bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Diverse Early Life-History Strategies in Migratory Amazonian Catfish: Implications for Conservation and Management

Jens C. Hegg[1]*, Tommaso Giarrizzo[2], and Brian P. Kennedy[1,3]

[1] Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, USA

[2] Laboratório de Biologia Pesqueira - Manejo dos Recursos Aquáticos, Universidade Federal do Pará (UFPA), Belém, PA, Brazil

[3] Departments of Geological Sciences and Biological Sciences, University of Idaho, Moscow, ID, USA

* Corresponding Author

hegg1432@vandals.uidaho.edu (JH)

Abstract

Animal migrations provide important ecological functions and can allow for increased biodiversity through habitat and niche diversification. However, aquatic migrations in general, and those of the world's largest fish in particular, are imperiled worldwide and are often poorly understood. Several species of large Amazonian catfish carry out some of the longest freshwater fish migrations in the world, travelling from the Amazon River estuary to the Andes foothills. These species are important apex predators

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

in the main stem rivers of the Amazon Basin and make up the regions largest fishery. They are also the only species to utilize the entire Amazon Basin to complete their life cycle. Studies indicate both that the fisheries may be declining due to overfishing, and that the proposed and completed dams in their upstream range threaten spawning migrations. Despite this, surprisingly little is known about the details of these species' migrations, or their life history. Otolith microchemistry has been an effective method for quantifying and reconstructing fish migrations worldwide across multiple spatial scales and may provide a powerful tool to understand the movements of Amazonian migratory catfish. Our objective was to describe the migratory behaviors of the three most populous and commercially important migratory catfish species, Dourada (*Brachyplatystoma rousseauxii*), Piramutaba (*Brachyplatystoma vaillantii*), and Piraíba (*Brachyplatystoma filamentosum*). We collected fish from the mouth of the Amazon River and the Central Amazon and used strontium isotope signatures ($^{87}Sr/^{86}Sr$) recorded in their otoliths to determine the location of early rearing and subsequent. Fish location was determined through discriminant function classification, using water chemistry data from the literature as a training set. Where water chemistry data was unavailable, we successfully in predicted $^{87}Sr/^{86}Sr$ isotope values using a regression-based approach that related the geology of the upstream watershed to the Sr isotope ratio. Our results provide the first reported otolith microchemical reconstruction of *Brachyplatystoma* migratory movements in the Amazon Basin. Our results indicate that juveniles exhibit diverse rearing strategies, rearing in both upstream and estuary environments. This contrasts with the prevailing understanding that juveniles rear in the estuary before migrating upstream; however it is supported by some fisheries data that has indicated the presence of alternate

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

spawning and rearing life-histories. The presence of alternate juvenile rearing strategies may have important implications for conservation and management of the fisheries in the region.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Introduction

Animal migration provides many important ecological functions: they can be a stabilizing strategy in seasonal environments; offer transitory habitats for large populations; often transport materials across ecosystem boundaries; and may increase a regions biodiversity [1]. Large-scale migrations shed light on ecosystem connectivity across scales and can be used as a lens to understand broader behavioral responses to the environment and links to physical processes [2–4]. However, migrations worldwide are under threat from the alteration of migratory pathways, habitat loss, climatic changes and anthropogenic changes to the landscape [5]. In aquatic systems, changes in upstream land use and the placement of dams have had significant impacts on ecosystems and migrations worldwide [6–11]. This is particularly true for large migratory fish that are under threat in many of the world's largest river systems [12–14]. Despite this, many large migratory fish species are not well understood [14].

Globally, dams and water resources challenges in the two largest rivers in China provide an example of the ongoing changes to large rivers and their effects on aquatic species, including sturgeon and paddlefish [15]. In South America, transnational river systems and a lack of coordinated research of aquatic systems may result in losses to unspecified levels of biodiversity [16–20]. New dams present a unique challenge to migratory fish in the region. Because the young of many Amazonian species undergo a drifting larval stage, even if adults can pass above dams the lack of flow in reservoirs creates a barrier that drifting juveniles are unable to surmount on their way downstream [21].

Several species of Amazonian catfish in the genus *Brachyplatystoma* carry out some of the longest freshwater fish migrations in the world, travelling over 4,500 km from rearing areas

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

in the Amazon estuary to spawning grounds in rivers in the foothills of the Andes [22–24]. These species largely inhabit whitewater and clearwater rivers within the Amazon Basin [sensu 25,26], with rare reports in tannic blackwater rivers [23]. These catfish species are the only known organisms, terrestrial or aquatic, that require the entire length of the Amazon basin to complete their life cycle [23]. They are also one of the few apex predators in the pelagic and demersal zones of the largest Amazonian rivers, playing an important role in trophic dynamics and ecosystem functioning within the entire basin [27]. However, evidence indicates that the fisheries for the most populous species are in decline, potentially due to overfishing [22,28]. The reliance of these species on headwater streams for spawning leaves adults and larva vulnerable to blocking of their migration paths by dams and their reservoirs [21,29].

Surprisingly little is known about the life history of migratory Amazonian catfish given that the three most abundant *Brachyplatystoma* taxa support the largest fisheries in the Amazon Basin [23,24]. Dourada (*Brachyplatystoma rousseauxii*) is a pelagic predator found throughout the whitewater and clearwater rivers of the Amazon and supports the largest fishery in the Amazon [27,29]. Piramutaba (*Brachyplatystoma vaillantii*) make up a second large export fishery and are found almost exclusively in the Amazon River mainstem, whitewater tributaries, and the estuary [30–32]. Piraíba (*Brachyplatystoma filamentosum*) is the largest of the migratory catfish, present in whitewater rivers throughout the Amazon basin. It is also the most locally exploited and least understood of these three species [22]. The expansive scale of the Amazon Basin, and the large size of the rivers these fish inhabit, have made tracking and reconstructing their movements very difficult [32]. Our current understanding of the migratory behavior of migratory Amazonian catfish is based on fishing records (including the catch timing and size of fish across the Amazon basin) and a growing number of scientific sampling efforts [23,28,31,33–

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

36]. After hatching in the upper reaches of the whitewater rivers originating in the Andes, larvae of these species drift downstream for two to four weeks before reaching the Amazon estuary. Juveniles rear in the estuary before commencing an upstream migration that coincides with the seasonal flood pulse. Genetic data indicate that dourada may home to natal tributaries in the basin to spawn [37,38].

Otolith microchemistry has been an effective method for quantifying and reconstructing fish migrations worldwide across multiple spatial scales [39–46]. Strontium ratio in particular has become a powerful tool for determining movement and location because it is not fractionated biologically. Thus, the signatures recorded in otoliths match the water through which fish pass [43,47–50]. Studies of geological weathering throughout the Amazon basin have provided detailed, multi-year records of micro-chemical and isotopic chemistry in the largest rivers of the basin. These data provide the required background sampling necessary to tie regional otolith signatures to geographic location [51–53] (Figure 1A, Table 1). Recent studies have also shown the feasibility of predicting $^{87}Sr/^{86}Sr$ signatures of unknown watersheds using the geologic makeup of the basin, allowing researchers to characterize strontium signatures of unsampled areas [54,55]. These advances point to otolith microchemistry as a potentially powerful tool to understand the movements of Amazonian migratory catfish.

Our objective was to describe the migratory behaviors of large, migratory catfish in the Amazon River basin using otolith microchemistry. We focused our study on the three most populous and commercially important species in the Amazon Basin. We sought to determine the location of early rearing and subsequent movement in dourada, pirimutaba, and piraíba using samples collected from two, large fish markets at the mouth of the Amazon River and in the central Amazon. We determined the movement patterns over the lifetime of individual fish using

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

laser ablation isotope mass spectrometry of their otoliths. Areas of stable signature were identified statistically throughout the chemical profile of the otolith, which were then classified to their location within the basin using discriminant function analysis. The discriminant function was created using a training set of $^{87}Sr/^{86}Sr$ samples from rivers throughout the Amazon basin. These samples were obtained from the geological literature. Where river $^{87}Sr/^{86}Sr$ values were unknown, we used established relationships between surface water $^{87}Sr/^{86}Sr$ values and the age and composition of the underlying watershed geology to predict these signatures.

Ethical statement

Ethical approval was not required for this study, as all fish were collected as part of routine fishing procedures. Fish were sacrificed by the artisanal fishermen in Manaus and Belém using standard fisheries practices and donated to the authors.

No field permits were demanded to collect any samples from any location, since all samples derived from commercial catch. None of the species included in this investigation are currently protected or endangered. Therefore, no additional special permits were necessary. Permission to export the otolith samples was granted by the Brazilian Government with permit number: 116217 (MMA, IBAMA, CITES 09/01/2013).

Methods

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Otolith Collection

In March 2012, a total of 24 paired lapillus otolith samples (16 pairs for dourada, 5 for piramutaba and 3 for piraíba) were collected from the two major fishing ports of Brazilian Amazonia, the cities of Manaus and Belém (Table 1, Figure 1A). These cities are located 1,606 river kilometers apart. Manaus (03°05'39.60"S, 60°01'33.63"W), is the largest city in the central Amazon, located at the confluence of the whitewater Solimões River with the blackwater Negro River. Belém (01°27'18.04"S 48°30'08.90"W), is situated on the banks of the Amazon estuary and is the main landing port of large migratory catfishes fisheries in Brazil [30]. Prior to otolith collection the total length (TL) and weight (W) of each fish was recorded: dourada: mean TL = 83.6 cm, mean W = 8.58 kg; piramutaba: mean TL = 67.6 cm, mean W = 3.34 kg; piraíba: mean TL =186.6 cm, mean W = 86.6 kg. Piramutaba were gutted prior to collection so weight was estimated using a length-to-weight ratio from Pirker [56].

