

Meta-analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in otoliths to establish thresholds for determining fish movement

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Abstract

Unpublished data were combined with a literature review to test a hypothesis of whether there is a pattern for classifying fish as “movers” or “residents” according to variability in strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios in otoliths as a function of its environmental fingerprint. The variability in Sr ratios found in the otoliths of fish specimens as a percentage of isotopic environmental variability was used to determine the intensity of movement in a given study area (POEVSri index). A classic meta-analysis and a frequentist regression were applied to obtain a logistic model to describe the pattern. The meta-analysis returned a POEVSri limit of 28.95% for sedentary individuals and the logistic model shows a high probability of movement for POEVSri indices over 32%. There is a gradient of movement probabilities in the POEVSri interval from 8 to 32%, with each class having equal odds when POEVSri is approximately 20%. Regarding applicability for future studies, if aspects such as sufficient spatial and seasonal water sampling are addressed, the model provides two different thresholds for fish: a priori “movers” are those with $\text{POEVSri} \geq 32\%$, and resident fish have $\text{POEVSri} \leq 8\%$.

Keywords: Migratory fish; Fish home range; Strontium isotopes; Geochemistry; Rheophilic fish.

Metanálise de razões $^{87}\text{Sr}/^{86}\text{Sr}$ em otólitos para estabelecer limiares para determinar o movimento de peixes

Resumo

Dados não publicados em conjunto com revisão da literatura foram combinados para testar a hipótese de que existe um padrão para classificar peixes como “migradores” ou “residentes” de acordo com a variabilidade nas proporções de isótopos de estrôncio ($^{87}\text{Sr}/^{86}\text{Sr}$) em otólitos em função das assinaturas isotópicas ambientais. A variabilidade nas razões de Sr encontradas nos otólitos dos espécimes de peixes como porcentagem da variabilidade ambiental isotópica foi utilizada para determinar a intensidade do movimento em uma determinada área de estudo (índice POEVSri). Uma meta-análise clássica e uma regressão frequentista foram aplicadas para obter um modelo logístico para descrever o padrão. A meta-análise retornou um POEVSri limite de 28,95% para indivíduos sedentários, e o modelo logístico demonstra alta probabilidade de migração para índices POEVSri superiores a 32%. Há um gradiente de probabilidades de movimento no intervalo de POEVSri entre 8 e 32%, com cada classe tendo probabilidades iguais quando POEVSri é de aproximadamente 20%. Quanto à aplicabilidade para estudos futuros, se aspectos como amostragem espacial e sazonal suficiente da água forem abordados, o modelo fornece dois limites diferentes para os peixes: “movers” a priori são aqueles com $\text{POEVSri} \geq 32\%$, e os peixes residentes têm $\text{POEVSri} \leq 8\%$.

Palavras-chave: Peixes migratórios; Área de vida de peixes; Isótopos de estrôncio; Geoquímica; Peixe reofílico.

Received: March 30, 2023 | **Approved:** November 23, 2023

INTRODUCTION

Fish migration can be defined as a strategy to increase fitness, in which part or all the population moves between at least two places based on both biotic and abiotic factors (Secor, 2015). Movements are constrained by the trade-off of staying in one location versus moving to a new location. In many ecosystems, as habitat conditions change seasonally, seasonal movement can allow individuals to optimize access to the best possible environmental conditions (Leggett, 1985). External drivers (*e.g.*, prey, predators, physicochemical factors, mating opportunities, and environmental changes) and internal motivations (*e.g.*, energetic status, size, experience, navigational capacity, and maturity level) influence the costs and benefits of movement (Nathan et al., 2008).

Duponchelle et al. (2021) present a more defined concept: “Migrations are considered periodic or seasonal synchronized movements of adaptive value (critical for individual fitness and population persistence) between two or more separate habitats involving a large portion of the population and which are repeated within or across generations”. This definition of migration fits well for homing behavior. Although isotope tracking does provide information on homing behavior, any mover fish can be also tracked, regardless of whether it is either a true migration or an opportunistic dispersion. Therefore, in this study, both movers *lato sensu* and migrators *strictu sensu* are being considered.

