts hundreds of thousands of small, nonadhe-

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sive eggs in a single batch in the rainy season between November and February (Bazzoli 2003; Sato et al. 2003b). Eggs are semibuoyant, drift downstream with river flow (A. Godinho and B. Kynard, unpublished), and hatch in 19 h at 24°C (Sato et al. 2003b). Drifting eggs and larvae are in the water column and density is highest during floods when spawning occurs (A. Godinho and B. Kynard, unpublished). Larvae drift into floodplain lakes, which are important nursery grounds for early juveniles (Sato et al. 1987; Pompeu and Godinho 2003). Some larvae may also rear in the river, but data are lacking. Preliminary observations suggest that at some point in ontogenetic development, juveniles migrate upriver in the dry season and join adults (A. Godinho, unpublished).

Migrations of several South American fishes have been studied, mostly using mark–recapture (Petrere 1985; Carolsfeld et al. 2003). Telemetry has rarely been used in South America to study migratory fish (e.g., Mochek et al. 1991). We radio-tracked zulegas in three reaches of the São Francisco River for 2.5 years. We identified the sex and reproductive stage at the time of tagging to link movements and behavior of ripe fish to likely spawning. Our objectives were to identify migrations, determine linear home ranges, identify spawning and nonspawning habitats, determine timing of spawning relative to river conditions, and develop a conceptual model of migrations that would contribute to understanding the species' life history migrations.

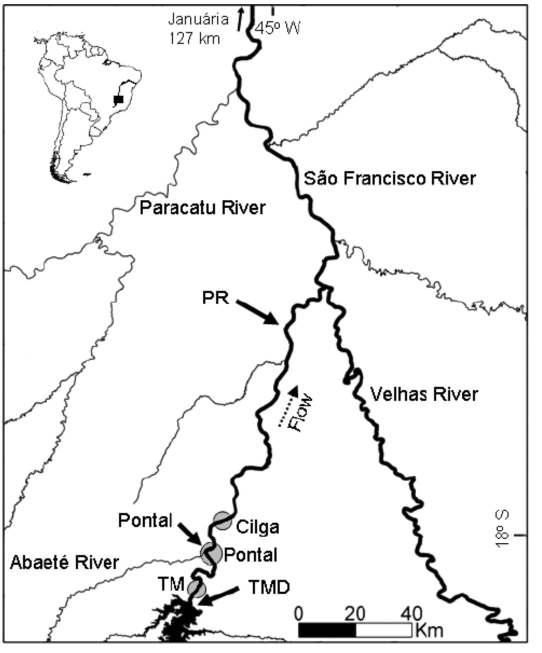

FIGURE 1.—The study area for zulega in the São Francisco River basin. Bold arrows show the three sites with data-logging receivers: Três Marias Dam (TMD; rkm 2,109), Pontal (rkm 2,077), and Pirapora Rapids (PR; rkm 1,980). Shaded circles show the fish-tagging sites: Três Marias (TM; 5-km reach), Pontal (8-km reach including the Abaeté River mouth), and Cilga (5-km reach).

Methods

Study area.—The São Francisco River is a large river on the east coast of South America that flows mostly northward for 3,160 km (Kohler 2003). The reach where we tracked fish most intensively extended 282 km downstream from Três Marias Dam (18°12′S, 45°15′W), which is located at river km (rkm) 2,109 (measuring from the mouth of the São Francisco River; Figure 1). From this dam downstream to Pirapora Rapids at rkm 1,980, the river has a high gradient with fast current, rapids, and runs. The bottom is mostly rocky. There are only a few narrow floodplains that seldom flood because of regulated flow at Três Marias Dam. Abaeté River is the largest of the three major tributaries in the Três Marias Dam–Pirapora Rapids reach. At Pirapora Rapids, the river level declines 8 m over a distance of 1 km. Downstream of Pirapora Rapids, the river gradient is low, the current is slow, the bottom is mostly sand, and the channel meanders. Many wide floodplains are present, mostly below the Paracatu River mouth at rkm 1,866. Within 506 km downstream of Três Marias Dam, four dams are planned that will convert that segment of the main stem into a series of large reservoirs. In the free-flowing Abaeté River, nine potential sites for dams have been identified.

Tagging and tracking.—We captured and tagged fish at three main-stem locations: Três Marias (4–9 km downstream from Três Marias Dam), Pontal (1 km downstream and 7 km upstream from the Abaeté River mouth), and Cilga (a 5-km reach centered on Cilga Island) (Figure 1). We tagged fish in January–February 2001 and January 2002, that is, during the November–February spawning seasons of 2000–2001 and 2001–2002.

We captured fish with gill nets or cast nets and held them in a nearby floating net-pen for as long as 2 h before tagging. We held fish for tagging in a small portable tank filled with 30 L of river water and immobilized them using electronarcosis with non-pulsed 30 V DC (Kynard and Lonsdale 1975; Ross and Ross 1999). Prior to tagging, we determined fish weight (*W*) and standard length (SL). During tagging, we kept fish submersed in water except for part of the lateral body wall where we made the incision. We renewed the holding water frequently to maintain a suitable dissolved oxygen level for fish during tagging.

Tags were inserted into the body cavity through a 5-cm long incision. We made the incision on the left lateral body wall about 4 cm behind the pelvic fin base and 2 cm above the ventral line. The 43-cm long antenna extended posterior through the body wall and exited the body about 2 cm below the lateral line. Tags were Lotek Model MCFT-3FM coded radio transmitters (frequency = 149.780 mHz, diameter = 11 mm, length = 59 mm) with a transmission life of 25 months at a 10-s burst rate. Tag weight in air (10 g) as a percent of fish weight was 1.3% or less. During the last minutes of surgery, we added Stress Coat or LabProtect to the tank's water to aid recovery of fish.