Fish collected from Manaus were captured in the mainstem Amazon River between the mouth of the Madeira River and Manaus as reported by the fisherman. Thus, we would expect the chemical signatures representing the end of the fish's life (signatures from the edge of the otolith) of fish caught in Manaus to represent signatures in the mainstem Amazon River or its tributaries upstream of the Madeira River. Fish collected in Belém were captured in the estuary between 60 km and 150 km from Belém according to the fisherman. The otolith edge chemistry of fish caught in Belém are therefore assumed to match the signature of the estuary, the lower Amazon tributaries, or the lower Amazon River mainstem. Because the $^{87}Sr/^{86}Sr$ signature can take days to weeks to equilibrate and accumulate enough material to reliably sample, it is possible that fish could exhibit signatures other than the location of capture if they had recently

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

moved from a habitat with a different signature.

Otolith Analysis

The left lapillus otolith from each sample was prepared using standard methods of mounting, transverse sectioning with a high precision saw, and abrasive polishing to reveal the rings [34,57] (Figure 2). If the left otolith was missing or unavailable the right otolith was used for analysis. Otoliths were then analyzed at the GeoAnalytical Laboratory at Washington State University using a Finnigan Neptune (ThermoScientific) multi-collector inductively coupled plasma mass spectrometer coupled with a New Wave UP-213 laser ablation sampling system (LA-MC-ICPMS). We used a marine shell standard to evaluate measurement error relative to the global marine signature of 0.70918 [58]. Repeated analyses of a marine shell signature provided an average $^{87}Sr/^{86}Sr$ value of 0.70914 during the course of the study (N=22, St. Error=0.00002). The laser was used to ablate a sampling transect from the core of the otolith section to the edge (30 μm/s scan speed, 40 μm spot size, 0.262 s integration speed, ~7 J/cm). This resulted in a continuous time-series of $^{87}Sr/^{86}Sr$ data from the birth of the fish (core) to its death (edge) which was used for subsequent analysis. For more detailed methods see Hegg et. al [40]. The asteriscus was used for one sample for which the lapilli were not available; however, the strontium concentration was low and the unreliable results were not included.

Baseline Water Sampling and Prediction

Twenty-four water sampling points located throughout the Amazon River basin (Figure 1A) from three published studies provided baseline $^{87}Sr/^{86}Sr$ values for our study (Table 2, Figure 3). Santos et al. [53] provided thirteen samples from the Ore-HYBAM project (www.ore-

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

hybam.org), a multi-year research effort with a comprehensive sampling design covering the mainstem Amazon River and all of the major tributaries above Obidos, Brazil. Nine additional samples from Gaillardet et al. [52] covered the mainstem Amazon and the mouths of the major tributaries as far east as Santarem, Brazil. Finally, Queiroz et al. [51] provided two samples from the Lower Solimões and Upper Purus Rivers. Our intention was to include samples that represented all major Amazon tributaries at a regional scale, while excluding smaller tributaries that were unlikely to provide long-term habitat for our study species. Smaller tributaries in the Amazon Basin have been shown to exhibit much different isotopic chemistry from their mainstem rivers [51]. The scale and geologic heterogeneity of these smaller tributaries could jeopardize assignment accuracy [54].

The isotopic chemistry of a few significant locations were not available in the literature. Notably missing were samples from the mouth of the Amazon River, its tributaries below Obidos, and the Tocantins River which contributes to the estuary habitat of our study species. To account for the $^{87}Sr/^{86}Sr$ of these locations we used the relationship between the geologic makeup of a watershed and its $^{87}Sr/^{86}Sr$ signature to predict these points, following a similar regression approach to Hegg et al. [54]. Watersheds were delineated in qGIS (http://www.qgis.org), an open-source geographic information system, using the GRASS analysis plugin, which contains advanced watershed analysis tools from the open-source GRASS GIS platform (http://grass.osgeo.org). All analysis layers were procured from open-access datasets. Water sampling points were manually digitized by the authors based on location descriptions from Santos et al. [53], Gaillardet et al. [52], and Queiroz et al. [51]. Topography layers were taken from the GTOPO30 dataset [59] and stream courses from the HydroSHED dataset [60]. Geologic information came from the World Energy Assessment Geologic Map of the Amazon Region

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

[61].

We used geologic age as the primary candidate independent variables in our regression to predict the $^{87}Sr/^{86}Sr$ signatures for unsampled tributaries, along with very general intrusive and extrusive rock-type categories (Figure 1B). Our methods differed from Hegg et al. [54], who used rock type as the primary explanatory variable rather than age. We did this because the very generic designations of intrusive or extrusive rock available in our dataset were insufficient to provide explanatory power. The values for these candidate variables were calculated by converting the geologic age codes from the map attribute table to continuous variables using the mean age (Ma) of the geologic periods encompassed by each code using the International Chronostratigraphic Chart [62]. The percentage area of each rock age and type was then calculated within the watershed upstream of each $^{87}Sr/^{86}Sr$ sample point. The mean age of each watershed, weighted by area, was also included as a potential explanatory variable for the regression, leaving twenty-four potential explanatory variables for the regression.

Model selection used a genetic algorithm selection procedure in the {glmulti} package for R [63]. We limited models to four terms to limit the number of potential models and included interaction terms. The genetic algorithm uses a search algorithm based on Darwinian natural selection, an efficient method for model optimization when the number of potential models is large, as was the case with our geologic data [64]. Akaike's Information Criterion optimized for small datasets (AICc) was used as the optimization criteria for the genetic algorithm, a criterion that penalizes over-parameterization [65]. One third of the sample points were randomly selected as a validation set, withheld from the model selection procedure, and used to assess prediction accuracy of the best model. The best model was then used to calculate the $^{87}Sr/^{86}Sr$ values for the unsampled points in the basin, using the geology upstream of these points.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Grouping of Distinguishable Watersheds

The water sample points were grouped into three distinguishable geographic regions using prior knowledge of the geography and geology of the watersheds (Table 1, Fig. 1A, Fig. 3). River basins that were geographically contiguous and broadly geologically and chemically similar were grouped. The Amazon River mainstem and western tributaries, all considered whitewater rivers [26], were grouped together due to the overwhelming influence of the Andes on their chemistry. The Beni-Madeira River and lower Negro River were grouped due to similar chemical signatures from a mix of upland mountainous geology and old, lowland, Amazon and Guyana shield geology. The Negro River, being blackwater, would not be expected to contain large numbers of our target species, while the whitewater Madeira is a known fishery [23,26]. The lower Amazon tributaries (below the Madeira River) were grouped due to the their similarly old, shield geologies resulting in high $^{87}Sr/^{86}Sr$ values. These rivers are all considered clearwater tributaries [26]. These group assignments were then used as the training set, with $^{87}Sr/^{86}Sr$ as the predictor and group as the response, to create a quadratic discriminant function. This discriminant function was then used in the following section to classify the $^{87}Sr/^{86}Sr$ signatures recovered from fish otoliths to these three distinguishable river groups.

Determining Fish Movement and Location

The transect of $^{87}Sr/^{86}Sr$ values from the core to the rim of each otolith was analyzed using a PELT algorithm changepoint analysis (using the {changepoint} package in R [66]) to determine when the mean $^{87}Sr/^{86}Sr$ values changed to a new stable signature. This changepoint

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

algorithm generated mean values and starting points for each stable region within the otolith transect using a penalty value of 0.0001 [67]. Each stable signature was assumed to correspond to movement into a new river signature, with the first stable signature corresponding to early rearing. In some cases the changepoint algorithm returned erroneous means for small portions of the signature, in locations were the means was obviously unstable. Such fragments were manually removed.

Stable otolith signatures were then classified to their likely location using the discriminant function developed from known and predicted water sampling points in the prior section. Because *a priori* probability of group membership was unknown, the prior probabilities for the discriminant function were set to be equal among groups. After classification, the results were plotted and the data were assessed to determine trends in early rearing and movement both within and among the three sampled species.

Results

Baseline Water Sampling and Prediction

The most parsimonious model without interaction terms explained ~80% of the variation in the data but provided an unreasonably high prediction for the mouth of the Amazon River. We had no direct evidence of significant geologic interactions; however, we included interactions in a second model selection exercise in hopes of finding a parsimonious model that better fit the available data. We limited the maximum number of model terms to four to limit the number of potential models available from the twenty-four available variables plus interactions. This limit

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

is reasonable since more terms would risk over parameterization given the number of observations used to build the model. Under these conditions the AICc model-selection algorithm selected three models that were greater than two AICc points superior to the next most parsimonious model. The top model,

$$^{87}Sr/^{86}Sr = (0.0263)Precambrian - (0.676)Precambrian{:}Tertiary - (0.0011)Mean\ Watershed\ Age^{(weighted\ by\ area)} + \varepsilon \qquad (1)$$

explained 89% (Adjusted R^2) of the variation in the data, provided the best prediction residuals for the validation set, and resulted in a more reasonable prediction of the mouth of the Amazon. This equation was used to predict the $^{87}Sr/^{86}Sr$ signatures for the five unsampled watersheds.

