

Article

Migratory Ecology of *Pseudoplatystoma fasciatum* in the Amazon Basin Revealed by Otolith Microchemistry

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Abstract: Fish migrate for varied reasons, including to avoid predators and to access feeding, spawning, and nursery habitats, behaviors that enhance their survival and reproductive rates. However, the migratory ecology of many important fishes, especially those in river–floodplain ecosystems, remains poorly understood. One fish of the Amazon Basin whose migratory behavior is poorly understood is the catfish *Pseudoplatystoma fasciatum*. Here, we used otolith elemental microchemistry to characterize the migration ecology of *P. fasciatum* in the Amazon Basin. The main research questions of this study were: (1) does *P. fasciatum* move between waters with different Sr isotopic signatures (⁸⁷Sr/⁸⁶Sr) and chemical compositions? (2) What distance do they migrate? (3) Is the migration of *P. fasciatum* related to age? And (4) does *P. fasciatum* migrate mainly upstream, downstream, or in both directions? We assessed whether *P. fasciatum* migrates between waters with different ⁸⁷Sr/⁸⁶Sr values, comparing the Sr isotopic signature of otolith transects of each individual with the range of Sr isotopic signatures within the respective rivers. We found that 34% of the 71 fish analyzed migrated between rivers with different Sr isotopic signatures and 66% did not. The mean migration distance migrated was 126 km, with most specimens migrating between 72 and 237 km. Apparently, no fish of age one or age six or older migrated. All fish that migrated were between two and five years of age, with 20% of the specimens that migrated being two years old, 40% three years old, 30% four years old, and 20% five years old. Sixty-six percent of all individuals that migrated between rivers with different Sr signatures did so bidirectionally, while 33% moved unidirectionally. According to our definition of homing behavior in which fish migrated back to the same river where they were born, 41% of all fish that migrated displayed apparent homing behavior. Our findings provide insights into the migratory ecology of *P. fasciatum*, corroborating and refining knowledge reported in the literature. Our results on the migratory ecology of *P. fasciatum* have implications for sustainable fisheries conservation and management: conserving *P. fasciatum* requires habitat maintenance and suitable fishing practices in spawning and nursery habitats, and managers must consider large geographic areas for effective fishery management and conservation.

Keywords: Sr isotopic ratios; ontogenetic migration; reproductive migration; life history; barred surubim catfish



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1. Introduction

Fish migrate for varied reasons, including avoiding predators and accessing feeding, spawning, and nursery habitats [1], p. 5, behaviors that enhance their survival and reproductive rates and, thus, their fitness [2]. The topic of fish migration is relatively well-understood in many ecosystems of the world [2,3]. However, the migratory ecology of many important fishes, especially those in river–floodplain ecosystems, remains poorly understood. An improved understanding of fish migration in such systems is necessary because many tropical river floodplains are undergoing major transformations. Rapidly

growing human activities—such as overexploitation of natural resources, climate change, land-cover change, and construction of hydropower dams—are threatening the viability of many migratory fish populations in these ecosystems, and hence ecological and social dependence upon them [4,5].

Prior studies have shown that fish migration in tropical river–floodplains is usually driven by predictable, seasonal variations in river water levels, known as flood pulses [6,7]. Most known upstream fish movements in river–floodplains coincide with different phases of the flood pulse [8,9], allowing fish populations to compensate for the downstream drift of eggs and larvae, and thereby maintain their position in these systems [10,11]. Prior studies of fish migration in the Amazon River basin have shown that fish migrations vary, depending upon: (1) the geographical scale of the movements, from tens to hundreds to thousands of kilometers [12–15]; (2) the type of movements, which can be longitudinal or lateral [16,17]; and (3) timing of the movements, which occur at different life stages and have various durations over the individual’s life span [17,18]. While this knowledge of fish migrations in the Amazon has been useful in framing its consideration, it is based on a limited number of studies [19], with the migratory ecology of many important species remaining largely unstudied.

One fish of the Amazon Basin whose migratory behavior is poorly understood is the surubim catfish *Pseudoplatystoma fasciatum*. The few studies on its migratory ecology showed that its migrations mediate energy flows among habitats and food webs while supporting valuable fisheries that sustain food security and income for Amazonians [20,21]. *P. fasciatum* males usually inhabit rivers, while females inhabit floodplain lakes during the low-water season [22]. Adult *P. fasciatum* migrate upstream for spawning during the beginning of high waters in the Mamoré River Basin, Bolivia. Juvenile *P. fasciatum* are believed to be non-migratory, growing in the floodplains until adulthood [22]. In the Colombian Amazon, Diaz-Sarmiento and Alvarez-León [23] indicated that *Pseudoplatystoma* spp. migrate between 300 and 500 km. However, these studies inferred migration distances using circumstantial evidence from mean sizes and gonad maturity in capture data. Only one study has produced movement data on *P. fasciatum*. Using telemetry methods in the Xingu River, Brazil, Hahn et al. [24] found that *P. punctifer* (renamed *P. fasciatum* afterward [21]) performs bidirectional movements and that most movements occur between the dry season and the rising water period. Hahn et al. [24] also found that *P. punctifer* can migrate up to 164 km between the low and rising water periods. Therefore, there are many open questions about the migratory ecology of *P. fasciatum*, including why, how far, when, and where they migrate.

This uncertainty about the migratory ecology of *P. fasciatum* limits its management and conservation. Although *P. fasciatum* is not considered to be widely overexploited, and is classified as “Least Concern”, the species is the focus of major fishing pressure. Landings of *P. fasciatum* have been declining in some regions, and it has been captured at increasingly small body sizes due to growing fishing pressure [25,26]. Isaac et al. [27] found that *P. fasciatum* was overexploited, being caught at a very small size near Santarem on the Amazon River in Brazil. Another source of pressure on *P. fasciatum* is the growing construction of hydropower dams in the Amazon basin [21]. As barriers to upstream migrations, dams can prevent adults from reaching spawning grounds during the breeding season, resulting in recruitment failure and eventual population extirpation above the dam [28]. Dams may also disrupt downstream migrations. In particular, the modification of the downstream river-flow regime can cause a loss of migration stimuli, routes, and spawning grounds, disrupting the life cycle of migratory species by decreasing the survival of eggs and juveniles along with recruitment to the mature life stage [29].

One approach to gain insight into the migratory ecology of *P. fasciatum* is through the use of otolith microchemistry analysis [9]. Otolith microchemistry offers a robust and cost-effective way to unravel the migratory ecology of fish species where there are enormous challenges but few human and economic resources to study them. Over time, otoliths record the strontium (Sr) isotope signature of the water in which fish grow [3,30,31], providing

reliable records of past movement patterns over the individual's lifetime. Analysis of such chronologic Sr signatures across the otolith thus provides a cost-effective means to infer the migratory ecology of individual fish in river–floodplain systems like the Amazon. Sr isotopes have been successfully used to study the migratory behavior of other pimelodid catfishes [14,17,32,33] and cichlids [34,35] in the Amazon basin.