We determined the sex and reproductive stage of fish during surgery using unaided visual observations of gonads through the incision or, for fish with undeveloped gonads, using a fiber optic bioscope inserted through the incision (Kynard and Kieffer 2002). Undeveloped ovaries are ribbon-like organs, translucent and pinkish. Undeveloped testicles are thin, very translucent, filament-like organs. Due to their larger size, undeveloped ovaries are easier to locate and see with a bioscope than testicles. We classified the reproductive stage of females as early stage (ES, undeveloped ovary not containing visible maturing or mature eggs) or late stage (LS, ripe gonads) following Kynard and Kieffer (2002). We classified the reproductive stage of males as ES if testicles could not be identified with the bioscope, or LS if testicles could be identified with the bioscope or the male was releasing sperm

The ES category included adults that might have spawned and juveniles that would not spawn during the spawning period when they were tagged. We tracked some ES fish during a second spawning season, when they were most likely to be adults, and reclassified these fish during the second year as presumed LS adult fish. In analysis of adult home range, we did not use the ES fish tracked for only 1 year, because they might have been juveniles.

We completed surgery within 30–40 min. This length of time was necessary to carefully make an incision through the thick body wall, determine sex and reproductive stage, insert the tag and antenna, close the incision, and hold the fish in the recovery bath. Tagging could be done slowly and carefully because fish that were held immobilized for 2 h by means of electronarcosis recovered quickly and had no deleterious effects (Kynard and Lonsdale 1975). We held fish in the net pen for 1–3 h to ensure recovery before release. We released fish within 1–3 km of their capture site, except for three fish released 5–7 km from their capture sites.

We tracked fish from January 2001 to July 2003, which included three spawning seasons: 2000–2001, 2001–2002, and 2002–2003. We manually tracked fish using a Lotek SRX_400 receiver by boat or by helicopter. We tracked fish almost every month during each spawning season (November–February) and at least every other month during nonspawning seasons. We searched a total of about 7,500 km of river to locate tagged fish. We also tracked fish using Lotek SRX_400 fixed-location, data-logging receivers at Três Marias Dam, Pontal, and Pirapora Rapids from January 2001 to July 2003 (Figure 1). We used multiple antennas on the receivers at the Pontal and Pirapora Rapids sites to determine fish movement direction. Further details on tracking methods are available in Godinho (2005).

We recorded temperature at the Abaeté River mouth every 3 h using an Onset StowAway temperature logger. Daily river discharge of the Abaeté River was provided by CEMIG (Minas Gerais Power Company).

Data analysis.—The continuous record time-out function of the data-logging receivers was set at 10 min, so receivers recorded tag code and number of tag detections (signal hits) for each 10-min interval. Receivers logged signal hits of tag codes used in the study (present codes); however, due to background noise, the receivers also logged signal hits of codes not used in the study (absent codes). If the receivers logged signal hits of absent codes, they also logged signal hits of present codes when they were not in the receiver's range. We called these as false-positive records of present codes.

We developed two procedures to eliminate false-positive records of present codes. The first procedure was based on P_k, the probability of a record with k signal hits being a false positive. We calculated P_k using records of absent codes with the formula (Table 1)

$$P_k = 100F_k / \sum_{k=1}^{m} F_k,$$

where F_k = the frequency of records with k signal hits. We considered a record of present code as false-positive if $P_k > 1.0\%$ for the Pontal receiver and if the cumulative $P_k > 99.0\%$ for Três Marias Dam and Pirapora Rapids receivers. For the last two receivers, we used a higher threshold than for the Pontal receiver because of the higher level of background noise in those areas. Because the maximum number of possible signal detections for a 10-s burst-rate tag in 10 min is 60, we excluded from analysis all records with more than 60 signal hits.

The second procedure was to check data log records for consistency. When a receiver recorded a tag signal, the tag code and time of the first and last signal hits were recorded for each 10-min interval. We considered

TABLE 1.—Actual logs of absent codes (i.e., tag codes not used in the present study) by the Pontal receiver. The record with k signal hits is the number of absent code signal hits, and F_k is the frequency of absent codes with k signal hits. Thus, the Pontal receiver logged 10,159 records of absent codes with only one signal hit. The P_k is the probability that a record with k signal hits is a false positive. We calculated P_k as a percentage of all F_k. For the Pontal receiver, we considered all records of present tags with P_k exceeding 1.0% as false positive. So, we only used records with four or more signal hits in the analysis of movement of zulegas because records with three or fewer signal hits had a probability of more than 1.0% of being false positives. For the Três Marias and Pirapora Rapids receivers, we used the cumulative P_k to eliminate false-positive records of present codes.

Record with k signal hits	F_k	P_k
1	10,159	86.81
2	1,274	10.89
3	225	1.92
4	35	0.30
5	8	0.07
6	1	0.01
8	1	0.01
All	11,703	100.00

the signal hit as a positive record if a false-positive record, as determined by the first procedure, was within 30 min of a positive record. We excluded all other false-positive records of present codes.

The Pontal receiver detected short-term movements (visits) of ES, LS, and presumed LS fish to Pontal during the spawning season. We determined frequency and duration of visits using arrival and departure day and time. We also determined the arrival and departure direction. We analyzed the frequency of visits for relationship with Abaeté River discharge and temperature. These two variables behaved like a periodic function presenting a complete cycle in a matter of days during the rainy season. As a periodic function, the variability of the variables ranged from peak (maximum point of a complete cycle) to trough (minimum point) and then back to peak. Using this variability, we classified each visit as peak (during peak day or 1 d postpeak), decreasing (decreasing from peak), trough (during trough or 1 d posttrough), increasing (increasing from trough), or stable (variable unchanged for $\geq$3 d). If a visit lasted longer than 1 d, we characterized the visit day as the day with the greatest number of signal hits. We tested data for differences in visit frequency and duration among classes of discharge and temperature.

We calculated total linear home range (the distance between the most upstream and downstream locations; Young 1998) of all fish tracked during spawning and nonspawning seasons. For these fish, we calculated the Fulton condition factor ($K = W/\,SL^3$). We used only LS and presumed LS fish in the calculation of total linear home range. We excluded ES fish because we could not distinguish between adult ES and juvenile ES fish. We also excluded ES fish because total linear home range of juvenile fish may have a different adaptive significance than that of adult fish.

We calculated the nonspawning linear home range (distance between the most upstream and downstream locations) using fish located at least twice during the nonspawning season. We excluded the locations of fish during prespawning or postspawning migration periods. Two fish used different river reaches in different nonspawning seasons, so we estimated the nonspawning linear home range of the fish for each season.