Grouping of Distinguishable Watersheds

A quadratic discriminant function provided the best cross-validation error rate (3.6%) for discriminating all the watersheds into the three regions. One predicted value for the Madeira River was the lone misclassification from the validation set, being classified to the Lower Amazon Tributaries group. One sample from the Solimões River was dropped from the training set as an outlier (Table 2). The value for this site was unexplainably high in comparison to the multi-year samples above and below it on the river. While no explanation for this discrepancy was forthcoming from the original study, Bouchez et al. [68] found that lateral heterogeneity in $^{87}Sr/^{86}Sr$ signatures can persist for long distances below confluences in the Solimões.

Determining Fish Movement and Location

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Changes in $^{87}Sr/^{86}Sr$ ratio, indicating movement, were common across each of the three species. Movement between distinguishable river groups, as determined by discriminant function classification, was less frequent. Over 70% of dourada exhibited movement between stable signatures based on changepoint analysis, however only two (14%) showed movement between distinguishable river groups after discrimant function classification (Figure 4A). Sample BR24 started life in the Amazon Mainstem and Western Tributaries signature before moving to a signature consistent with the Lower Amazon Tributaries river group. Sample BR25 began life with a signature consistent with the Lower Amazon Tributaries river group, before moving twice to a signature consistent with the Beni-Madeira and Lower Negro group with a small region consistent with the Amazon Mainstem and Western Tributaries river group.

Of five piramutaba, two (40%) were shown to move between stable signatures but none moved outside the Amazon Mainstem and Western Tributaries river group based on discriminant function classification (Figure 4B). Of the three piraíba samples two showed movement, both of which moved between the Beni-Madeira and Lower Negro River group and the Amazon Mainstem and Western Tributaries (Figure 4C).

Overall, these results indicated that the majority of fish begin life in the Amazon Mainstem and Western Tributaries signature, a signature which contains within it the estuary signature, the expected location of early rearing [23]. Our results were unable to distinguish the Amazon mainstem signature from that of the estuary, the expected location of early rearing. However, we would expect the signature to be intermediate between that of the signature of the Amazon River mouth and the global marine signature of 0.70918 resulting from the mixing of the two water bodies. The resulting estuary signature would be contained with the range of the Amazon Mainstem and Western Tributaries classification.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Conversely, some portion of fish begin life, and undergo some or all of their rearing, in signatures indicative of freshwater (Figure 4A, B &C). Sample BR25 (dourada) and BF1 (piraíba) were the two most obvious examples, starting life with signatures that correspond to the Beni-Madeira and Lower Negro and Lower Amazon Tributary signatures. Many of the fish that remained within the Amazon Mainstem and Western Tributaries river group began life with signatures > 0.71, significantly higher than the Mainstem Amazon River signatures (Table 2)and the global marine signature, and thus likely an upriver signature. Others (BR6, BR8, BV1, BF2) spent large portions of their lives in distinctly upriver environments.

Otolith microchemistry data is available in the supporting information for this publication (S1 Table).

Discussion

Understanding the migration ecology of Amazon catfish represents an opportunity to understand the large-scale ecosystem processes of long distance aquatic migration in an intact, native fish population. These fish also represent an international conservation challenge, as their movements stretch across multiple national boundaries [35] and are potentially threatened by several hydropower projects [16–19]. The first step in understanding these ecological processes, and their effects on the fishery, is a robust understanding of their migratory movements at a finer scale than is currently available from fisheries data.

Our results provide the first reported reconstruction of movements and migrations of individual *Brachyplatystoma* spp. in the Amazon Basin using chemical signatures from otoliths.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Applying these techniques in this system appears promising for improving our understanding of the migratory movements of these species, which are currently understood only at the most basic level. While this work is preliminary, $^{87}Sr/^{86}Sr$ signatures appear capable of identifying large-scale fish movements at a meaningful spatial scale; between important river systems within the basin. Further, movement between areas with stable signatures can be observed within statistically distinguishable river groups, indicating that improved baselines and larger sample collections should allow greater resolution. Discrimination of fish location and movement may also be improved by applying multivariate analyses of elemental signatures in concert with $^{87}Sr/^{86}Sr$ signatures [69–71].

We observed diversity in rearing location and behavior among a minority of individuals in each of the three species sampled using otolith $^{87}Sr/^{86}Sr$ movement reconstructions and discriminant function classification to location. For example, fish BR25 (a dourada caught in Manaus) appears to have spent most of its early life in areas with very high $^{87}Sr/^{86}Sr$ ratios assigned to the Lower Amazon Tributaries river group (Figure 4A). The chemical signatures of this fish indicate that rather than drifting to the estuary to rear, it spent the first third of its life in a lower tributary of the Amazon River before moving to a signature indicative of areas between the Madeira and Amazon Rivers, finally being caught near between Manaus and the mouth of the Madeira (as reported by the fishermen who provided the samples in Manaus). Notably, the signatures appear to support the idea that this fish never traveled to the estuary. Fish BF1 (piraíba) also showed a significant length of freshwater rearing in a signature assigned to the Beni-Madeira and Lower Negro river group (Figure 4C).

Indeed, several additional dourada and piraíba, and one piramutaba all appeared to have spent significant time in $^{87}Sr/^{86}Sr$ signatures greater than 0.7100 (Figure 4A, B &C). This

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

signature is higher than all but one location on the mainstem Amazon River and significantly higher than the accepted global marine signature of 0.70918 considering the analytical precision that is possible for otolith measurements. We would expect estuarian signatures to fall between the $^{87}Sr/^{86}Sr$ signature of the Amazon mouth and the global marine signature except very near the mouth of the Tocantins. The Tocantins signature is likely attenuated significantly by Amazon River water flowing through the Canal de Breves which noticeably muddies the water flowing from the Tocantins [23]. Further, the estuary signature should converge to the marine signature at relatively low salinities due to the much higher strontium concentration of the ocean [72]. This indicates the possibility that a larger percentage of our samples may have reared upriver of the estuary as well, but our methods were unable to detect it.

Ecologically, the presence of upriver $^{87}Sr/^{86}Sr$ signatures during the rearing phase indicates that in some situations a rearing strategy that forgoes the high growth potential of the estuary may provide overall fitness benefits. This finding suggests that the life-history of these species is more complex than has been previously understood. The potential existence of a freshwater rearing life-history, based on evidence for alternative spawning periods in the upper reaches which do not fit the conventional estuary rearing model, was theorized by García Vasquez et al. [33]. This model is supported by evidence of young and immature fish present in the far western Amazon before and during the spawning season when the prevailing hypothesis would place these fish in the estuary [24,35,36].

Understanding the extent of diversity in life history strategies is critical for managing these little-studied native species, especially in habitats facing current and future perturbations. Variations in life history have been shown to affect recruitment, survival, and fisheries sustainability in other long-distance migratory fish [73–75]. These species may home to their

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

natal rivers, and sub-population structure and associated differences in life history may exist [37,38], which may have important implications for planning and policy decisions related to dam placement and fishery management. For instance, fishing pressure in the estuary is high, potentially limiting juvenile escapement to upriver fisheries [24,35]. Freshwater rearing life-histories would avoid the high fishing pressures in the estuary, potentially increasing survival and providing important recruitment to upriver fisheries in the Western Amazon, fisheries which appear to be overfished [24,25,31].

Dams in particular have been shown to decrease life-history diversity of other major migratory fisher species, with consequences for their conservation and fisheries sustainability [76,77] and diverse source populations appear to provide resilient fisheries over time [74]. So, the extent to which dams or other anthropogenic disturbances decrease the diversity of source populations in dourada, piramutaba, and piraíba could have adverse impacts on the sustainability of the fishery. The pace of dam building in the major Amazon Basin tributaries [16,17,19]; the difficulty of providing significant fish passage in Amazonian rivers [21]; and the known and suspected effects of dams on the migration of these migratory catfish species [6,29,78] increase the need to understand the details of their migration ecology. Only with detailed knowledge of *Brachyplatystoma* migration ecology can policymakers weigh the effects of dams on the sustainability of this important fishery.

Our study raises numerous important questions and opportunities for future research. While it is clear that water chemistry signatures for the Amazon basin can be classified into meaningful groups, such results do not necessarily translate into concrete interpretation of fish movement at anything but the largest of scales. Our understanding of the degree to which the movements and migrations of individual fish can be interpreted at the scale of the entire Amazon

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

basin is in its infancy. At smaller spatial scales, many of the local tributaries to the major rivers of the Amazon basin exhibit vastly different signatures than those of the main channels, which reflect the headwater signature of the Andes or the Brazilian and Guyana Shield geology [51]. Incomplete or slow mixing of different signatures, especially across muddy whitewater and tannic blackwater rivers, may occur over extended river distances, which may create unexpected intermediate signatures [68]. Furthermore, our understanding of temporal variation associated with available empirical data is limited. Especially in the Amazon estuary our understanding of the $^{87}Sr/^{86}Sr$ signatures in this seasonally dynamic environment are limited. Increased understanding of these estuarian signatures is critically important to understanding these species using otolith microchemistry studies. Our study species are thought to inhabit only the larger, mainstem tributaries, making large scale location classification useful. At smaller geographic scales additional ground truth sampling of fish and water chemistry is needed to constrain the scale at which movements and migrations can be accurately interpreted from otolith data. Otolith sampling across larger areas of the Amazon may also allow elemental ratios, which are fractionated biologically unlike $^{87}Sr/^{86}Sr$, to be used in addition to $^{87}Sr/^{86}Sr$ to improve location analysis.