Here, we used otolith microchemistry to characterize the migration ecology of *P. fasciatus* in the Amazon Basin. The main research questions of this study were: (1) does *P. fasciatus* move between waters with different Sr and chemical compositions? (2) What distance do they migrate? (3) Is the migration of *P. fasciatus* related to age? And (4) what is the directionality of the migration of *P. fasciatus*?

2. Materials and Methods

2.1. Area of Study and Sampling

We collected field samples from 2019 to 2021 in five localities (Figure 1), each from a different river of the Amazon Basin in which *P. fasciatus* is distributed: (1) Manacapuru on the Solimões River, (2), Santarem, and (3) Itacoatiara on the Amazon River, (4) Porto Velho on the Madeira River, and (5) Guajara-Mirim, where the fish come from the Yata River. We collected samples in these localities because they are located at or near the confluence between rivers, presenting Sr isotopic heterogeneity. Rivers of the Amazon Basin drain geological units with a wide range of Sr isotope compositions [36]. For example, the Negro rivers drain old rock formations that imprint a strong radiogenic Sr isotope signature in their waters. In contrast, the Solimões River drains younger formations, draining water characterized by less radiogenic Sr isotope signatures. Thus, the heterogeneity of the Amazon Basin in terms of strontium (Sr) isotope signatures allowed us to analyze the Sr isotopic signature in the otoliths of *P. fasciatus* to understand its migratory ecology.

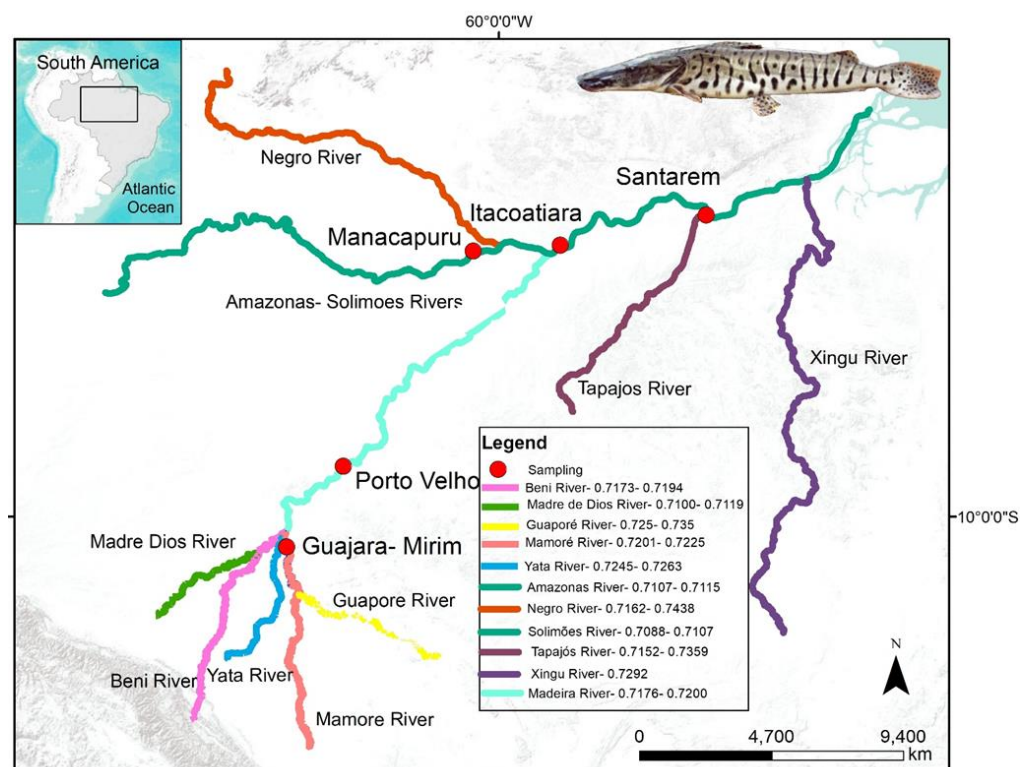


Figure 1. Map of the Amazon basin showing the sampling sites for the 71 *P. fasciatus* (red circles). The rivers with different colors have different $^{87}\text{Sr}/^{86}\text{Sr}$ signatures. Values beside the rivers' names represent the range of $^{87}\text{Sr}/^{86}\text{Sr}$ values known for each of these river basins, following Hauser et al. [32] and Hauser et al. [37].

We sampled 71 specimens of *P. fasciatum*, 10 from Guajara-Mirim, 11 from Itacoatiara, 13 from Manacapuru, 16 from Porto Velho, and 20 from Santarem (Table 1). The length of the specimens varied from 23 cm to 105 cm, with very few specimens being smaller than 50 cm or larger than 70 cm. Specimens were aged in another study using vertebrae [38], following [22], with ages ranging from one to seven years old. Our handling and use of fish complied with permit 20–176 issued by the Virginia Tech Institutional Animal Care and Use Committee on 23 September 2020.

Table 1. Number of *P. fasciatum* sampled per basin, range of total lengths, and estimated age ranges.

Site	N	Length Range	Age Range
Guajara-Mirim	10	50–70 cm	2–5 years
Itacoatiara	11	23–68 cm	1–5 years
Manacapuru	13	52–85 cm	4–7 years
Porto Velho	16	57–105 cm	2–6 years
Santarem	20	50–73 cm	2–5 years
Total	71	23–105 cm	1–7 years

To analyze the Sr isotope signature in the otoliths, we followed established methodology [8,14,17]. We mounted each otolith in Araldite epoxy resin (Huntsman Advanced Materials, Basel, Switzerland) and cut them transversally with a low-speed saw (Isomed Buehler, Düsseldorf, Germany, 2009) to obtain a section that included the otolith core. The sections were fine-polished until the core could be seen, sonicated in distilled water, and mounted on a glass slide using crystal bond glue.