We tested continuous data sets for normality (Shapiro–Wilk test, SAS Univariate procedure) using statistical software SAS for data analysis (SAS Institute 1999). In case of nonnormality, we transformed the data following transformations of Sokal and Rohlf (1995), and then tested again for normality. If normality was achieved after transformation, we used the following analyses: (1) Student's t-test (SAS t-test procedure) according to the homogeneity of variances for comparisons of data between two groups (i.e., standard length between ES versus LS, total linear home range size between males and females, nonspawning linear home range between males and females, and duration of visits between males and females); (2) analysis of variance (ANOVA) (SAS GLM procedure) for comparisons among three or more classes (i.e., duration of fish visits among classes of water discharge and temperature and total linear home-range size and nonspawning linear home-range size among fish from different tagging sites); and (3) Pearson correlation (SAS Corr procedure) to test relationships between continuous variables (i.e., total linear home-range size and nonspawning linear home range with the number of days we tracked fish, SL, and K). We determined the power of the test (Borenstein and Cohen 1988; Cohen 1988) in cases where we did not reject the null hypothesis. In case of nonnormality, we used Wilcoxon two-sample test with normal approximation and continuity correction of 0.5 (SAS Npar1way procedure) to compare data between two groups (i.e., number of visits by males versus females, visit duration of ES versus LS and presumed LS fish, and distance from prespawning staging sites to spawning sites of males versus females). We used chi-square to test for frequency of fish visits to Pontal among the classes of Abaeté River temperature and discharge. We set $\alpha = 0.05$ and power $= 0.80$.

Results

We tagged 37 fish. Six fish did not provide long-term movement data because they were tracked $\leq$28 d and moved only a small distance (≤2.6 km) from their release site, so we excluded them from the analysis. The remaining 31 fish were tagged during two spawning seasons: 16 were tagged in January–February 2001 and 15 were tagged in January 2002. We tagged 10 fish at Três Marias (7 ES fish and 3 LS fish), 11 fish at Pontal (6 ES fish and 5 LS fish) and 10 fish at Cilga (all LS fish). Twenty fish were females (36.0–50.5 cm) and 11 fish were males (32.0–49.0 cm). Thirteen fish were ES (11 females and 2 males) and 18 fish were LS (10 females and 8 males). There was no significant difference between standard lengths of ES and LS fish ($t = 1.83$, df $= 30$, $P = 0.08$, power $= 0.03$). We tracked the fish for 34–554 d (mean = 228). The number of locations per fish was 3–329 (mean = 21). The reach where all fish were manually tracked was less than 0.4 km wide, less than 10 m deep, and the tag detection range was 0.5–1.8 km (n = 7), so the likelihood of detecting a tagged fish during manual tracking was virtually 100%.

Tagging Mortality and Disappearance of Tagged Fish

We found immobile tagged fish (tag not moving) from 6 to 256 d after tagging; 11 of 37 tagged fish were immobile sometime during the study. Some immobility of tagged fish may be related to tagging mortality in cases where tags became immobile soon after release (<36 d, $n = 6$). Other fish were immobile at more than 80 d ($n = 5$). Although tagging-related mortality cannot be discarded in these five cases, death of these fish was probably due to other causes.

Five of 17 tags used in 2001 stopped transmitting after 224–514 d instead of the specified 755 d. All five tags were either returned by fishers or were found on the river bottom.

The signals of 19 fish could not be found after 19–554 d. Seventeen of these fish were probably harvested or the tag stopped transmitting because we last tracked them in the main stem upstream of Pirapora Rapids and the data-logging receivers did not detect them moving out this reach, which is a popular fishing area.

General Fish Movements

We grouped fish according to the river reach where they were located most frequently during the spawning season (Figure 2). Using this procedure, we categorized 9 fish as Três Marias fish (all tagged at Três Marias), 16 fish as Pontal fish (1 fish tagged at Três Marias, 11 fish tagged at Pontal, and 4 fish tagged at Cilga), and 4 fish as Cilga fish (all tagged at Cilga). We located most Três Marias fish and all Pontal fish most frequently at the tagging site during the first spawning season they were tagged. Twelve fish stayed at the tagging site during the following nonspawning season. Two Três Marias fish and one Pontal fish stayed at the tagging site two consecutive spawning seasons. Four Pontal fish migrated to a nonspawning habitat during or after the spawning season and then returned to Pontal the following spawning season.

Visits to Pontal from Prespawning Staging Areas

After LS and presumed LS fish arrived at Pontal during the spawning season, they stayed for a short time (visit), then usually moved to a nearby prespawning staging area, and later returned to visit Pontal (Figure 3). The Pontal receiver detected 26 visits by five females and four males. The number of visits to Pontal per fish ranged from one to nine. The four males visited Pontal one to nine times (mean = 3.3) and the five females visited two to four times (mean = 2.6). We tracked all fish that visited Pontal for a period of time shorter than the expected tag transmitting life, so the actual number of visits per fish is probably greater than we observed.

There was no difference in the number of visits between males and females (Wilcoxon two-sample test: $W = 16.5$, df $= 1$, $P = 0.44$). Males and females visited Pontal all months of the spawning season. Number of visits per month ranged from one to five for males and two to five for females. Visit duration ranged from 1 to 10 d (mean ± SD = 1.8 ± 1.9) and most visits lasted 1 (65%) or 2 d (19%). There was no difference in duration of visits (min) between males and females ($t = -1.17$, df $= 23$, $P = 0.25$, power $= 0.20$). Arrival time at Pontal for 18 of 25 visits was during the day between 0632 and 1757 hours. For 12 of 18 visits, fish arrived between 0632 and 1300 hours Three visits occurred at night between 2147 and 0325 hours. Two visits occurred at dawn and one visit occurred at dusk.

Four ES fish visited Pontal during the spawning season, and we tagged three additional fish at Pontal. They swam away from Pontal after tagging, but returned to Pontal after 5–10 d and stayed at Pontal for 11–15 d from late January to mid-February 2002. The other ES fish visited Pontal for 2 d. No ES fish visited Pontal more than once during the spawning season. Visit duration of ES fish was longer than the visit duration of LS and presumed LS fish (Wilcoxon two-sample test: $W = 107.5$, df $= 1$, $P = 0.002$). The ES fish visited Pontal from late January to late February while LS and presumed LS fish visited Pontal during all months of the spawning season.