Overall, this study highlights the feasibility and utility of the latest otolith chemistry techniques to greatly improve our understanding of the movements and ecology of these important native fishes throughout the entire Amazon basin. Recent declines in the fishery point to the necessity of conducting this research [22,28,79]. Migratory catfish in the Amazon Basin are several of only a few large, freshwater fishes worldwide that are not currently imperiled due to anthropogenic changes to freshwater ecosystems [12]. However, as fishing pressure increases, land use and forest clearing affect the river system, and dams threaten migration routes and

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

access to critical habitats, these populations will likely be affected. The sustainability of these populations and the fisheries they support, especially across international borders, continues to depend on accurate population assessments of based on detailed knowledge of their behavior and ecology.

Acknowledgements

Thanks to A. Fremier and P. Anders for their encouragement and help in framing the project at the earliest stages, as well as sharp outside editing. Thanks to C. Cooper for editing and moral support. Thanks to L. Rayala for applying his practiced editing eye. Thank you to Z. Hogan for providing constructive feedback on the project proposal. Thanks to M. Andrade, A. Zuluaga and D. Bastos for help with sample collection in Manaus and Belém, as well as to the fishermen who volunteered their catch for sampling. Thanks to J. Vervoort and C. Knaack at the Washington State University Geoanalytical Laboratory for use of their equipment for isotopic analysis. T. Giarrizzo received a productivity grant from CNPq (process: 308278/2012-7), and was funded by CAPES (PNPD and Pró-Amazônia: biodiversidade e sustentabilidade).

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

References Cited

1. Bauer S, Hoye BJ (2014) Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. Science (80-) 344: 54–54(8). Available: http://www.sciencemag.org/cgi/doi/10.1126/science.1242552. Accessed 3 April 2014.

2. Bowlin MS, Bisson I-A, Shamoun-Baranes J, Reichard JD, Sapir N, et al. (2010) Grand challenges in migration biology. Integr Comp Biol 50: 261–279. Available: http://www.ncbi.nlm.nih.gov/pubmed/21558203. Accessed 30 April 2014.

3. Poiani K a., Richter BD, Anderson MG, Richter HE (2000) Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks. Bioscience 50: 133. Available: http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568(2000)050[0133:BCAMSF]2.3.CO;2.

4. Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17: 76–83. Available: http://linkinghub.elsevier.com/retrieve/pii/S0169534701023801.

5. Wilcove DS, Wikelski M (2008) Going, going, gone: is animal migration disappearing. PLoS Biol 6: e188. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2486312&tool=pmcentrez&rendertype=abstract. Accessed 15 May 2014.

6. Freeman BJF (2003) Ecosystem-Level Consequences of Migratory Faunal Depletion Caused by Dams. Am Fish Soc Symp 35: 255–266. Available: http://www.esf.edu/efb/limburg/watershedEcology/Readings/Freeman-dams.pdf.

7. Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev Camb Philos Soc 81: 163–182. Available: http://www.ncbi.nlm.nih.gov/pubmed/16336747. Accessed 29 April 2014.

8. Tockner K, Pusch M, Gessner J, Wolter C (2011) Domesticated ecosystems and novel communities: challenges for the management of large rivers. Ecohydrol Hydrobiol 11: 167–174. Available: http://linkinghub.elsevier.com/retrieve/pii/S1642359311700131. Accessed 5 May 2014.

9. Rosenberg DM, Mccully P, Pringle CM (2000) Global-Scale Environmental Effects of Hydrological Alterations: Introduction. Bioscience 50: 746. Available: http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568(2000)050[0746:GSEEOH]2.0.CO;2. Accessed 19 May 2014.

10. Foley JA, DeFries R, Asner GP, Barford C, Bonan G, et al. (2005) Global consequences of land use. Science (80-) 309: 570.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

11. Carpenter SR, Stanley EH, Vander Zanden MJ (2011) State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes. Annu Rev Environ Resour 36: 75–99. Available: http://www.annualreviews.org/doi/abs/10.1146/annurev-environ-021810-094524. Accessed 21 March 2014.

12. Allan JD, Abell R, Hogan Z, Revenga C, Taylor BW, et al. (2005) Overfishing of Inland Waters. Bioscience 55: 1041. Available: http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2.

13. Pikitch EK, Doukakis P, Lauck L, Chakrabarty P, Erickson DL (2005) Status, trends and management of sturgeon and paddlefish fisheries. Fish Fish 6: 233–265. Available: http://doi.wiley.com/10.1111/j.1467-2979.2005.00190.x.

14. Stone R (2007) The last of the leviathans. Science (80-) 316: 1684. Available: http://www.sciencemag.org/content/316/5832/1684.short. Accessed 30 May 2014.

15. Dudgeon D (2011) Asian river fishes in the Anthropocene: threats and conservation challenges in an era of rapid environmental change. J Fish Biol 79: 1487–1524. Available: http://www.ncbi.nlm.nih.gov/pubmed/22136237. Accessed 15 May 2014.

16. Fearnside PM (2006) Dams in the Amazon : Belo Monte and Brazil's Hydroelectric Development of the Xingu River Basin. Environ Manage 38: 16–27.

17. Fearnside PM (2014) Impacts of Brazil's Madeira River Dams: Unlearned lessons for hydroelectric development in Amazonia. Environ Sci Policy 38: 164–172. Available: http://www.sciencedirect.com/science/article/pii/S1462901113002724. Accessed 12 May 2014.

18. Tavener B (2012) New Dams Planned for Heart of Amazon. Rio Times. Available: http://riotimesonline.com/brazil-news/rio-politics/new-dams-planned-for-heart-of-amazon/.

19. Finer M, Jenkins CN (2012) Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. PLoS One 7: e35126. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3329437&tool=pmcentrez&rendertype=abstract. Accessed 1 May 2014.

20. Forero J (2013) Power-hungry Brazil builds dams, and more dams, across the Amazon. Washington Post. Available: http://www.washingtonpost.com/world/the_americas/brazil-building-more-dams-across-amazon/2013/02/09/f23a63ca-6fba-11e2-b35a-0ee56f0518d2_story.html. Accessed 20 May 2014.

21. Pompeu PS, Agostinho AA, Pelicice FM (2012) Existing and Future Challenges : The Concept of Successful Fish Passage in South America. River Res Appl 512: 504–512. doi:10.1002/rra.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

22. Petrere M, Barthem RB, Córdoba EA, Gómez BC (2005) Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraíba (*Brachyplatystoma filamentosum* Lichtenstein). Rev Fish Biol Fish 14: 403–414. Available: http://link.springer.com/10.1007/s11160-004-8362-7. Accessed 4 April 2014.

23. Barthem R, Goulding M (1997) The Catfish Connection: Ecology, Migration, and Conservation of Amazon Predators. New York: Columbia University Press. 144 p.

24. Fabré NN, Barthem RB (2005) O manejo da pesca dos grandes bagres migradores: Piramutaba e Dourada no Eixo Solimões-Amazonas. Ruffino ML, editor Manaus, Amazonas, Brazil: ProVárzea/Ibama. 116 p. Available: http://www.ibcperu.org/doc/isis/6464.pdf.

25. Sioli H (1956) As aguas da regiao do alto Rio Negro [Biologia aquatica; Fisica da agua; Quimica da agua; Hidrogeologia; Hidrografia; Amazonia; Brasil]. Bol Técnico Inst Agronômico do Norte 32: 117–155.

26. Junk WJ, Piedade MTF, Schöngart J, Cohn-Haft M, Adeney JM, et al. (2011) A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. Wetlands 31: 623–640. Available: http://link.springer.com/10.1007/s13157-011-0190-7. Accessed 27 May 2014.

27. Angelini R, Fabrè NN, Silva-jr UL (2006) Trophic analysis and fishing simulation of the biggest Amazonian catfish. J Agric Res 1: 151–158.

28. Córdoba EA, Viviana Á, León J, Bonilla-castillo CA, Junior MP, et al. (2013) Breeding , growth and exploitation of *Brachyplatystoma rousseauxii* Castelnau , 1855 in the Caqueta River , Colombia. Neotrop Icthyology 11: 637–647. Available: http://www.scielo.br/pdf/ni/v11n3/1679-6225-ni-11-03-00637.pdf.

29. Barthem B, Ribeiro M, Petrere M (1991) Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon Basin. Biol Conserv 55: 339–345.

30. Jimenez EA, Filho MA, Frédou FL (2013) Fish Bycatch of the Laulao catfish *Brachyplatystoma vaillantii* (Valencienes, 1840) Trawl Fishery in the the Amazon Basin. Brazilian J Oceanogr 61: 129–140. doi:http://dx.doi.org/10.1590/S1679-87592013000200005.

31. Barthem RB, Petrere Jr M (1995) Fisheries and population dynamics of *Brachyplatystoma vaillantii* (Pimelodidae) in the Amazon Estuary. In: Armantrout NB, Wolotira R, editors. Proceedings of the World Fisheries Congress, Theme 1. Condition of the World's Aquatic Habitats. New Delhi, India: Oxford and IBH Publishing Co. Pvt. Ltd., Vol. 1. pp. 329–340.