2.2. Analytical Design

2.2.1. Laboratory Analysis

Sr isotope analyses were performed at the University of Brasilia and at the University of Montpellier. The isotope ratios measured at the University of Brasilia were measured using an Analyte Excite ArF laser ablation system (LA) coupled to a Thermo Fischer Neptune XT sector-field multi-collector (MC)-ICP-MS following the procedures detailed by Claverie et al. [39] and Tabouret et al. [40]. Laser ablation conditions were adjusted according to the concentration of Sr in the otoliths. Analyses were performed using a square-shaped laser raster with an aperture diameter of 80–150 μm , advancing with a speed of 10 $\mu\text{m}/\text{s}$, operating at 20 Hz, and using a nominal energy of 7.55 J/cm². The ablated aerosol was flushed from the HelEx II two-volume laser cell using 0.7 L/min (0.35 + 0.35) of He. The Neptune XT is equipped with 9 Faraday detectors, which measured the masses 82 to 88 in static mode and using 10¹¹ Ω amplifiers. The Neptune XT is equipped with the Jet interface, a combination of a high-efficiency dry mechanical pump and a combination of the “Jet” and “X” cones, offering higher sensitivity during the analytical session. The background was measured before each raster for 20 s, and the measured data were each integrated for 0.262 s. Mass bias was corrected by normalizing to $^{88}\text{Sr}/^{86}\text{Sr} = 8.375209$. Rb and Kr interferences were corrected using exponential law, and the natural ratios of $^{87}\text{Rb}/^{85}\text{Rb} = 0.38560$, $^{84}\text{Kr}/^{83}\text{Kr} = 4.95565$, and $^{86}\text{Kr}/^{83}\text{Kr} = 1.5026$. Any residual bias was corrected by normalization to our in-house otolith (ID-TIMS $^{87}\text{Sr}/^{86}\text{Sr} = 0.70968$), which has an isotopic composition of the present-day modern ocean water (0.70918; e.g., [41]), bracketed before and after each group of six samples. Uncertainties are reported at 2 s.

Measurement of Sr isotopes at the University of Montpellier (AETE-ISO Plateform of the OSU OREME) used a ThermoFinnigan Neptune+ multicollector inductively-coupled plasma mass spectrometer (MC-ICP-MS) coupled with a Teledyne Analyte G2 Excimer laser (193 nm wavelength). Before each ablation experiment, a pre-ablation step was conducted, consisting of smoothly ablating the linescan used for the Sr isotopic analyses, but with lower laser parameters (3 J/cm², 4 Hz) and using a larger spot size (145 μm). This pre-ablation step allows for the cleaning of the top of the track used later for Sr isotopic measurements.

Ablation experiments were performed in a two-volume sample cell under ultrapure helium. The sample + He aerosol is then mixed with ultrapure N₂ and subsequently with Ar before entering the plasma source. Ablation was performed using a 130 µm spot size. Laser frequency was 8 Hz and the energy density of the laser beam was 4 J/cm². A typical analysis included a 30 s background measurement followed by an ablation period whose duration depended on the otolith size (between 30 and 180 s). Integration time for each measurement was 1.04 s, and all isotopes were measured on Faraday cups equipped with 10¹¹ ohm resistors. Corrections for Kr and Rb interferences and mass bias followed a routine procedure using known isotopic ratios [42]. No corrections were applied for interferences from doubly charged REE, Ca argides, Ca dimers, or polyatomic interferences, since numerous studies have shown that Ca argides and dimers have no significant influence on Sr isotopic data during MC-ICP-MS analyses (e.g., in Yang et al. [43]), and for material with high Sr (Sr > 300 ppm) and low REE contents, Ca-P-O and doubly charged ions are insignificant as well. Krypton interferences (^{84,86}Kr on ^{84,86}Sr) originating from the argon tank were corrected for by measuring the background level before the analysis and then by subtracting the background from the data. Rubidium interferences (⁸⁷Rb on ⁸⁷Sr) were corrected for by monitoring ⁸⁵Rb and subtracting the signal at mass 87 amu assuming a natural ⁸⁵Rb/⁸⁷Rb of 2.59262 [44]. The ⁸⁵Rb/⁸⁷Rb ratio was corrected for mass bias using the mass discrimination factor calculated from Sr, using an exponential law and a natural ⁸⁸Sr/⁸⁶Sr = 8.375209, and assuming no differential mass discrimination between Sr and Rb. The accuracy and long-term reproducibility of the measurements were gauged by analyzing an in-house reference material constituted by a modern Atlantic bivalve shell with a reference value of ⁸⁷Sr/⁸⁶Sr = 0.709178 ± 10 (2 s) comparable to modern seawater.

In order to ensure the repeatability and comparability of the analyses performed at the University of Brasilia and at the University of Montpellier, several otoliths were analyzed in both laboratories (i.e., Figure S1).

2.2.2. Migration in Different Waters

To infer whether *P. fasciatum* migrates between waters with different Sr and chemical compositions, we compared the Sr signature of otolith core-to-edge otolith transects of each specimen with the range of Sr signatures in the respective rivers. For those specimens whose Sr signatures in the otolith transects differed from the range of one river to the range of the other river, we concluded that the individual had migrated between those rivers. We considered specimens that moved between rivers with different Sr signatures as those that had differences in the otolith transect Sr signatures of at least two µms along the x-axis and more than 0.003 Sr isotope signature variation in the river.

For reference, we used the most recent review on Sr isotope signatures in rivers of the Amazon [32]. Because the ranges from Hauser et al. [32] included the maximum and minimum values ever registered for the rivers, and in some of them they also included seasonal variations of Sr [36], we note that they account for natural variability that is expected in such natural environments. While such fluidity could hamper our analyses, we note that the data in Hauser et al. [32] did not show overlap in the range of Sr signatures, allowing us to reliably infer movement among rivers.

A limitation of otolith microchemistry is that it can identify movements only when there is spatial heterogeneity in Sr isotopic signatures among rivers. Specimens that did not have changes in Sr isotopic signatures along the otolith transects were assumed not to have moved between rivers with different Sr signatures. However, they might have migrated between river waters with identical Sr signatures or migrated within the same river system. As such, for those specimens whose otolith Sr signatures did not change in relation to the range of Sr signatures of the respective rivers, we inferred that they did not migrate among rivers with different Sr signatures and considered conservatively that they did not migrate.

We also analyzed whether *P. fasciatum* migrated between rivers with different physiochemical compositions; to answer this question, we compared the core-to-edge transect Sr signatures of each fish with the type of water of each river (white, clear, or black) in

which they moved using the classifications of Sioli [45]. When the Sr signature of the otolith transect changed for different types of water, we inferred that the fish had moved among different types of water.

2.2.3. Distance Migrated

To estimate the minimum distance (possibly) migrated by *P. fasciatum*, we inferred the migration routes of each specimen by tracing back the differences of Sr signatures of the Sr transects and determining the most probable river from which each specimen originated and the river to which it migrated. We then used ArcGIS (<https://www.arcgis.com/index.html> accessed on 1 August 2023) to measure the distance between 20 km from the confluence of the river from which the fish started migrating and 20 km past the confluence into the river where it migrated (Figure 2). Conservatively, we measured just the first 20 km in the river because we could not confirm how far the fish migrated within either the origin or destination rivers; we could only determine that the fish was in that river. We then calculated the average and range of estimated distance migrated for that individual.