Abaeté River Conditions during Visits

There was no significant association between the frequency of visits of LS and presumed LS fish to

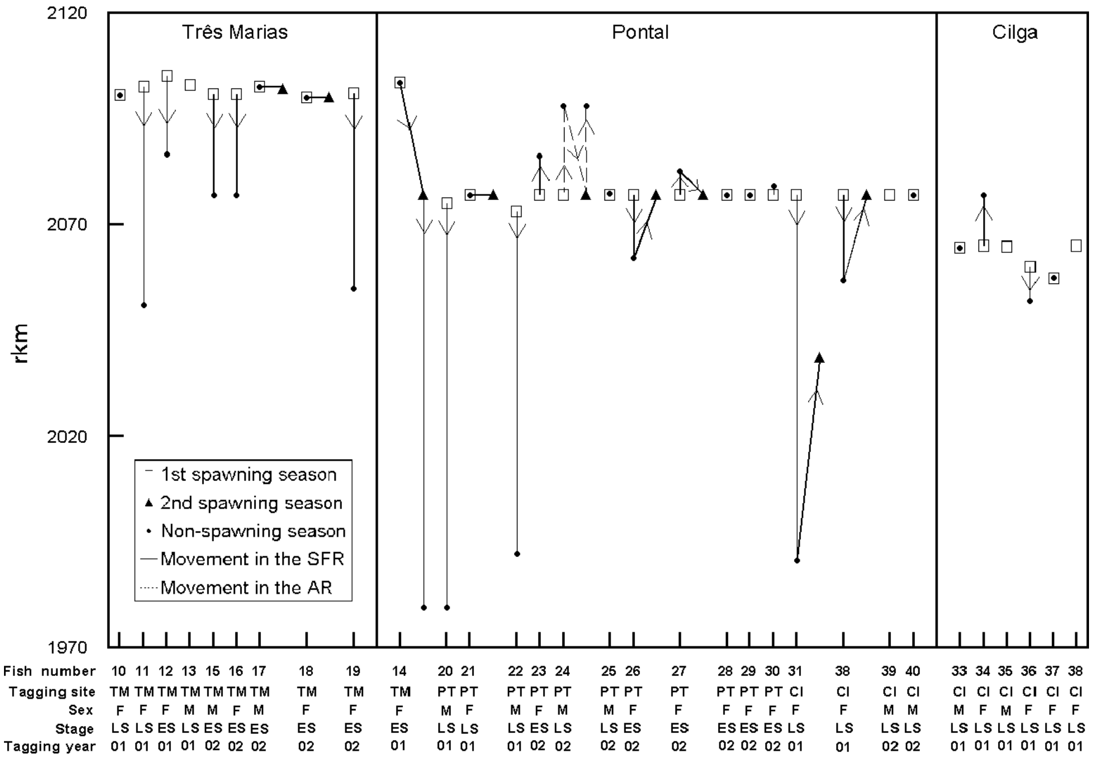

FIGURE 2.—Zulega movements in the São Francisco River basin. Fish were grouped in three clusters (Três Marias, Pontal, and Cilga) according to the river reach in which they were located most frequently during the spawning season. The *x*-axis shows the fish identification number, tagging site (TM = Três Marias, PT = Pontal, CI = Cilga), sex (F = female, M = male), reproductive stage at tagging (LS = late stage, ES = early stage), and tagging year. Squares indicate locations during the first spawning season and triangles show locations during the second spawning season. Dots mark the farthest fish locations during the nonspawning season. Solid lines show movements in the São Francisco River (SFR), and dashed lines show movements in the Abaeté River (AR). Arrows indicate the direction of fish movement.

Pontal and water temperature ($\chi^2 = 4.38$, df = 4, $P = 0.36$) or river discharge ($\chi^2 = 1.31$, df = 4, $P = 0.86$; Figure 4). Two ES fish visited Pontal during the discharge trough and three ES fish visits occurred during the temperature trough. There was no difference in the duration of visits (min) in LS and presumed LS fish among the different classes of water discharge (ANOVA: $F = 0.88$, df = 4, $P = 0.50$, power = 0.40) and temperature (ANOVA: $F = 2.14$, df = 4, $P = 0.11$, power = 0.59).

Prespawning Staging Areas Near Pontal

During the spawning season, fish were present at the nearby prespawning staging areas before and after visiting Pontal (Figure 3). We located fish that visited Pontal a total of 18 times at prespawning staging sites. All prespawning staging sites were upstream of Pontal 0.3–12.3 km (mean ± SD = 5.5 ± 3.9). One fish staged once in the Abaeté River. Males staged nearer Pontal than females (Wilcoxon two-sample test: $W = 6.5$, df = 1, $P = 0.01$).

Main Stem and Tributary Use

Zulegas used the main stem and two tributaries during the nonspawning season. They were present in 128 km of the main stem from 2 km downstream of Três Marias Dam to Pirapora Rapids. We detected two fish in tributaries as well as a few in the main stem during some surveys, but not during others. Because the tag detection range was greater than the river width, fish could not go undetected during tracking if they were in the main stem. Therefore, these fish probably moved back and forth between the main stem and tributaries.

Homing Fidelity

Some zulegas, all LS or presumed LS fish, returned (homed) to the same prespawning staging site. During the 2002–2003 spawning season, fish 27 and 28 visited