32. Godoy MP (1979) Marcação e migração de piramutaba *Brachyplatystoma vaillanti* (Val., 1840. na Bacia Amazonica (Pará e Amazonas), Brasil (Pisces, Nematognathi, Pimelodidae). Bol Fac Ceincias do Pará, Belém 11: 3–21.

33. García Vásquez A, Alonso J-C, Carvajal F, Moreau J, Nuñez J, et al. (2009) Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Iquitos region, Peru. J Fish Biol 75: 2527–2551. Available: http://ida.lib.uidaho.edu:3278/doi/10.1111/j.1095-8649.2009.02444.x/full. Accessed 7 November 2013.

34. Pirker LEM (2008) Morfometria e Descrição de Otólitos Dourada (*Brachyplaystoma rousseauxii*) (Castelnau, 1855) e de Piramutaba (*B. vaillantii*) (Valenciennes, 1840)(Siluriformes: Pimolodidae) e Verificação de Anéis de Crescemento em Otólitos de Juvenis de Dourada e de Pirimut Museu Paraense Emílio Goeldi - Universidade Federal Do Pará. Available: http://repositorio.ufpa.br/jspui/bitstream/2011/3445/1/Tese_MorfometriaDescricaoOtolitos.pdf.

35. Agudelo E, Salinas Y, Sanchez CL, Munoz_Sosa DL, Alonso JC, et al. (2000) Bagres de la Amazonia Colombiana: un Recurso sin Fronteras. Santa Fé de Bogota D.C., Columbia: Editorial Scripto Ltda. 253 p. Available: http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=BAC.xis&method=post&formato=2&cantidad=1&expresion=mfn=025972.

36. Alonso JC, Fabré NN (2002) Padrão espaço-temporal da estrutura populacional e estado atual de exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões Manaus: Universidade Federal do Amazonas.

37. Batista JS, Alves-Gomes JA (2006) Phylogeography of *Brachyplatystoma rousseauxii* (Siluriformes - Pimelodidae) in the Amazon Basin offers preliminary evidence for the first case of "homing" for and Amazonian migratory catfish. Genet Mol Res 5: 723–740.

38. Carvajal F (2013) Phylogeny and population genetics of the fish performing the largest migratin known in freshwater, the Amazonian catfish "*Brachyplatystoma rousseauxii*" : revelations from the upper Madera Basin Montpellier 2. Available: http://www.biu-montpellier.fr/florabium/jsp/nnt.jsp?nnt=2012MON20149. Accessed 30 May 2014.

39. Hamann EJ, Kennedy BP (2012) Juvenile dispersal affects straying behaviors of adults in a migratory population. Ecology 93: 733–740.

40. Hegg JC, Kennedy BP, Chittaro PM, Zabel RW (2013) Spatial structuring of an evolving life-history strategy under altered environmental conditions. Oecologia 172: 1017–1029. Available: http://dx.doi.org/10.1007/s00442-012-2564-9. Accessed 12 April 2013.

41. Hogan Z, Baird IG, Radtke R, Vander Zanden MJ (2007) Long distance migration and marine habitation in the tropical Asian catfish, Pangasius krempfi. J Fish Biol 71: 818–832.

42. Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal homing in a marine fish metapopulation. Science (80-) 291: 297–299.

43. Kennedy BP, Klaue A, Blum JD, Folt CL, Nislow KH (2002) Reconstructing the lives of fish using Sr isotopes in otoliths. Can J Fish Aquat Sci 59: 925–929.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

44. Walther BD, Dempster T, Letnic M, McCulloch MT (2011) Movements of diadromous fish in large unregulated tropical rivers inferred from geochemical tracers. PLoS One 6. doi:10.1371/journal.pone.0018351.

45. Garcez RCS, Humston R, Harbor D, Freitas CEC (2014) Otolith geochemistry in young-of-the-year peacock bass *Cichla temensis* for investigating natal dispersal in the Rio Negro (Amazon - Brazil) river system. Ecol Freshw Fish: n/a – n/a. Available: http://doi.wiley.com/10.1111/eff.12142. Accessed 29 April 2014.

46. Collins SM, Bickford N, McIntyre PB, Coulon A, Ulseth AJ, et al. (2013) Population Structure of a Neotropical Migratory Fish: Contrasting Perspectives from Genetics and Otolith Microchemistry. Trans Am Fish Soc 142: 1192–1201. Available: http://www.tandfonline.com/doi/abs/10.1080/00028487.2013.804005. Accessed 11 April 2014.

47. Hobson KA, Barnett-Johnson R, Cerling T (2010) Using isoscapes to track animal migration. Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping. Springer Verlag. pp. 273–298.

48. Kennedy BP, Blum JD, Folt CL, Nislow KH (2000) Using natural strontium isotopic signatures as fish markers: methodology and application. Can J Fish Aquat Sci 57: 2280–2292.

49. Kennedy BP, Folt CL, Blum JD, Chamberlain CP (1997) Natural isotope markers in salmon. Nature 387: 766–767.

50. Barnett-Johnson R, Pearson TE, Ramos FC, Grimes CB, MacFarlane RB (2008) Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. Limnol Oceanogr 53: 1633–1642.

51. Queiroz MMA, Horbe AMC, Seyler P, Moura CAV (2009) Hidroquímica do rio Solimões na região entre Manacapuru e Alvarães: Amazonas - Brasil. Acta Amaz 39: 943–952. Available: http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0044-59672009000400022&lng=en&nrm=iso&tlng=ES. Accessed 23 January 2014.

52. Gaillardet J, Dupre B, Allegre CJ, Négrel P (1997) Chemical and physical denudation in the Amazon River Basin. Chem Geol 142: 141–173.

53. Santos R V., Sondag F, Cochonneau G, Lagane C, Brunet P, et al. (2013) Source area and seasonal $^{87}Sr/^{86}Sr$ variations in rivers of the Amazon basin. Hydrol Process: n/a – n/a. Available: http://doi.wiley.com/10.1002/hyp.10131. Accessed 27 January 2014.

54. Hegg JC, Kennedy BP, Fremier AK (2013) Predicting strontium isotope variation and fish location with bedrock geology: Understanding the effects of geologic heterogeneity. Chem Geol 360-361: 89–98. Available: http://ida.lib.uidaho.edu:2104/science/article/pii/S0009254113004464#. Accessed 4 November 2013.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

55. Bataille CP, Bowen GJ (2012) Mapping $^{87}Sr/^{86}Sr$ variations in bedrock and water for large scale provenance studies. Chem Geol 304: 39–52.

56. Pirker LEM (2001) Determinação da idade e crecimento da Piramutaba Brachyplatystoma vaillantii (Valenciennes, 1840) (Siluriformes: Pimilodidae) capturada no estuário Amazônico Universidade Federal do Pará/Museo Paraense Emílio Goeldi. Available: http://www.repositorio.ufpa.br/jspui/bitstream/2011/4153/1/Dissertacao_DeterminacaoIdadeCrescimento.pdf.

57. Secor DH, Dean JM, Laban EH (1991) Manual for otolith removal and preparation for microstructural examination. 1: 85. Available: http://www.cbl.umces.edu/~secor/manual/manual.pdf.

58. Faure G, Mensing TM (2004) Isotopes: principles and applications. John Wiley & Sons Inc.

59. USGS (1996) GTOPO30 30-Arc-Second Elevation Data Set of South America. Sioux Falls, South Dakota: United States Geological Survey. Available: https://lta.cr.usgs.gov/GTOPO30.

60. Lehner B, Verdin K, Jarvis A (2008) New global hydrography derived from spaceborne elevation data. Eos (Washington DC) 89: 93–94.

61. USGS (1999) Geologic Map of the Amazon Region. Denver, Colorado: United States Geological Survey. Available: http://energy.cr.usgs.gov/energy/WorldEnergy/WEnergy.html.

62. Cohen KM, Finney S, Bibbard PL (2013) International Chronostratigraphic Chart. International Commission on Stratigraphy.

63. Calcagno V, Mazancourt C de (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. J Stat Softw 34. Available: http://www.researchgate.net/publication/215991965_glmulti_An_R_Package_for_Easy_Automated_Model_Selection_with_(_Generalized_)_Linear_Models/file/e0b4952a1b23cf2236.pdf. Accessed 28 November 2014.

64. Tang KS, Man KF, Kwong S, He Q (1996) Genetic algorithms and their applications. IEEE Signal Process Mag 13: 22–37. Available: http://ieeexplore.ieee.org/xpls/abs_all.jsp?arnumber=543973. Accessed 28 November 2014.

65. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag.

66. Killick R, Eckley IA (2013) Changepoint: An R Package for changepoint analysis. R Packag version 06, URL http//CRANR-project.org/package=changepoint: 1–15. Available: http://www.lancs.ac.uk/~killick/Pub/KillickEckley2011.pdf.

67. Killick R, Fearnhead P, Eckley I (2012) Optimal detection of changepoints with a linear computational cost. J Am … 107: 1–25. Available:

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

http://www.tandfonline.com/doi/abs/10.1080/01621459.2012.737745. Accessed 30 May 2014.

68. Bouchez J, Lajeunesse E, Gaillardet J, France-Lanord C, Dutra-Maia P, et al. (2010) Turbulent mixing in the Amazon River: The isotopic memory of confluences. Earth Planet Sci Lett 290: 37–43. Available: http://linkinghub.elsevier.com/retrieve/pii/S0012821X0900716X. Accessed 2 February 2014.