Due to the increasing need for improved fisheries management and the logistical difficulties associated with long-term continuous tracking of particularly small aquatic animals, there has been a growing interest in studying fish life cycles/histories. This exploration involves the analysis of trace elements and isotopes found in hard structures such as otoliths, spines, and scales (Reis-Santos et al., 2022). Otoliths have one critical advantage over renewable hard structures like spines and scales, since they preserve elemental composition throughout the entire life of the fish (Thorrold and Hare, 2002). In comparison, spines and scales are composed of hydroxyapatite and are metabolically active (Tzadik et al., 2017). Moreover, it is possible to lose and regrow scales and fin bones. However, reabsorption or losses do not occur in otoliths because they are metabolically inert. Otolith growth occurs from the very beginning of ontogenetic development and is relatively protected from contamination and dissolution in its cephalic chamber.

Among trace chemical elements, strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) are extensively used in geochemical fingerprinting, source tracking, contamination prediction, and migration/mobility studies. As part of source tracking and migration/

mobility studies, strontium isotopes can help provide useful information about fish life ranges over different watersheds within a particular hydrographic basin (Hegg et al., 2013).

Unlike elemental ratios, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio is mainly related to the age and type of rock in the watershed, and its incorporation into otoliths is relatively unaffected by physiological processes (Reis-Santos et al., 2022). Because an otolith continually grows, changes in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio are incorporated into the bone structure, while the fish inhabits geochemically different water bodies throughout its life (Hauser et al., 2020; Avigliano et al., 2021). Therefore, tracking movements using strontium isotopes consists of comparing the environmental range of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios to the traces found in hard structures (such as bones, scales, and otoliths). As the fish grows, the structures receive new layers that accumulate while they are immersed in each habitat. Each layer is an indicator of the habitat's $^{87}\text{Sr}/^{86}\text{Sr}$ ratio at that time, and the variations between layers may constitute evidence of migration or dispersion. As a result, it is possible to compare the individual “time capsules” recorded by the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in fish otoliths with the $^{87}\text{Sr}/^{86}\text{Sr}$ signatures found in the fishes' watershed. However, there is a need to confront a critical question: what do variabilities in fish $^{87}\text{Sr}/^{86}\text{Sr}$ ratios indicate in terms of either migration or dispersal? In other words, how much variation of $^{87}\text{Sr}/^{86}\text{Sr}$ between fish's otolith layers in comparison to the environments “signatures” indicates movement? The many criteria in use in different studies should be compared.

Since many case studies cite fish habitat use derived from $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in otoliths, some contain enough data to be included in a meta-analysis involving this question. Therefore, the aim of this study was to generate a model that shows how variability in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in otoliths based on inter-habitat differences can reveal changes in habitat; thereby indicating either migration or dispersal. It was hypothesized that there is a minimum $^{87}\text{Sr}/^{86}\text{Sr}$ range in otoliths, expressed as a percentage of the environmental $^{87}\text{Sr}/^{86}\text{Sr}$ range, which, if statistically significant, can indicate *a priori* movement through any given area, regardless of the species.

METHODS

Due to the sophisticated technology required to analyze $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in otoliths, this type of study has only become common in the last few decades (Campana, 1999). In the meta-analysis of the scientific literature associated with this topic, unpublished doctorate theses, master's dissertations, and technical reports, as well as published scientific papers, were all included to reduce the “risk of publication bias” (Field and

Gillett, 2010). When raw data was available as a supplement for the respective articles, dissertations and theses, written permission was sought from the corresponding authors to use the data in this new approach.

Many studies have plotted the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio data for the total transects of laser ablation of otoliths (for typical methodological settings, see Duponchelle et al., 2016). Furthermore, as these studies showed the variability of environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for nine published datasets, the data was included in the meta-analysis. Each one of the four unpublished datasets consists of methodologies and experimental designs that were specified. This reduced the “risk of publication bias”, a meta-analysis requirement, without compromising comparability among subsets of data.