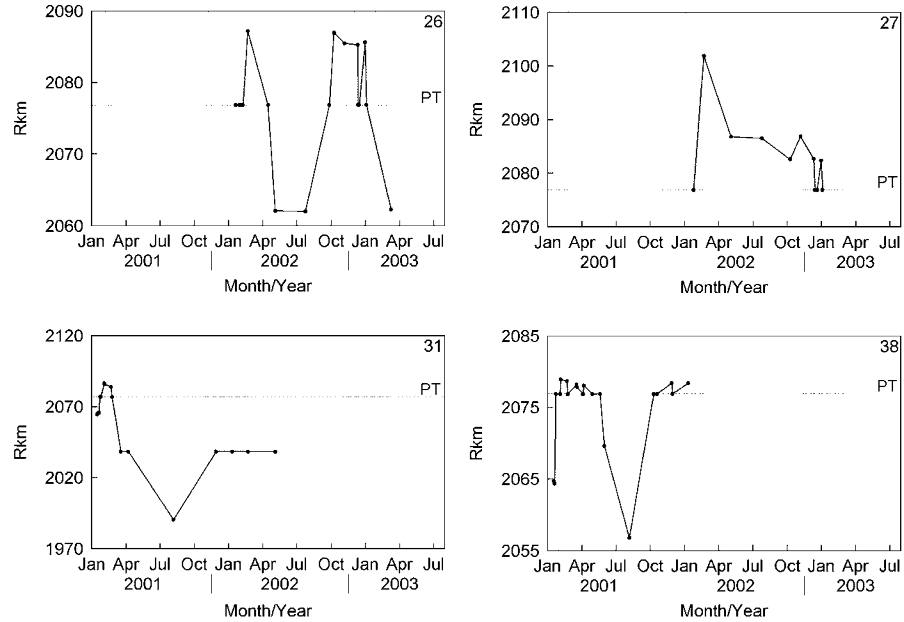

FIGURE 3.—Migration of four zulegas in the São Francisco River (numbers 26, 27, 31, and 38). Gray vertical bars show spawning seasons and unshaded areas show nonspawning seasons. The horizontal dashed line shows the rkm location of the Pontal (PT) receiver.

Pontal and then returned to the same 300-m-long prespawning staging site 6–9 km upstream from Pontal (Figure 3). Female 38 visited Pontal four times and used the same prespawning staging site about 3 km upstream from Pontal during the 2 years (Figure 3).

Some zulegas returned to the same nonspawning and spawning locations during two seasons. During the nonspawning season, two Três Marias fish moved downstream 19 and more than 23 km, respectively, before returning upstream to Três Marias after 3–5 months. Fish 26 returned to the same nonspawning spot (170 m long) downstream of Pontal during 2002 and 2003 (Figure 3). During the 2001 spawning season, fishes 31 and 38 were at rkm 2,039 and 2,077, respectively. They migrated downstream 20–48 km in the nonspawning season, and then returned upstream to the same rkm just before or at the beginning of the 2002 spawning season (Figure 3). Fish 26 occupied a spot at rkm 2,087 at the end of the 2001–2002 spawning season, spent the nonspawning period downstream, then returned to the same spot (190 m long) at rkm 2,087 before the 2002–2003 spawning season (Figure 3). Fish 24 returned to the same rkm in the Abaeté River during the nonspawning seasons of 2002 and 2003 (Figure 2).

Home Range

We located most fish in the 60 km downstream from Três Marias Dam (Figure 5). The greatest numbers of fish locations were at or near Três Marias, Pontal, and Cilga (the original tagging sites). Tagged fish were present mostly in the main stem during the spawning season. The main stem near Pirapora Rapids and the Abaeté River was also used by tagged fish during the nonspawning season.

We tracked 19 fish during both the spawning season (November–February) and the nonspawning season. Total linear home range for these fish was 1–127 km (mean $\pm$ SD = 33 $\pm$ 39 km). Four fish had a total

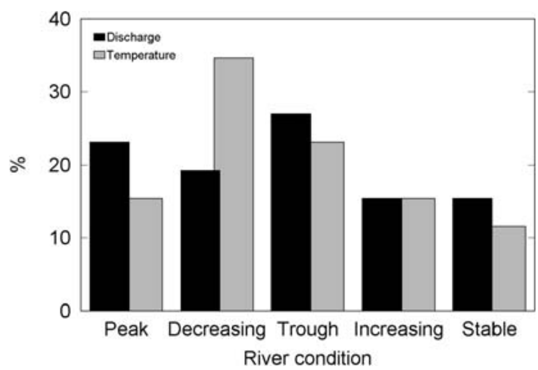

FIGURE 4.—Frequency (y-axis) of visits by zulegas to Pontal in the São Francisco main stem during varying discharge and temperature conditions in the Abaeté River mouth where it joins the São Francisco River.

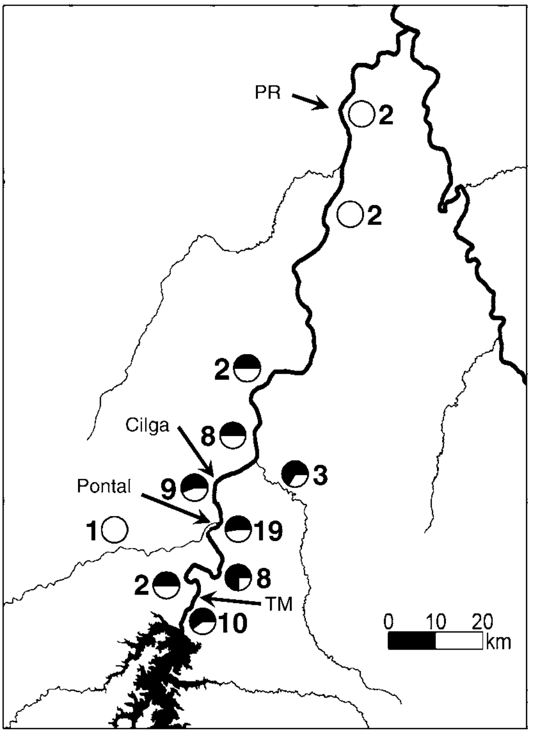

FIGURE 5.—Frequency of occurrence of 19 zulegas among 10-km-long segments of the main-stem São Francisco River and two tributaries. Numbers represent the total number of fish located in each segment. Pie charts show the percentages of fish located in each segment during spawning (black) and nonspawning (white) seasons. Map also shows the three fish-tagging sites (Três Marias [TM], Pontal, and Cilga), and Pirapora Rapids (PR, the most downstream location site for any fish).

linear home range greater than 80 km. Fourteen fish had a total linear home range less than 26 km; six fish had a total linear home range less than 6 km. There was no significant relationship between total linear home range size and the number of days we tracked fish (Pearson correlation: $r = -0.07$, df $= 17$, $P = 0.79$, power $= 0.05$), SL (Pearson correlation: $r = 0.26$, df $=$ 17, $P = 0.29$, power $= 0.19$), and K (Pearson correlation: $r = 0.02$, df $= 17$, $P = 0.93$, power $=$ 0.03). Also, total linear home range size was not different between males and females ($t = 0.31$, df $= 17$, $P = 0.76$, power $= 0.07$) or among Três Marias, Pontal, and Cilga fish (ANOVA: $F = 2.20$, df $= 2$, $P = 0.14$, power $= 0.50$).