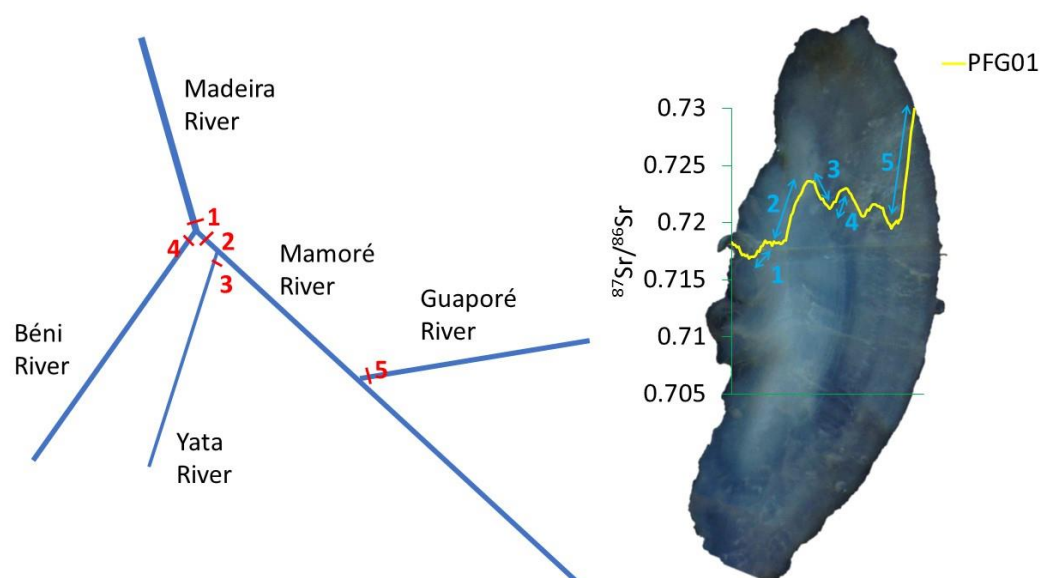


Figure 2. Diagram showing the calculation of the minimum distance migrated. The blue lines represent the geographic orientations of the respective rivers, and the numbers on the left represent points on the inferred migration route that this specimen completed based on the Sr isotope signature in its otoliths. Each number represents a point 20 km into the river that the fish presumably migrated to record the Sr isotope signature exhibited in the otolith shown on the right. The exact location in each river to or through which the specimen migrated was arbitrarily and tentatively set at 20 km of distance from the nearest river confluence. Each section of the profile corresponds to the isotopic values of one particular river; hence, we deduced that the fish was in that river at that time. To reach that river from the precedent section of the profile, the fish had to travel at least from point A of that river to point B of the other river. For example, for fish PFG 01, the first part of the profile corresponds to the chemical signature of the Madeira River. We then conservatively estimated that the fish had migrated at least 20 km within the Madeira River (point 1 of the diagram) to the confluence with the Mamore River. Then we added to this value 20 km at least that the fish might have made into the Mamore River (point 2), plus the distance between point 2 and the confluence with the Yata River, plus the 20 km into the Yata River (point 3). The profile then indicated that the fish went into the Beni River. We then added the 20 km from point 3 to the confluence with the Mamoré, plus the distance to the confluence of the Mamoré with the Beni, plus 20 km into the Beni River until point 4. The profile then indicated that the fish moved into the Guapore River. We therefore added the 20 km from point 4 to the confluence with the Mamoré, plus the distance to the confluence with the Guapore River, and finally another 20 km in the Guapore to point 5.

2.2.4. What Is the Directionality of the Migrations of *P. fasciatum*?

To determine the directionality of migration, we inferred whether specimens of *P. fasciatum* migrated up or downstream based on the Sr isotope signature throughout the otolith transects, considering the migration routes inferred above and the Sr signature of the respective rivers. We calculated the percentage of specimens that migrated bidirectionally and unidirectionally.

2.2.5. Is the Migration of *P. fasciatum* Related to Age?

To assess whether the migration of *P. fasciatum* is related to age, we calculated the proportion of specimens that migrated per age class for both specimens that migrated between rivers and those that did not migrate among rivers. To investigate whether specimens that migrated among rivers returned to the river of origin (i.e., displayed homing behavior), we classified the specimens as those exhibiting the same Sr isotopic ratios of the same river before and after apparent migration behavior.

3. Results

Our data show that individual *P. fasciatum* varied regarding their migratory patterns, with some migrating between rivers with different Sr isotopic signatures while others did not. Table 2 and Figures 3 and 4 summarize the main data and outputs from this study. Figure 2 shows the Sr signature of specimens that performed migrations between rivers and those that did not. For each fish, information about the estimated age, total length at capture (TL), movements between rivers with different Sr isotopic ratios and types of water, the minimum estimated distance migrated, the direction of the migration, and the presence or absence of apparent homing behavior is reported in Table 2. A detailed explanation of how these data and results answer our research questions is presented next.

Table 2. Data for each individual *P. fasciatum*, showing sample locality, estimated age, length at capture, migration between rivers with different Sr signatures and types of water, minimum distance migrated, directionality of migration, and performance of homing behavior. Individuals were aged in another study using vertebrae [38]. Sampling localities: GUA—Guajara, ITA—Itacoatiara, Mana—Manaus, PV—Porto Velho, and Santa—Santarem.

Fish	Locality	Age	Length TL (mm)	Moved between Rivers?	Moved between Water Types?	Minimum Estimated Distance Migrated	Direction	Homing?
PFG01	GUA	4.0	660	yes	yes	232	Bi	no
PFG04	GUA	3.0	600	yes	no	372	Bi	no
PFG05	GUA	4.7	800	yes	yes	474	Bi	yes
PFG07	GUA	2.8	630	yes	no	72	Bi	yes
PFG14	GUA	2.3	640	yes	no	180	Bi	no
PFG15	GUA	2.3	570	no	no	166	NA	no
PFG16	GUA	3.3	550	yes	no	252	Uni	no
PFG19	GUA	3.4	590	no	no	36	NA	no
PFG20	GUA	5.4	660	yes	yes	252	Uni	no
PFG21	GUA	2.4	700	no	no	80	NA	no
PFG24	GUA	3.5	700	yes	yes	36	Uni	no
PFG27	GUA	3.5	610	no	no	1020	NA	no
PFI01	ITA	3.2	680	yes	no	264	Bi	yes
PFI09	ITA	3.2	570	no	no	252	NA	no
PFI11	ITA	3.2	557	yes	yes	80	Bi	yes
PFI14	ITA	1.2	460	no	no	172	NA	no
PFI19	ITA	3.2	545	yes	no	40	Uni	no

Table 2. Cont.