Once the data was obtained, the greatest $^{87}\text{Sr}/^{86}\text{Sr}$ value minus the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ value for the environments in each study area was used to determine the known range of environmental variation. Similarly, the greatest $^{87}\text{Sr}/^{86}\text{Sr}$ value for each fish minus the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ value in the otolith rings was used to determine the internal variation. Next, the isotope variability of each otolith was standardized as a percentage of environmental isotope variability for each fish in a given study area. The percentage of the otolith/environmental variability of Strontium isotopes (POEVSri) (acronym as preconized by Sand-Jensen, 2007) was calculated by Eq. 1:

$$\text{POEVSri} = \frac{(\text{Max} - \text{Min otolith } ^{87}\text{Sr}/^{86}\text{Sr}) \times 100}{(\text{Max} - \text{Min environmental } ^{87}\text{Sr}/^{86}\text{Sr})} \quad (1)$$

Seaborn/MatPlot/Pandas libraries on the Jupyter Notebook platform for Python 3 programming language were used to plot the data distribution and explore its variability.

To determine the minimum threshold indicating fish movement in the POEVSri gradient, the end of the distribution of sedentary individuals in the same gradient was calculated. Therefore, a meta-analysis was performed only on the datasets of individuals classified as sedentary.

To consider both sample sizes and/or variance for weight measures, fixed-effect and random-effects meta-analyses were conducted, as well as the most common heterogeneity test for fixed-effects models, the Homogeneity “Q” (DerSimonian and Laird, 1986) (Eq. 2):

$$Q = \sum (d^2/\text{var}) - \frac{(\sum d/\text{var})^2}{\sum 1/\text{var}} \quad (2)$$

Where: d: Cohen’s d (see below); var: the variance in each dataset.

The assumptions of fixed-effects models are that:

- Among the set of studies, there is a common cause for variation (Fleiss, 1993);
- The differences among the results in the studies occur by chance (Deeks et al., 2001; Konstantopoulos and Hedges, 2009).

The variability among datasets can occur at random for random-effects models, irrespective of a common causal mechanism. This assumption ensures the random-effects models to be predictive (Field and Gillett, 2010), which corresponds with the purposes of this study.

To measure the datasets effects, Hedge’s g (Hedges, 1984) was selected, a complement to Cohen’s d coefficient (Cohen, 1992), which in turn uses the sum of squared errors to standardize the difference between means (Hedges and Olkin, 1983; Fleiss, 1993) (Eq. 3).

$$D = \frac{M1 - M2}{\sigma} \quad (3)$$

Where: M: the means; σ : the sum of squared errors.

Cohen’s d coefficient is easy to obtain from different datasets, and it fits nicely for sample sizes below 10, capturing both the weight of the sampling number and the importance of the variance in each dataset (Field and Gillett, 2010). Therefore, it became the default option in the procedures using the meta package for meta-analysis in R (Schwarzer et al., 2015).

Using the above combination of coefficients and assumptions, the meta-analysis was performed with the “metamean” option of the “meta” package (Schwarzer et al., 2015) in R language (R Core Team, 2000). The function “forest” of the “metafor” package (Viechtbauer and Viechtbauer, 2015) was also used to plot the generated object (the models and statistics) as a “forest plot.”

Using all the datasets for movers and sedentary individuals, a general linear model (limited dependent variable/logit/binary) considered the categories (movers or sedentary) as dependent on POEVSri, in the GRETl cross-platform software package for econometric analysis (Cottrell and Lucchetti, 2021). The output logistic model was exported to a “csv” file and plotted on a histogram distribution background calling for functions from the “popbio” package/library (Stubben et al., 2022) in R language (R Core Team, 2000) on the R Studio platform (R Studio Team, 2022).