Twenty-one fish provided data on size of the nonspawning linear home range. The nonspawning linear home range was 0–48 km (mean $\pm$ SD $= 11 \pm$ 15 km). All nonspawning linear home ranges except one were either less than 5 km or more than 20 km. There was no difference between males and females for size of nonspawning linear home range ($t = 0.81$, df $=$ 19, $P = 0.43$, power $= 0.12$) or among Três Marias, Pontal, and Cilga fish (ANOVA: $F = 0.82$, df $= 2$, $P =$ 0.45, power $= 0.20$). Also, there was no relationship between nonspawning linear home range and number of days we tracked fish (Pearson correlation: $r = 0.22$, df $= 21$, $P = 0.32$, power $= 0.17$), SL (Pearson correlation: $r = 0.26$, df $= 19$, $P = 0.26$, power $= 0.21$), and K (Pearson correlation: $r = 0.09$, df $= 18$, $P = 0.71$, power $= 0.06$).

Among the 19 fish that provided data on total linear home range, 15 fish also provided data on nonspawning linear home range. The nonspawning linear home ranges represented 2–100% (48 $\pm$ 41%) of the total linear home ranges.

Spawning during Successive Years

Spawning during successive years of both females and males was indicated by movements of LS fish that were at Pontal in two consecutive spawning seasons. For example, fish 38 moved upstream to Pontal soon after tagging in January 2001 (Figure 3). After the spawning season, this female moved downstream past Cilga for the nonspawning season; then returned upstream to Pontal the next spawning season. Pontal male 24, which used the Abaeté River during the nonspawning season, was at Pontal during two consecutive spawning seasons (Figure 2).

Discussion

Spawning Grounds

Movements of tagged zulegas indicated that Pontal was the major spawning ground. Zulegas migrated to Pontal from main-stem nonspawning locations upstream and downstream of Pontal and from the Abaeté River. While we did not monitor the actual spawning at Pontal of tagged fish, we know spawning occurred at Pontal while our fish were present, because we frequently used passive acoustic techniques to detect male mating calls in the main stem at the mouth of the Abaeté River during floods (A. Godinho and B. Kynard, unpublished). Zulegas also probably spawned at Cilga, just downstream from Pontal, where spawning could be triggered by Abaeté River floods, but detailed information is lacking.

Only a few or no zulegas probably spawn between Pontal and Três Marias Dam, a reach where no large tributaries bring flood waters into the main stem and main-stem flow is mainly a result of discharge from the Três Marias Reservoir. We found no zulega eggs or larvae drifting from that reach of the river while this species was spawning nearby downstream (A. Godinho and B. Kynard, unpublished). Also, Sato et al. (2003a) compared reproduction of zulegas from upstream and downstream of Pontal and concluded that hypolimnetic water from the Três Marias Reservoir creates unfavorable conditions for spawning upstream of Pontal, whereas spawning conditions are favorable at and downstream of Pontal because of the inflow from the Abaeté River.

Visits to Pontal

Zulega females are total spawners (Bazzoli 2003; Sato and Godinho 2003). So, why do zulegas visit the Pontal spawning grounds multiple times? It is possible that the proper spawning cues at the prespawning staging area upstream from Pontal are not present. Fish staging upstream from Pontal are in water from the Três Marias Reservoir, which has very different characteristics than the historical main-stem water before 1963 (i.e., before Três Marias Dam); thus, the present water probably lacks spawning cues. This explanation is supported by the absence of a relationship between the frequency of fish visits to Pontal and discharge of the Abaeté River. A significant relationship was expected because spawning, as indicated by the presence of male spawning calls, occurs almost exclusively during the few days of an Abaeté River flood, which probably has the correct spawning cues (A. Godinho and B. Kynard, unpublished). During the evolution of prespawning staging behavior, the water characteristics of the main stem and Abaeté River were more similar then than they are now. Presently, there seems to be a mismatch; fish prefer the main-stem prespawning staging area upstream of the Abaeté River inflow, even though there is an absence of spawning cues in the main-stem water at this area.

Males may also return multiple times for the following reason. Because spermiogenesis occurs even in ripe males (Sato et al. 2003a), males are ripe much of the spawning season, and consequently, they can visit the spawning area many times to mate. Visits to Pontal of ES fish had different characteristics (i.e., duration and number of visits per fish) than LS and presumed LS fish visits. Further study is needed.

Prespawning Staging and Nonspawning Areas

During the spawning season we found zulegas in sections of a river reach unfavorable for spawning, but from which they could visit the spawning ground, suggesting the site was a prespawning staging ground. The most important of these was in the main stem 0.3–12.5 km upstream of Pontal. Prespawning staging areas are known for several fish species (Pegg et al. 1997; Paragamian and Kruse 2001; Godinho 2005) and in all cases the prespawning staging area was within a few kilometers of the spawning area. Staging close to the spawning ground allows zulegas and other fishes rapid access to the spawning ground with low energetic costs to the fish.

Lucas and Baras (2001) identified two types of nonspawning grounds for riverine fishes: feeding and refuge. In our study, we termed the river reaches used by tagged zulegas outside the spawning season as nonspawning grounds. We did not gather data to determine whether fish were foraging, but all nonspawning grounds of zulegas in our study were likely feeding grounds, not refuge grounds. River conditions during the entire year are suitable for foraging, so no refuge grounds are probably needed.

Homing

Homing is defined as returning to a place formerly occupied instead of going to other equally probable places (Gerking 1959). In South American fishes, which have rarely been studied for homing, homing has only been found in tagged adults of *Prochilodus lineatus* returning to a spawning area in the Mogi-Guaçu River, Brazil (Godoy 1959, 1975). This spawning-site homing is similar to that of tagged zulegas to Pontal, and suggests spawning-site homing is widespread within the genus *Prochilodus*. The return of LS fish (two males and one female) to Pontal in two consecutive spawning seasons suggests some fish of both sexes spawn again after 1 year. In addition to spawning-site homing, some zulegas showed very precise homing to prespawning staging and nonspawning sites. Zulegas seem to have evolved the ability, possibly by imprinting, to identify and return to small river reaches for critical life history activities.