Fish	Locality	Age	Length TL (mm)	Moved between Rivers?	Moved between Water Types?	Minimum Estimated Distance Migrated	Direction	Homing?
PFI23	ITA	5.2	230	yes	no	1020	Uni	no
PFI28	ITA	3.2	620	no	no	40	NA	no
PFI29	ITA	3.3	600	yes	no	40	Uni	no
PFI33	ITA	2.3	505	no	no	72	NA	no
PFI37	ITA	3.3	573	no	no	144	NA	no
PFM02	MANA	3.7	600	no	no	108	NA	no
PFM05	MANA	3.7	600	no	no	72	NA	no
PFM07	MANA	3.7	740	no	no	NA	NA	no
PFM12	MANA	4.7	850	no	no	NA	NA	no
PFM18	MANA	4.7	780	no	no	NA	NA	no
PFM20	MANA	4.7	580	no	no	NA	NA	no
PFM27	MANA	5.7	520	no	no	NA	NA	no
PFM29	MANA	5.7	570	no	no	NA	NA	no
PFM30	MANA	5.7	560	no	no	NA	NA	no
PFM34	MANA	5.7	550	no	no	NA	NA	no
PFM37	MANA	6.7	700	no	no	NA	NA	no
PFM38	MANA	6.7	690	no	no	NA	NA	no
PFM41	MANA	6.7	600	no	no	NA	NA	no
PFP01	PV	2.9	750	yes	yes	252	Uni	no
PFP07	PV	4.0	600	no	no	NA	NA	no
PFP09	PV	5.0	690	yes	no	108	Bi	no
PFP10	PV	4.0	660	yes	yes	172	Bi	no
PFP12	PV	3.4	580	yes	no	80	Uni	yes
PFP13	PV	3.4	570	yes	no	72	Bi	yes
PFP15	PV	3.7	570	yes	no	40	Uni	no
PFP17	PV	4.9	620	yes	no	144	Bi	yes
PFP20	PV	5.9	105	no	no	NA	NA	no
PFP23	PV	5.9	770	no	no	NA	NA	no
PFP26	PV	3.5	570	yes	no	72	Bi	yes
PFP28	PV	5.8	870	yes	no	144	Bi	yes
PFP29	PV	4.8	810	yes	no	108	Bi	no
PFP35	PV	5.9	840	no	no	NA	NA	no
PFP42	PV	4.0	660	yes	no	72	Bi	yes
PFP43	PV	5.0	590	no	no	NA	NA	no
PFS05	SANTA	4.8	635	no	no	NA	NA	no
PFS06	SANTA	4.8	610	no	no	NA	NA	no
PFS09	SANTA	2.8	535	no	no	NA	NA	no
PFS14	SANTA	4.8	542	no	no	NA	NA	no
PFS15	SANTA	5.7	572	no	no	NA	NA	no
PFS18	SANTA	3.6	526	no	no	NA	NA	no
PFS19	SANTA	3.1	510	no	no	NA	NA	no
PFS22	SANTA	3.5	560	no	no	NA	NA	no
PFS23	SANTA	3.1	510	no	no	NA	NA	no
PFS25	SANTA	2.0	520	no	no	NA	NA	no
PFS31	SANTA	3.1	510	no	no	NA	NA	no
PFS32	SANTA	2.1	520	no	no	NA	NA	no
PFS33	SANTA	3.1	540	no	no	NA	NA	no
PFS34	SANTA	3.1	500	no	no	NA	NA	no
PFS35	SANTA	4.1	500	no	no	NA	NA	no
PFS36	SANTA	2.1	500	no	no	NA	NA	no
PFS38	SANTA	2.1	520	no	no	NA	NA	no
PFS44	SANTA	3.5	520	no	no	NA	NA	no
PFS46	SANTA	3.5	550	no	no	NA	NA	no
PFS48	SANTA	3.5	730	no	no	NA	NA	no