69. Crook DA, Macdonald JI, McNeil DG, Gilligan DM, Asmus M, et al. (2013) Recruitment sources and dispersal of an invasive fish in a large river system as revealed by otolith chemistry analysis. Can J Fish Aquat Sci 70: 953–963. Available: http://www.nrcresearchpress.com/doi/abs/10.1139/cjfas-2012-0504#.U1ha9P12Vy4. Accessed 24 April 2014.

70. Hughes JM, Schmidt DJ, Macdonald JI, Huey JA, Crook DA (2014) Low interbasin connectivity in a facultatively diadromous fish: evidence from genetics and otolith chemistry. Mol Ecol 23: 1000–1013. Available: http://www.ncbi.nlm.nih.gov/pubmed/24410817. Accessed 24 April 2014.

71. Muhlfeld CC, Thorrold SR, McMahon TE, Marotz B, Gillanders B (2012) Estimating westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) movements in a river network using strontium isoscapes. Can J Fish Aquat Sci 69: 906–915.

72. Hobbs JA, Lewis LS, Ikemiyagi N, Sommer T, Baxter RD (2010) The use of otolith strontium isotopes ($^{87}Sr/^{86}Sr$) to identify nursery habitat for a threatened estuarine fish. Environ Biol Fishes 89: 557–569. Available: http://link.springer.com/article/10.1007/s10641-010-9672-3/fulltext.html. Accessed 3 December 2014.

73. Winemiller KO (2005) Life history strategies , population regulation , and implications for fisheries management. Can J Fish Aquat Sci 885: 872–885. doi:10.1139/F05-040.

74. Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci U S A 100: 6564–6568. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=164486&tool=pmcentrez&rendertype=abstract. Accessed 18 March 2013.

75. Copeland T, Venditti DA (2009) Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. Can J Fish Aquat Sci 66: 1658–1665.

76. Burke JL (2004) Life histories of juvenile chinook salmon in the Columbia River estuary: 1916 to the present Oregon State University.

77. Beechie T, Buhle E, Ruckelshaus M, Fullerton A, Holsinger L (2006) Hydrologic regime and the conservation of salmon life history diversity. Biol Conserv 130: 560–572. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320706000450. Accessed 15 March 2013.

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

78. De Mérona B, Mendes dos Santos G, Goncçalves de Almeida R (2001) Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Biol Fishes 60: 375–392. Available: http://link.springer.com/article/10.1023/A:1011033025706. Accessed 30 May 2014.

79. JICA, Japan International Cooperation Agency: Sanyo Techno Marine I, IBAMA, Japan (1998) The fishery resources study of the Amazon and Tocantins river mouth areas in the Federative Republic of Brazil: final report. Tokyo. 332 p. Available: http://lvzopac.jica.go.jp/external/library?func=function.opacsch.mmindex&view=view.opacsch.toshoshozodsp&lang=eng&shoshisbt=1&shoshino=0000097380&volno=0

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Tables

Table 1. *Brachyplaystoma* spp. sample information

Species	Sample Number	Location	Total Length (cm)	Weight (kg)
Brachyplatystoma rousseauxii	BR1	Belém	75	8.00
(dourada)	BR3	Belém	75	8.00
	BR6	Belém	75	8.00
	BR7	Belém	75	8.00
	BR8	Belém	75	8.00
	BR10	Belém	75	8.00
	BR12	Belém	75	8.00
	BR14	Belém	75	8.00
	BR16	Belém	75	8.00
	BR18	Belém	100	22.00
	BR19	Manaus	110	11.00
	BR21	Manaus	100	6.00
	BR23	Manaus	115	10.00
	BR24	Manaus	75	3.70
	BR25	Manaus	80	4.00
	BR26*	Manaus	-	-
Brachyplatystoma vaillanti	BV1	Manaus	75	4.19°
(piramutaba)	BV2	Manaus	70	3.38°
	BV3	Manaus	68	3.09°
	BV4	Manaus	65	2.68°
	BV5	Manaus	70	3.38°
Brachyplatystoma filamentosum	BF1	Belém	220	110.00
(piraíba)	BF3	Belém	250	130.00
	BF5	Belém	90	20.00

* Asterisci otolith. Analysis was excluded due to low Sr concentrations
° Weights are estimated from length-to-weight ratios
Fish were collected from two locations in the Brazilian Amazon; in the cities of Belém near the mouth of the Amazon River, and Manaus in the central Amazon Basin. Piramutaba were gutted prior to otolith collection. Their weights are estimated from a length-to-weight relationship from Pirker [56].

Table 2. Isotopic and geologic makeup of major watersheds of the Amazon River basin

Sample Point Name (From Literature)	Literature Source	River	River Group Classification	$^{87}Sr/^{86}Sr$	St. Dev.	N	Geology Percent Area			Mean Age (Ma)
							Carboniferous	Tertiary	Precambrian	
Amazon 13	Gaillardet et al. 1997	Amazon	Wester Tributaries & Amazon Mainstem	0.710728	-	1	1%	47%	21%	409
Amazon 14	Gaillardet et al. 1997	Amazon	Wester Tributaries & Amazon Mainstem	0.71112	-	1	1%	47%	21%	409
Amazon 20	Gaillardet et al. 1997	Amazon	Wester Tributaries & Amazon Mainstem	0.711478	-	1	2%	42%	25%	429
Amazon 6	Gaillardet et al. 1997	Amazon	Wester Tributaries & Amazon Mainstem	0.709172	-	1	0%	60%	17%	407
Rio Madeira	Gaillardet et al. 1997	Lower Madeira	Beni-Madeira & Lower Negro	0.720036	-	1	2%	20%	30%	412
Rio Negro	Gaillardet et al. 1997	Lower Negro	Beni-Madeira & Lower Negro	0.716223	-	1	0%	21%	68%	1243
Rio Topajos	Gaillardet et al. 1997	Lower Topajos	Lower Amazon Tributaries	0.733172	-	1	10%	8%	48%	658
Rio Trombetas	Gaillardet et al. 1997	Lower Trombetas	Lower Amazon Tributaries	0.732295	-	1	3%	7%	78%	515
Uracara	Gaillardet et al. 1997	Lower Uracara	Lower Amazon Tributaries	0.723584	-	1	2%	19%	62%	558
Purus	Queiroz et al. 2009	Lower Purus	Wester Tributaries & Amazon Mainstem	0.711135	-	1	0%	92%	4%	564
Solimões*	Queiroz et al. 2009	Lower Solimões	Wester Tributaries & Amazon Mainstem	0.714461	-	1	0%	63%	1%	289
Atalaya	Santos et al. 2013	Upper Solimões	Wester Tributaries & Amazon Mainstem	0.70887	-	1	0%	20%	0%	331
Borba	Santos et al. 2013	Lower Madeira	Beni-Madeira & Lower Negro	0.71762	-	1	2%	20%	30%	412
Borja	Santos et al. 2013	Upper Solimões	Wester Tributaries & Amazon Mainstem	0.7085	-	1	0%	13%	0%	426
Caracarai	Santos et al. 2013	Upper Negro	Beni-Madeira & Lower Negro	0.72238	-	1	0%	0%	74%	1650
Francisco de Orellana	Santos et al. 2013	Upper Solimões	Wester Tributaries & Amazon Mainstem	0.70592	0.00037	26	0%	67%	10%	287
Itiatuba	Santos et al. 2013	Lower Tapajos	Lower Amazon Tributaries	0.72964	0.00587	27	10%	4%	51%	671
LaBrea	Santos et al. 2013	Lower Purus	Wester Tributaries & Amazon Mainstem	0.71012	-	1	0%	90%	6%	1126
Manacapuru	Santos et al. 2013	Lower Solimões	Wester Tributaries & Amazon Mainstem	0.70907	0.00025	38	0%	72%	2%	312
Obidos	Santos et al. 2013	Amazon	Wester Tributaries & Amazon Mainstem	0.71154	0.00053	46	1%	46%	23%	408
PortoVelho	Santos et al. 2013	Lower Madeira	Beni-Madeira & Lower Negro	0.71677	0.00073	9	3%	17%	22%	379
Ruranbaque	Santos et al. 2013	Upper Madeira	Beni-Madeira & Lower Negro	0.71730	0.00126	38	17%	13%	1%	433
Serrinha	Santos et al. 2013	Upper Negro	Lower Amazon Tributaries	0.73183	0.00737	16	0%	19%	80%	614
Tabitinga	Santos et al. 2013	Upper Solimões	Wester Tributaries & Amazon Mainstem	0.70881	0.00029	9	0%	75%	3%	200
Amazon Mouth (Predicted)	Predicted from regression	Amazon	Wester Tributaries & Amazon Mainstem	0.71625	0.00787°	-	2%	40%	29%	482
Jari (Predicted)	Predicted from regression	Lower Jari	Lower Amazon Tributaries	0.72928	0.00873°	-	0%	2%	89%	718
Paru (Predicted)	Predicted from regression	Lower Paru	Lower Amazon Tributaries	0.72703	0.00845°	-	1%	4%	78%	515
Tocantins (Predicted)	Predicted from regression	Lower Tocantins	Lower Amazon Tributaries	0.72683	0.00884°	-	13%	22%	36%	877
Xingu (Predicted)	Predicted from regression	Lower Xingu	Lower Amazon Tributaries	0.72633	0.00827°	-	2%	13%	70%	1091

* Outlier dropped from regression analysis

° Values are prediction intervals of the regression from Equation 1.