Home Range

The distance between spawning and nonspawning grounds of our tagged fish was a maximum of 98 km, but for most zulegas (72%) it was no more than 22 km. Nonspawning grounds of zulegas in the main stem were located at Pontal and upstream and downstream of Pontal, including Cilga. Fish seeking to move downstream to nonspawning grounds had free movement, but fish seeking to move far upstream would be limited by the Três Marias Dam. However, no tagged Pontal or Cilga fish moved upstream to Três Marias, so this did not affect the total linear home range estimate of this group of fish.

Tagged zulegas had a total linear home range of 1–127 km. This is the smallest total linear home range found for any large South American migratory fish (Petrere 1985; Lucas and Baras 2001; Carolsfeld et al. 2003) and suggests that foraging habitat for adults is available near the spawning ground. Also, zulegas had two total linear home range sizes: small ($<$26 km) and large ($>$53 km). Reasons for this dualistic pattern of total linear home range are not known. The small and large total linear home range pattern was also reflected in the dualistic migration pattern of fish: resident and migratory. Some resident fish (21%) had a total linear home range $\leq$1 km, and thus, virtually used the same grounds for spawning and nonspawning. However, most fish were migratory using different reaches for spawning and foraging.

Juvenile Migration

Fish that have an early life history whereby eggs and larvae drift far downstream to rear also must return upstream eventually as juveniles or adults to rejoin the parental adults (Baras and Lucas 2001). In the nonspawning season of 2002, a school of about 1,000 young zulegas estimated at 20 cm SL arrived at the Três Marias Dam tailrace (A. Godinho, unpublished). They remained for several days swimming at the water's surface seemingly searching for upstream passage. Many fishers reported that this migration of juveniles, locally named "arribação," happens every year. A similar upstream migration of young *P. lineatus* occurs in the Mogi Guaçu River (Godoy 1954).

Metapopulation

The migration characteristics of zulegas inhabiting the area downstream of Pirapora Rapids appear similar to those of the zulegas tracked in our study. Paiva and Bastos (1982) tagged 1,594 fish (presumably, adults) at the Pirapora–Velhas River mouth reach and recaptured 18. Fourteen fish were recaptured less than 25 km from their original tagging site, including six fish marked one season and recaptured another season. Only three fish migrated a long distance (90–250 km). The group of zulegas studied by Paiva and Bastos (1982), and the Pontal group we studied, do not overlap in their spawning grounds and only overlap for a short distance at Pirapora Rapids.

Hatanaka and Galetti (2003) found that Três Marias zulegas had a significantly higher genetic similarity coefficient than Pontal (including Cilga) fish. They suggested that the two groups comprised different populations with separate spawning grounds. Our finding showed that Três Marias fish do not seem to be part of the Pontal group because all LS and presumed LS Três Marias fish, except one, stayed at Três Marias during the spawning season. Therefore, our data supports Hatanaka and Galetti's hypothesis that these two groups are different populations.

Mutually exclusive movement patterns and spatially distinct spawning grounds of the Três Marias, Pontal, and Pirapora Rapids groups of zulegas indicate these are three separate populations of a larger metapopulation. The Três Marias population seems to have only a small overlap in range with the upstream portion of the Pontal population. The Pirapora Rapids population has the largest range and some overlap with the Pontal population at Pirapora Rapids.

The Três Marias population may be the downstream part of another population of zulegas upstream of Três Marias Dam. The young zulegas that search for an upstream passage at the Três Marias Dam tailrace showed movements that would be expected if they were recruits from a population upstream of Três Marias Dam. These recruits cannot pass upstream of the dam and must stay downstream. They eventually become adults that are probably dysfunctional in many aspects because they are not at the correct place in the river. The tagged Três Marias adults remained near the dam during the spawning season even though conditions to spawn there were not favorable. This shows a strong behavioral drive to remain as far upstream as possible. Thus, genetic and life history data suggest that Três Marias fish are probably part of a larger upstream population that is segmented by the dam.

Population Structure

The zulegas in the three proposed populations differ in size at maturity. The Três Marias zulegas are largest at maturity (32.0–33.0 cm SL, Santos and Barbieri 1991). Size at maturity is 22.4–22.8 cm SL at Pirapora Rapids (Bazzoli 2003). We converted size at maturity in total length provided by Bazzoli (2003) to standard length using the equation $SL = 0.8 + 0.8$ total length ($r^2 = 0.99$, $n = 657$) using the same dataset used by Bazzoli. The Pirapora Rapids fish experience slightly warmer temperature than Três Marias fish (A. Godinho and B. Kynard, unpublished), and thus, reach sexual maturity at a smaller size. Due to an intermediate temperature at Pontal, we predict that Pontal zulegas mature at an intermediate size between fish at Pirapora Rapids and Três Marias.

Sato et al. (2003a) found more ES fish were present and their mean size was smaller at Três Marias than at Pontal (including Cilga). The mean size of the Três Marias fish was smaller than the size at maturity, which indicates a small proportion of adults at Três Marias. The mean size of Pontal fish was larger than the size at maturity, suggesting a larger percentage of adult fish.

The smaller mean size of fish at Três Marias was probably due to greater harvest at Três Marias. The 2,700 Três Marias commercial fishers (Franco de Camargo and Petrere 2001) are just a few kilometers away from the Três Marias population and much farther from the Pontal group. Also, anglers flock to the São Francisco River to fish for zulega at Três Marias in greater numbers than at any other area (A. Godinho, unpublished).

Conceptual Model

We propose the following metapopulation structure and conceptual model for life history movements of zulegas inhabiting the São Francisco River within 409 km downstream of Três Marias Dam (Figure 6). Three populations of zulegas (Três Marias, Pontal, and Pirapora Rapids) probably live in this reach with some overlap of nonspawning ranges among them. The Pontal population probably includes Cilga fish.

Eggs and larvae produced by each population disperse downstream during the spawning season (rainy season) to nursery grounds (floodplain lakes and probably within-river habitats). The Três Marias population probably produces few or no eggs. Floodplain lakes are abundant downstream of the Paracatu River mouth located 243 km downstream from Três Marias Dam. At about 20 cm SL, juveniles migrate upstream in schools from the nursery grounds to river reaches inhabited by adults of each population.