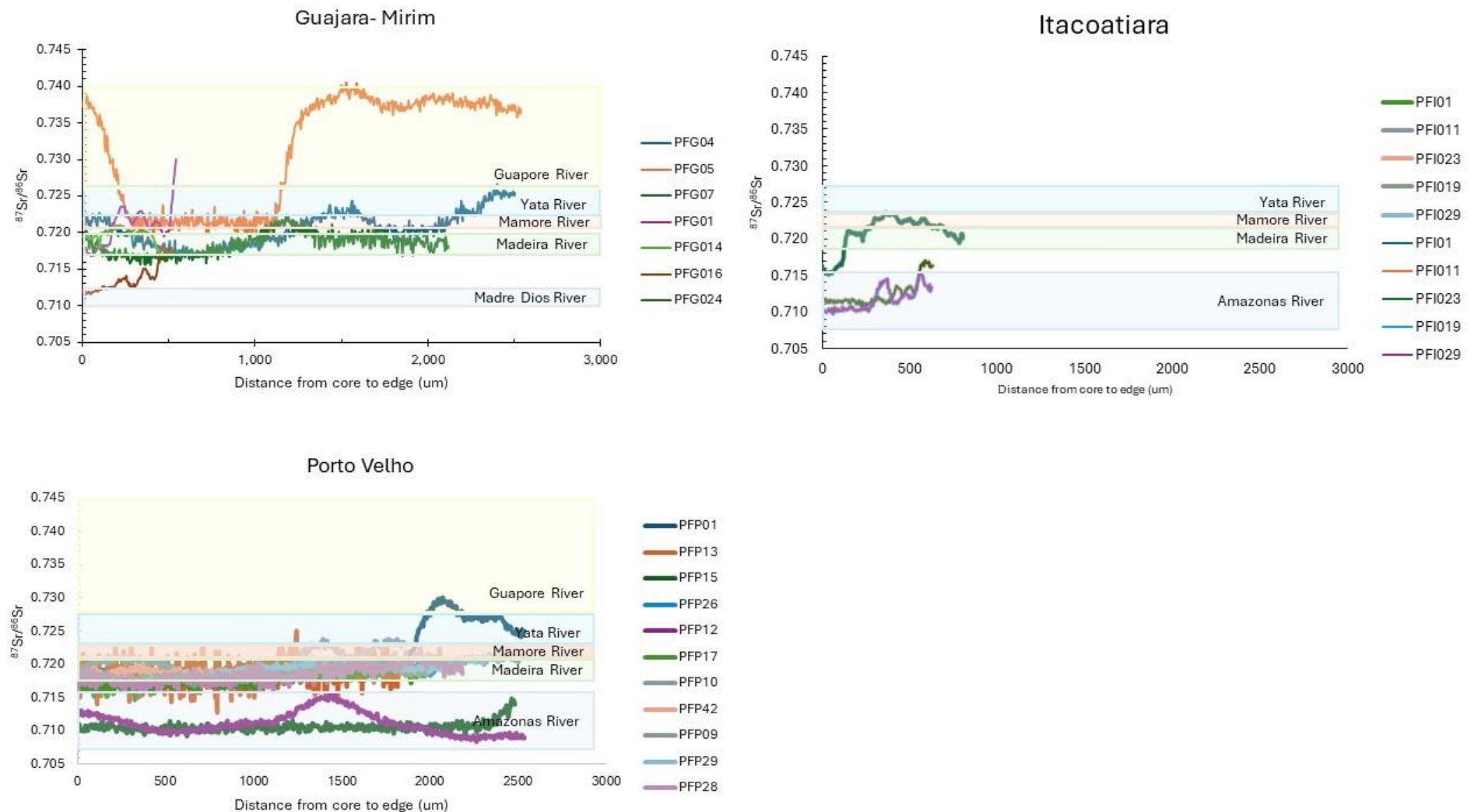


Figure 3. Sr isotopic signatures from core to edge of the otolith for *P. fasciatum* specimens collected in three rivers within the Amazon basin. The Sr range for each river is represented by boxes with different colors that include minimum and maximum Sr signature values for each river. Data show the Sr isotopic signatures of specimens that performed migrations between rivers with different Sr signatures in Guajara-Mirim, Itacoatiara, and Porto Velho.



Figure 4. Sr isotopic signatures from core to edge of the otolith for *P. fasciatum* individuals collected in five rivers within the Amazon basin. The Sr range for each river is represented by boxes with different colors that include minimum and maximum Sr signature values for each river. Data show the Sr isotopic signatures of specimens that did not perform migrations between rivers with different Sr signatures in Guajara-Mirim, Itacoatiara, Porto Velho, Manacapuru, and Santarem.

3.1. Migration of *P. fasciatum* between Waters with Different Sr and Chemical Compositions

Thirty-four percent of all fish analyzed migrated between rivers with different Sr signatures, and 66% did not (Table 3). The percentage of fish that migrated between rivers with different Sr signatures varied by locality; however, 53% of the fish sampled in Guajara-Mirim city migrated, as did 50% in Itacoatiara, 31% in Porto Velho, and 0% in Manacapuru and Santarem, which might be a reflection of the size range. Eighty percent of all fish migrated between rivers with the same type of water (i.e., whitewater and blackwater rivers), while only 10% migrated between different water types (Table 3).

Table 3. Proportions of *P. fasciatum* that migrated or did not migrate between rivers with different Sr signatures and types of water in five rivers within the Amazon Basin. The types of water in the Amazon Basin are white, black, and clear waters.

Sites	Size Range of Length (cm)	Percentage of Fish That Did Not Move between Rivers with Different Sr Signatures	Percentage of Fish That Did Move between Rivers with Different Sr Signatures	Percentage of Fish That Moved between Different Types of Water	Percentage of Fish That Did Not Moved between Different Types of Water
Guajara-Mirim	550–800	0.7	0.6	0.6	0.2
Itacoatiara	230–680	0.5	0.5	0.3	0.8
Manacapuru	520–850	0.0	1.0	NA	NA
Porto Velho	570–1050	0.7	0.3	0.3	0.8
Santarem	500–730	0.0	1.0	NA	NA
All	230–1050	0.7	0.3	0.1	0.8

3.2. Distance Migrated

The mean migration distance was 126 km, with most specimens migrating between 72 and 237 km. Migration distances were highly variable, however, with the minimum distance migrated being 36 km and the maximum being 1020 km (Figure 5).

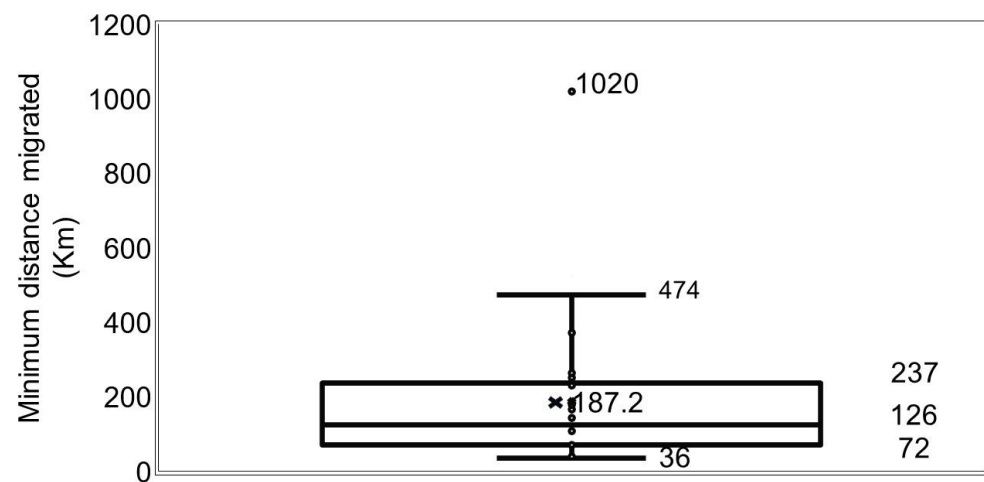


Figure 5. Box plot of the minimum estimated distance migrated by *P. fasciatum* showing the minimum and maximum values for estimated migration distance and standard deviation, with the average represented with an “x” and mean as a horizontal line.

3.3. Migration at Age

All fish of age one, six, or older either migrated only within the same river basin (within the same Sr signature) or did not migrate, which cannot be differentiated by our approach. All fish that migrated were between two and five years of age, with 20% of the specimens that migrated being two years old, 40% three years old, 30% four years old, and 20% five years old (Figure 6). However, we note that these results are based on an uneven number of fish per age class, with very few specimens over six years old and

only one of one year. This may explain why we did not find fish of age one or age six or older migrating.