Strontium ratios were taken from water samples reported in the literature for locations throughout the Amazon Basin and used as baselines to determine the likely location of fish movement. These samples were classified to three statistically distinguishable river group classifications using quadratic discriminant function analysis. Unsampled locations were predicted using geologic regression (Equation 1).

bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Figures

Figure 1. Water sampling points and geology of the Amazon River basin

Maps show (A) the location of $^{87}Sr/^{86}Sr$ water samples within the Amazon River basin digitized by the authors from location descriptions in the literature [51–53] and points predicted from Equation 1. The geological age and composition of the basin (B) used to predict the $^{87}Sr/^{86}Sr$ signatures of unsampled watersheds is also shown. Maps created using USGS datasets [59–61]

Figure 2. Otolith sectioning and analysis

Representative transverse section from a dourada lapillus otolith showing the analysis area (in red) used for all otoliths with the laser-ablation tracks indicated. All analyses were performed approximately perpendicular to the growth rings.

Figure 3. River isotopic signatures throughout the Amazon River basin

Strontium ratio values (y-axis) for each sampled and predicted watershed (x-axis) in the current study. Color indicates the classification to three river groups using quadratic discriminant function analysis. Solid error bars indicate the standard deviation where samples were repeated over time (See Table 1 for sample sizes). Dashed error bars indicate the prediction intervals from the geologic regression (Equation 1) used to predict that point. Points bordered in black were misclassified during cross validation of the quadratic discriminant function.

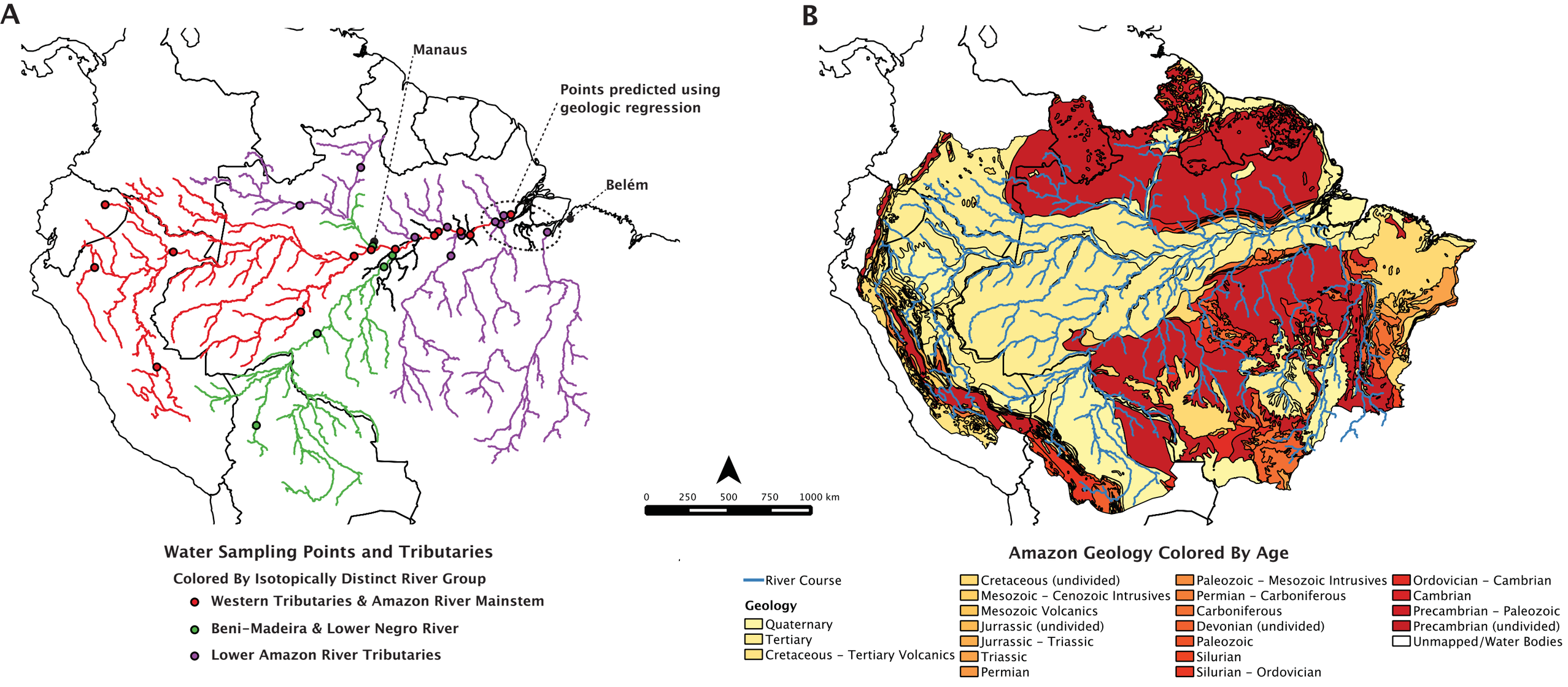
Figure 4. Location classification of $^{87}Sr/^{86}Sr$ signatures in otolith transects

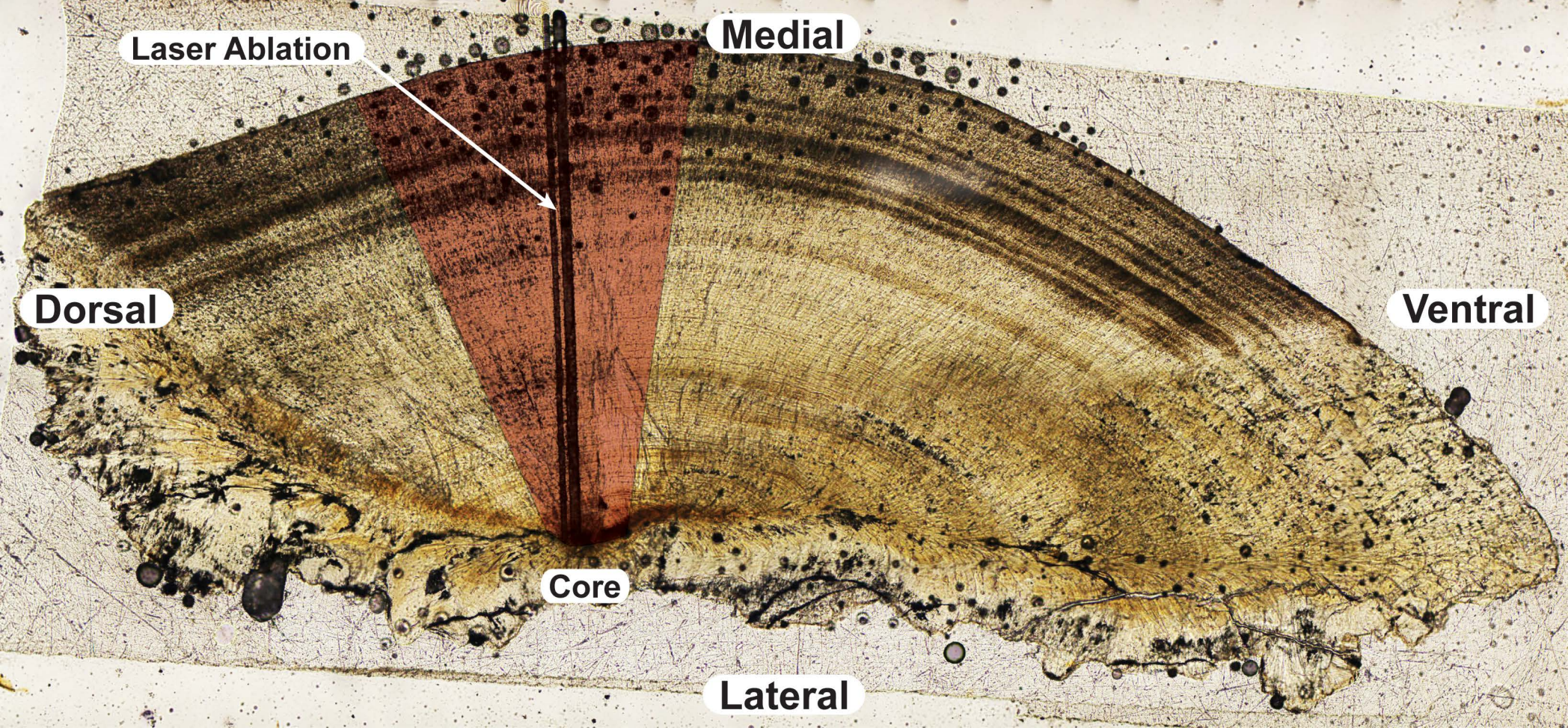
Plots show the variation in $^{87}Sr/^{86}Sr$ (y-axis) over the life of sampled fish, represented as distance from the otolith core in microns (x-axis). Horizontal colored lines indicate stable signatures identified using changepoint analysis, with colors representing inclusion in one of three statistically distinguishable river groups based on quadratic discriminant analysis. Fourteen samples of dourada (A) were collected in Belém and Manaus fish markets. Five samples of piramutaba (B) were collected in Manaus. Three samples of piraíba (C) were collected in Belém. Dark grey chart labels indicate a different y-axis scale was used to accommodate large variations in $^{87}Sr/^{86}Sr$. The x-axis scale differs for all fish depending on the width of the otolith, which varies based on age, growth and species specific factors.