The migration of adult zulegas to Pontal is the best documented (Figure 6), but similar movements probably occur in the Pirapora Rapids population. Adults upstream and downstream of the spawning area and from tributaries initiate a prespawning migration that is highly variable for timing, e.g., months, weeks or days before or during the spawning season (November–February). Prespawning adults move to Pontal or to a nearby prespawning staging area. They then move back and forth between prespawning staging areas and the spawning ground, usually visiting the spawning site several times (spawning-site homing). After a visit, they return to a prespawning staging site, but not always to the same spot (prespawning staging site homing). Some adults return to the same spawning site for more than one spawning season (spawning-site homing). A small fraction of the postspawned fish remains at the spawning site during the nonspawning season, but most migrate to nonspawning areas downstream in the main stem or into tributaries. Postspawned fish move mostly downstream as far as Pirapora Rapids. Timing of postspawning migration is highly variable, occurring any time during the spawning season or months after spawning ceases. Some postspawned fish return to the same nonspawning ground (nonspawning site homing) and others move to different areas. During the nonspawning season, zulegas are sedentary using a maximum of 4 km of river or occupying two or more different areas that are tens of kilometers apart.

The situation for Três Marias fish is a special case because they live in a river reach highly modified by

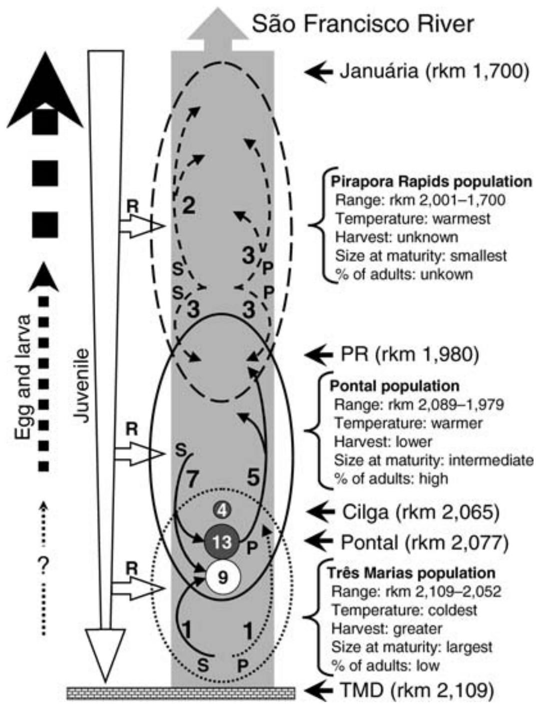

FIGURE 6.—Metapopulation structure and conceptual model of life history movements of zulegas in the São Francisco River between Três Marias Dam (TDM) and the city of Januária. Ellipses show the home ranges of adults in three populations: Três Marias (dotted lines), Pontal (solid lines), and Pirapora Rapids (dashed lines). Arrows within the ellipses show main-stem prespawning (S) and postspawning (P) migrations for the three populations. The range of Pirapora Rapids (PR) fish was determined by Paiva and Bastos (1982), that of the Três Marias and Pontal populations by radio-tracking in the present study. For each population, the range (km), water temperature (°C), harvest intensity, and two aspects of population structure are shown. The two larger circles show the spawning ground (dark) and prespawning staging area (white) for the Pontal population; the smaller dark circle shows the Cilga spawning ground. The large arrows on the left depict egg and larva downstream dispersal and a proposed upstream juvenile migration. The arrows connecting the juvenile upstream migration to the ellipses indicate recruitment (R). The numbers by the spawning grounds and migration arrows indicate the number of tracked fish that used that habitat or made the movement.

a dam. During the spawning season, prespawning Três Marias fish stay close to Três Marias Dam where the water probably lacks spawning cues and precludes spawning, so many fish reabsorb gametes. If spawning occurs, it is probably only by few fish, suggesting strong directional selection favoring those few fish that can mature and spawn under these conditions. After the spawning season, few fish migrate downstream (Figure 6). During the nonspawning season, Três Marias fish stay at or near Três Marias or migrate downstream only to return within a few months. When ES Três Marias fish develop into LS adults, most stay at Três Marias during the spawning season, but few adults go downstream and spawn at Pontal. If they do, they do not return to Três Marias, thus providing some genetic exchange between the two populations.

For Pirapora Rapids fish, only the total linear home range and migratory movements are known. Most fish have a small total linear home range (<25 km). They use tributaries and the main stem. Pre- and postspawning migrations are upstream or downstream, but location of spawning grounds and the details on nonspawning grounds are unknown (Figure 6).

Conservation and Management Implications

The São Francisco River Basin hydropower potential is 26.3 GW, of which 10.5 GW has already been developed (ANEEL 2002). Any of the nine new dams proposed for the free-flowing Abaeté River will stop floods that trigger spawning at Pontal and at other downstream locations. This will cause the collapse of the Pontal population. To maintain populations of zulegas and other migratory fishes that use the Pontal spawning area (A. Godinho and B. Kynard, unpublished), the Abaeté River must remain without dams.

Among the four dams planned for the main stem downstream of Três Marias Dam, the Formoso Dam is the most upstream one (Godinho 1993) and is located 10 km upstream from Pirapora Rapids. This dam will flood spawning and nonspawning grounds of the Pontal population. It will also impede free movement of adult zulegas and upstream movement of returning Pontal juveniles. The Formoso Resevoir will block downstream dispersing eggs and larvae of zulegas (Godinho 2005). Thus, it is hard to envision a scenario in which the Formoso Dam is constructed and the Pontal population survives. The three others planned mainsteam dams will probably impact the Pontal population by blocking downstream dispersal of eggs and larvae. They may also block returning juveniles if this life stage persists after dam construction. In this case, fish passage will be necessary to provide juveniles access to their nonspawning grounds.

Três Marias Dam does not have upstream or downstream fish passage facilities. The conceptual model indicates that the Três Marias population may be the downstream part of a population upstream of the dam, but there are many unanswered questions. Little is known about zulegas that occur upstream of Três Marias Dam other than they do occur; so the connection between Três Marias fish to an upstream population segment needs to be verified and understood in terms of life history movements. This information will provide agencies with the details of migrations and connections to upstream populations needed before pursuing development of fish passage facilities at the Três Marias Dam.

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