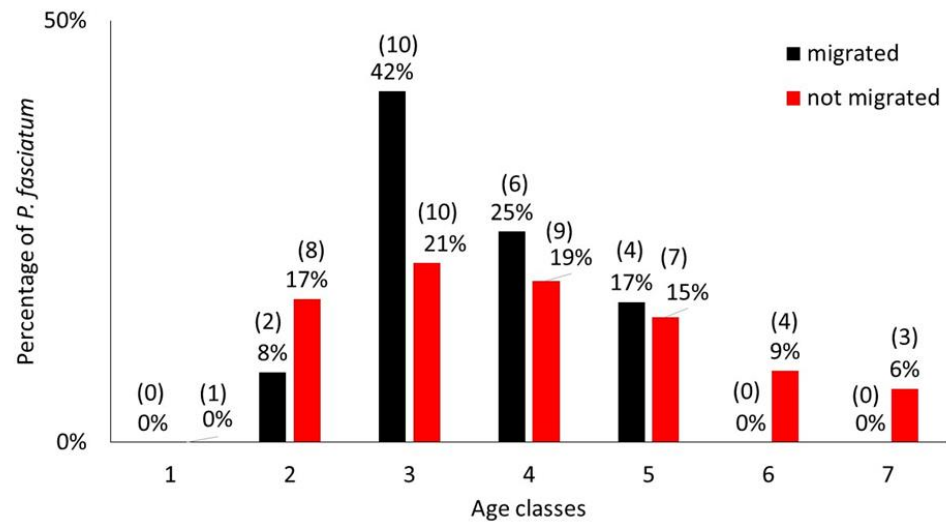


Figure 6. Percentage of *P. fasciatum* that migrated (black bars) and did not migrate (orange bars) between rivers with different Sr signatures per age class. The number of fish for each age class is presented in brackets.

3.4. Directionality of Migration

Sixty-six percent of all specimens that migrated between rivers with different Sr signatures did so bidirectionally, while 33% moved unidirectionally (Table 1). Of those that migrated bidirectionally, 10% migrated from whitewater rivers to blackwater rivers, while 80% migrated between whitewater rivers. Of those that migrated unidirectionally, 25% migrated from white- to blackwater rivers, while 75% migrated between whitewater rivers.

According to our definition of homing, 41% of all fish that migrated displayed apparent homing behavior. Of those, individual PFG05 presented a clear pattern of homing behavior (Figure 7). This specimen was born in the Guapore River and migrated to the Mamore River after it was two years old, and then it migrated back to the Guapore River at the time of capture, performing a bidirectional migration.

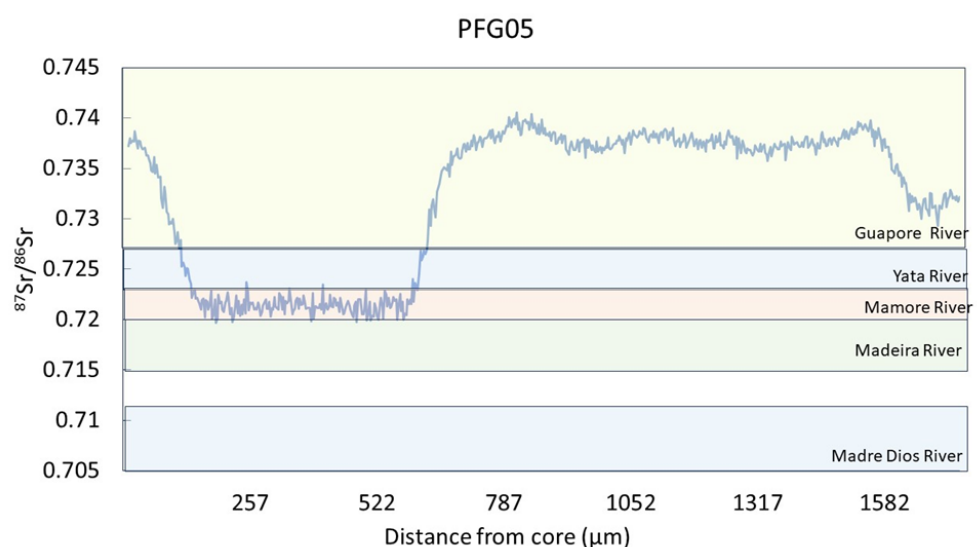


Figure 7. Sr isotopic signature of individual PFG05, which performed migrations between rivers with different Sr signatures and returned to its place of birth in the Guajara-Mirim Basin.

4. Discussion

Our findings provide insights into the migratory ecology of *P. fasciatum*, corroborating and refining knowledge reported in the literature. While many details of the life cycle of *P. fasciatum* remain elusive and patchily known across the Amazon Basin, available data mainly from Loubens and Panfili [22] present the following tentative sequence of events. Eggs and larvae drift downstream along river channels until they reach floodplains, where the structural complexity of vegetated habitats offers protection from predators and an abundance of food resources such as small fish and invertebrates [39,40]. Juveniles thrive in these floodplain habitats, feeding on abundant zooplankton, small fish, and invertebrates [46,47], and do not appear to exhibit migratory behavior until they grow to the age of two years [22]. Sexual maturation occurs at two years of age, and it appears to prompt migration during the rising-water season out of the floodplains and upstream in the main river channels [22]. Loubens and Panfili [22] suggested that this migration of *P. fasciatum* can reach up to 300 km. Hahn et al. [24] found that *P. fasciatum* moves an average distance of 25 km, but it is unclear whether that estimate is for routine everyday movements or for upstream migration. During these migrations, the stomachs of adults are commonly found empty, indicative of a non-feeding migration likely associated with reproduction, and adults from different populations appear to migrate to distinct spawning grounds [22]. *P. fasciatum* exhibits total spawning, i.e., releasing all their eggs at once each year and likely multiple times throughout their lives [21], with a longevity of ten years in the Beni River basin, Bolivia [22], and eight years for the studied populations [38].

Our study refines the current understanding of the migratory ecology of *P. fasciatum* in various ways. Our results support the view put forth by Loubens and Panfili [22] that its migration starts at the age of two years. We found that *P. fasciatum* does not migrate in the first year of its life, at least not in a way that could be detected by our approach (i.e., between rivers with different Sr signatures). This result agrees with Loubens and Panfili [22], who say that the juveniles are non-migratory and stay in the floodplains that are known to serve as nurseries [10], allowing them to grow to almost 40 cm in standard length in the first year [48]. In the floodplains, the juveniles find an abundance of zooplankton, and gradually, their diet shifts to aquatic insects and then to fishes [49,50], including the characiforms silver mylossoma *Mylossoma duriventre*, coporo *Prochilodus mariae*, and headstander *Schizodon* sp. [51]. Our finding that *P. fasciatum* starts its migration at the age of two years also supports the interpretation that its migration is for reproductive purposes. Reproductive migrations upstream have been documented many times in the literature and are thought to help maintain population position in river channels and prevent the washout of eggs and larvae [10,11].

Our results showing that the age classes where *P. fasciatum* migrates most frequently are ages three and four and that individuals older than five years do not migrate have to be taken with caution. Fecundity in fishes typically increases with biomass and, hence, with age [52]. It is thus improbable that *P. fasciatum* conducts reproductive migrations at ages three and four and does not migrate after the age of five. One possible explanation for these results is that our sample size of older specimens is small and thus not representative of the species. More studies are necessary to evaluate this pattern. It must also be kept in mind that a limitation of our microchemistry approach is that it requires different Sr isotopic gradients to infer movements. A fish could migrate long distances within the same river system (i.e., within the same Sr isotopic range), and some most likely do, without being detected by our approach.