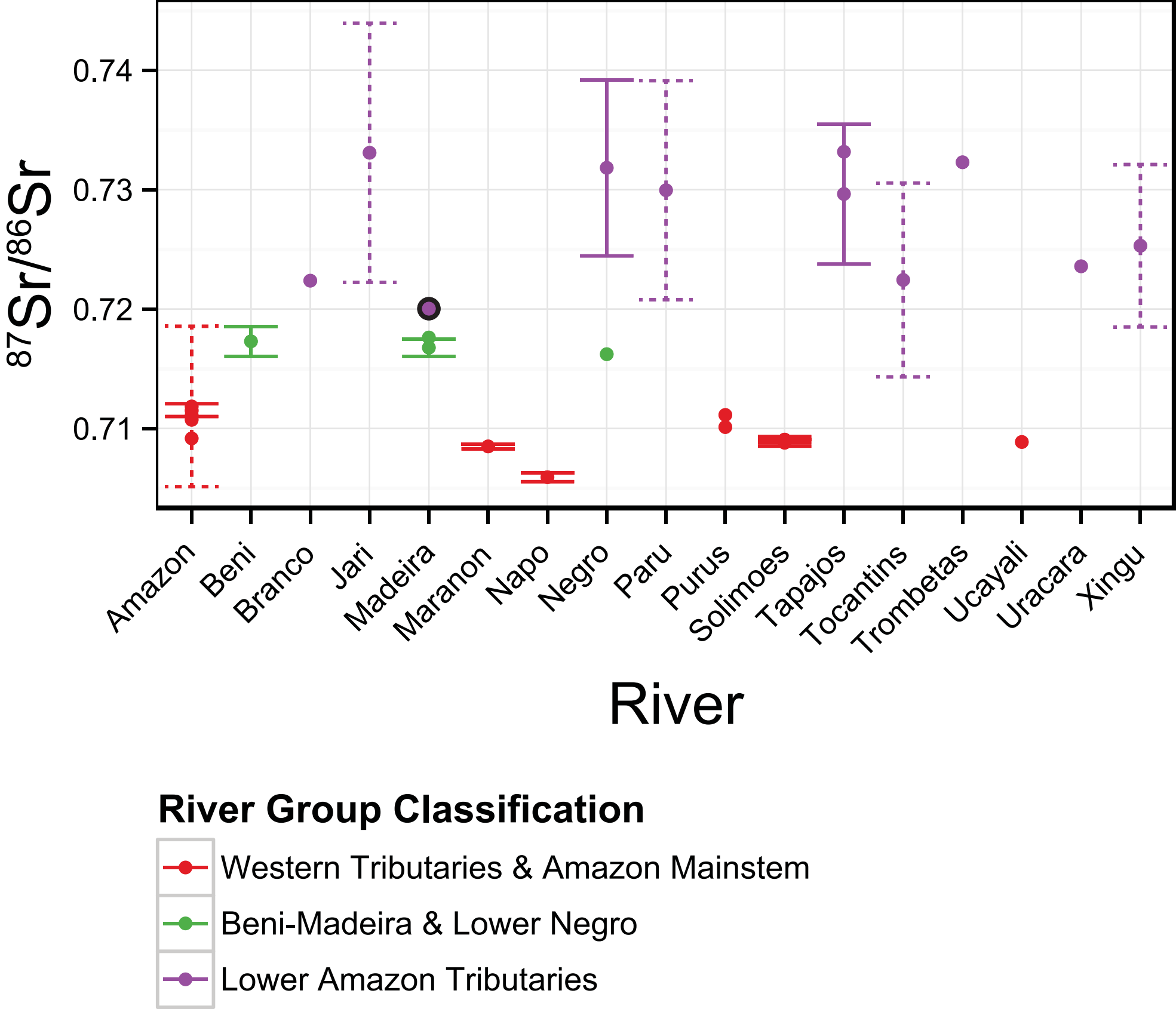
bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

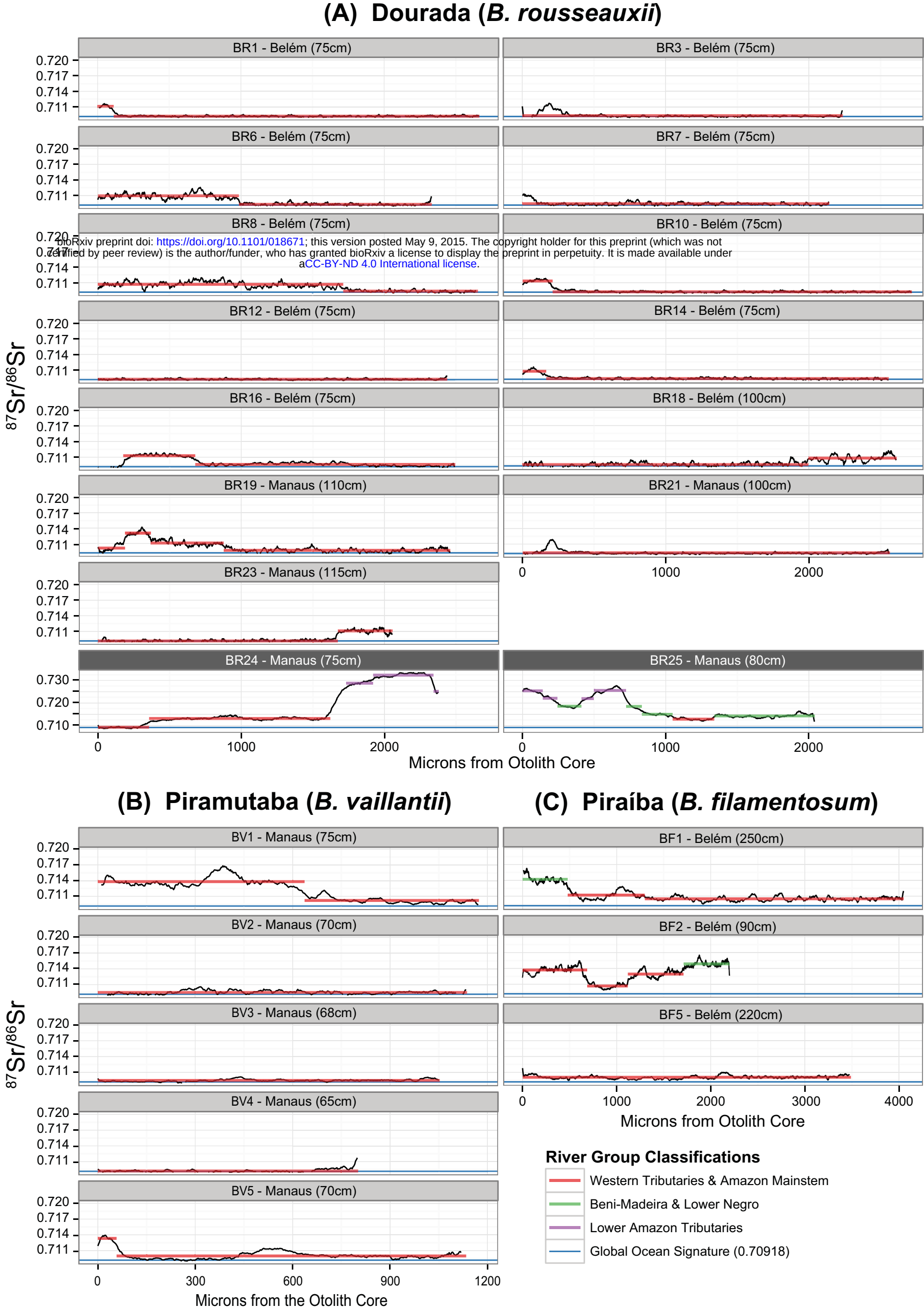
Supporting Information

S1 Table. Otolith transect data. Table of raw otolith transect data for each sample analyzed.


A
Manaus
Points predicted using geologic regression
Belém
0 250 500 750 1000 km
Water Sampling Points and Tributaries
Colored By Isotopically Distinct River Group
Western Tributaries & Amazon River Mainstem
Beni-Madeira & Lower Negro River
Lower Amazon River Tributaries
B
Amazon Geology Colored By Age
River Course
Geology
Quaternary
Tertiary
Cretaceous - Tertiary Volcanics
Cretaceous (undivided)
Mesozoic - Cenozoic Intrusives
Mesozoic Volcanics
Jurrassic (undivided)
Jurrassic - Triassic
Triassic
Permian
Paleozoic - Mesozoic Intrusives
Permian - Carboniferous
Carboniferous
Devonian (undivided)
Paleozoic
Silurian
Silurian - Ordovician
Ordovician - Cambrian
Cambrian
Precambrian - Paleozoic
Precambrian (undivided)
Unmapped/Water Bodies


Laser Ablation
Medial
Dorsal
Ventral
Core
Lateral


0.74
0.73
0.72
0.71
87Sr/86Sr
Amazon
Beni
Branco
Jari
Madeira
Maranon
Napo
Negro
Paru
Purus
Solimoes
Tapajos
Tocantins
Trombetas
Ucayali
Uracara
Xingu
River
River Group Classification
Western Tributaries & Amazon Mainstem
Beni-Madeira & Lower Negro
Lower Amazon Tributaries



bioRxiv preprint doi: https://doi.org/10.1101/018671; this version posted May 9, 2015. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.