RESULTS

Thirteen datasets were obtained, which covered sections of the two largest freshwater systems in South America, the Amazon and La Plata basins, the Mekong River in Asia, and the

Waikato River in Oceania. Those watersheds have different sizes, and the lengths of the study areas vary by more than an order of magnitude (Table 1). The lengths of the study areas showed no correlation with the environmental $^{87}\text{Sr}/^{86}\text{Sr}$ variability (Table 1).

Data was gathered for species showing very different life histories. Four are well-known potamodromous migratory fish: *Brachyplatystoma rousseauxii* (a giant catfish, data from Duponchelle et al., 2016), *Brachyplatystoma platynemum* (another giant catfish, data from Hauser et al., 2019), *P. lineatus*, and *Salminus brasiliensis* (Characiformes, data from Avigliano et al., 2021). *Arapaima* spp. (including *Arapaima gigas*) are giant Amazonian Osteoglossiformes and obligatory air-breathers that migrate between the floodplain and lacustrine habitats (Castello, 2008). One Asian equivalent of the Amazonian catfishes' migration is the dataset available for the anadromous catfish *Pangasius krempfi*, from the Mekong River (Tran et al., 2021). Two diadromous species were included, i.e., *Galaxias argenteus* and *Galaxias fasciatus* (Galaxiiformes, data from David et al., 2019). Three datasets covered freshwater perch-like species, one for *Cichla kelberi* (a small dataset from Sousa et al., unpublished) and two for *Cichla temensis*, known as sedentary until a few years ago, but they can move up to 100 km (Sousa et al., 2016; Barroco, 2019). The remaining species, *Galeocharax gulo* and *Hoplias*

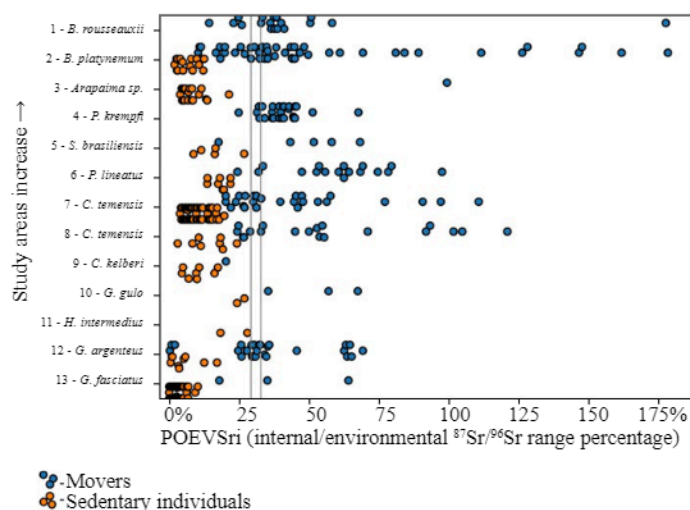
intermedius, are freshwater Characiformes (data from Sousa et al., unpublished) and known to be sedentary.

According to the criteria of the authors in Table 1, most species included both movers (migration and dispersion) and sedentary individuals in their study areas, thus resulting in 192 sedentary individuals and 196 movers, represented in Fig. 1. When the raw variations exemplified in Table 1 were standardized as individual percentages, as seen in Fig. 1, the distributions of each class were found to be much closer in the different studies. All the individuals classified as sedentary showed $^{87}\text{Sr}/^{86}\text{Sr}$ variations ranging from 0.08 to 27.75% of the $^{87}\text{Sr}/^{86}\text{Sr}$ environmental variation. For individuals classified as movers, the otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratio/environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratio percentage (POEV_{Sr}) showed a much larger range (from 0.31 to 177%). POEV_{Sr} values over 100% were expected for movers, as most studies have found their "isotopic signatures" to show divergence from the sampled home range environments, which indicates movement into areas that extend beyond the known environmental isotopic heterogeneity.

A partial overlay of movers and sedentary individuals is expected, mainly when the $^{87}\text{Sr}/^{86}\text{Sr}$ variation in otoliths is approximately 10 to 20% of the environmental $^{87}\text{Sr}/^{86}\text{Sr}$ variation (Fig. 1). However, POEV_{Sr} values above 25% are rarely found with sedentary individuals, with only movers

Table 1. The initial descriptors of each gathered dataset.