Our finding showing that *P. fasciatum* migrates an average of 126 km refines the three proposed migration models for fishes of the Amazon, whereby species are classified according to the geographical extent of movements and use of floodplain habitats [4]. Our results show that *P. fasciatum* conducts migrations that cover distances of the same magnitude as the migratory characiforms, which migrate in the order of hundreds of kilometers for reproductive purposes. The mean migration distance estimated by this study for *P. fasciatum* is approximately 126 km, which aligns with the results of Loubens

and Panfili [22], who proposed a migration distance of up to 300 km. The third quartile of distance migrated by *P. fasciatum* in our study was 237 km, which is close to the estimate of Loubens and Panfili [22] and that of Hahn et al. [24], who observed migrations of up to 164 km with radiotracking.

Our findings showing that 66% of *P. fasciatum* migrate bidirectionally and mostly between whitewater rivers (77%) align with those of prior studies and may indicate homing behavior. In a review paper, Herrera et al. [7] found that most migratory fishes of the Amazon basin migrate between whitewater rivers. In our study, the bidirectional migrations of *P. fasciatum* in whitewater rivers may indicate homing behavior, because almost half (41%) of our specimens returned to the same river of birth. Interpreted this way, our results indicate *P. fasciatum* perform homing behavior. However, the sizes of most rivers studied herein are enormous, and our methodology cannot precisely indicate whether our studied specimens of *P. fasciatum* returned to the same place of birth, only that they only returned to the river of birth. For example, a specimen born in the Guapore River that by the age of two years migrated to and spawned in the Mamore River (Figure 7), and then returned to the Guapore River would be indicated by our analyses to have performed homing. However, that specimen could have returned to many places in the Guapore River other than its place of birth. This lack of spatial resolution in our study is a limitation of the otolith microchemistry methodology. There are, however, a few reasons for *P. fasciatum* to perform homing. *P. corruscans*, a catfish species from the same genus distributed in the Parana and Sao Francisco basins in South America, has a strong tendency to perform homing to natal nursery areas for reproduction purposes [53]. Also, Herrera et al. [7] found that longitudinally migratory species present a strong phylogenetic signal, which means that the closer phylogenetically that species are, the higher their probability of presenting longitudinal migratory behavior. This migratory phylogenetic signal is found globally in the freshwater fish fauna [54]. Dorado catfish *Brachyplatystoma rousseauxii*, of the same family as *P. fasciatum* (Pimoliedae), also performs homing behavior [14,17,55], with most adult specimens returning from the estuary to the sub-basin where they were hatched in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru [14,17]. Fish homing behavior is an evolutionary strategy that increases fitness and produces reproductively isolated and adapted populations that maximally use diverse habitat conditions [56]. Homing behavior in *P. fasciatum* could be expected to increase the likelihood that reproductive-age individuals find mates and locate habitats favorable for both adult spawning and juvenile survival. However, if *P. fasciatum* does not perform homing, it could also benefit from straying (e.g., migration of specimens to locations that are not their natal places). Straying enables the colonization of new habitats and the recolonization of former habitats after the extinction of local populations [56]. Thus, more studies (e.g., using telemetry methods) are necessary to better understand the migratory ecology of *P. fasciatum* and determine whether it performs homing behavior.

Implications for Management and Conservation

Our results on the migratory ecology of *P. fasciatum* allow us to put forward two main implications for the sustainable management of its fisheries and species conservation. First, conserving *P. fasciatum* requires maintenance and suitable fishing practices in their nursery habitats. Building on and providing support to prior studies, our results show that *P. fasciatum* relies on the floodplains as its nursery habitat for the juveniles to grow until the age of two, emphasizing the need to protect these environments. Even though *P. fasciatum* does not feed directly on phytoplankton or tree leaves and fruits, which are key sources of energy for Amazon fishes [46,57,58], because it is a piscivorous species, we note that *P. fasciatum* does feed on a range of frugivorous and detritivorous fish species that feed directly on those sources of energy [51]. We also note that the floodplains are the target of intense fishing pressure [59], highlighting the need to avoid the capture of sexually immature specimens, which is common and leads to growth overfishing [59,60].

Our results on the migratory ecology of *P. fasciatum* inform managers about the extent of the geographic areas that should be considered for its management and conservation. Our results showing that the distance migrated by *P. fasciatum* is around 126 km (and mostly varies between 70 and 274 km) inform the minimum geographic extent of the home range of this species. Consequently, the area needed to manage populations of *P. fasciatum* should encompass river distances of that extent, including nurseries and floodplain habitats. Such management areas for *P. fasciatum* would require coordination within networks of fishing communities, which typically cover floodplain areas of only tens of kilometers, following existing rules of season and minimum size capture, in addition to other rules. The geographical extent of the home range of *P. fasciatum* also informs the likely area of population impacts produced by the construction of hydropower dams, considering only the effects related to disruption of upstream migrations. Disruption of river hydrology induced by hydropower dams is also expected to affect *P. fasciatum* via effects on growth and access to nursery and feeding areas [38], but such effects cannot be assessed given the results of the present study. Finally, we emphasize that our estimates are conservative in that we voluntarily restricted the distances migrated within a new river system to 20 km from the confluence of the river of origin because the microchemistry approach does not allow us to assess how far upstream the fish goes in the absence of a contrasted Sr signal. Although some fish could have migrated a bit less than 20 km, some might have migrated much further. Further studies, and particularly radio-telemetry studies, are needed to understand the home range for *P. fasciatum* in the Amazon to better manage it.

5. Conclusions

We found that 34% of all *P. fasciatum* in studied systems within the Amazon basin migrated between rivers with different Sr signatures. The mean distance of migration was 126 km, with most specimens migrating between 72 and 237 km. All migrating individuals were between two and five years of age, with 20% of such individuals being two years old, 40% three years old, 30% four years old, and 20% five years old. Sixty-six percent of all individuals migrating between rivers with different Sr signatures did so bidirectionally, and 33% moved unidirectionally. According to our definition of homing, 41% of all fish that migrated displayed apparent homing behavior. Our results on migration ecology inform managers that the minimum river length, including nurseries and floodplain habitats, that is needed to maintain populations of *P. fasciatum* is on the order of 126 km. Results will vary spatially and must be further investigated.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16070378/s1>, Figure S1: Comparison of 87Sr/86Sr profiles of otoliths from *Pseudoplatystoma fasciatum* analyzed in Brasilia (blue curve) and again in Montpellier (orange curve). The Montpellier profile was carried out above the same raster performed in Brasilia.

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