Authors	Watershed	Approximate length of the study area (km)	Variation in environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratio	Species	Mean variation in mover fish $^{87}\text{Sr}/^{86}\text{Sr}$ ratios	Mean variation in sedentary fish $^{87}\text{Sr}/^{86}\text{Sr}$ ratios
Duponchelle et al. (2016)	Amazon River	2,030	0.0319	<i>B. rousseauxii</i>	0.0139	
Hauser et al. (2019)	Amazon River	2,030	0.0319	<i>B. platynemum</i>	0.0167	0.0020
Pereira et al. (2019)	Amazon River	1,760	0.0150	<i>Arapaima</i> sp.	0.0148	0.0012
Tran et al. (2021)	Mekong	1,530	0.0050	<i>P. krempfi</i>	0.0016	
Avigliano et al. (2021)	La Plata	1,430	0.0085	<i>S. brasiliensis</i>	0.0040	0.0014
Avigliano et al. (2021)	La Plata	1,430	0.0085	<i>P. lineatus</i>	0.0051	0.0015
Barroco (2019)	Uatumã River	270	0.0253	<i>C. temensis</i>	0.0111	0.0025
Sousa et al. (2016)	Negro River	156	0.0413	<i>C. temensis</i>	0.0236	0.0058
Sousa et al. (Unpublished)	Verde River	151	0.0165	<i>C. kelberi</i>	0.0033	0.0017
Sousa et al. (Unpublished)	Verde River	151	0.0165	<i>G. gulo</i>	0.0087	0.0042
Sousa et al. (Unpublished)	Verde River	151	0.0165	<i>H. intermedius</i>		0.0038
David et al. (2019)	Waikato River	90	0.0022	<i>G. argenteus</i>	0.0007	0.0001
David et al. (2019)	Waikato River	90	0.0022	<i>G. fasciatus</i>	0.0008	0.0001



POEVSr: percentage of the otolith/environmental variability of Strontium isotopes.

Figure 1. Swarm plot of POEVSr (internal/environmental $^{87}\text{Sr}/^{86}\text{Sr}$ range percentage) for movers and sedentary fish in relation to the size of estimated home range areas of different fish species. The grey vertical lines demarcate the 95% random effects confidence interval (28.95%) and the 95% logistic model confidence interval (32%, $p^{\wedge} = 0.95$) to classify the individuals as movers. Dataset authors: 1) Duponchelle et al. (2016); 2) Hauser et al. (2019); 3) Pereira et al. (2019); 4) Tran et al. (2021); 5 and 6) Avigliano et al. (2021); 7) Barroco (2019); 8) Sousa et al. (2016); 9, 10, and 11) Sousa et al. (unpublished); 12 and 13) David et al. (2019).

showing POEVSr values above 30% (Fig. 1). The two models presented below exploit this pattern.

The pooled random-effects model

The meta-analysis indicated a significant heterogeneity ($Q = 508.76$, $p < 0.0001$), and the pooled random effects from the different studies resulted in a mean POEVSr of 12.36% for the distribution of sedentary individuals (Fig. 2).

By adding the meta-analysis' higher confidence interval (16.59%) plus the higher weighted range from the study's means (8.58%), it was expected that 95% of the sedentary individuals would be contained between 0 and 28.95% POEVSr (Fig. 1). Therefore, the interpretation of the meta-analysis indicates that, above 28.95% of POEVSr, there is a low probability of classifying a fish as sedentary and, consequently, a high *a priori* probability of classifying it as a mover.

Even though the random-effects model generated a *cut-off point*, as the minimum POEVSr to indicate a high *a priori* probability of migration/dispersal, it does not consider the

overlap of sedentary individuals and movers below this value. In this regard, a frequentist method for logistical classification probabilities could give us more information.

A logistic model for the dataset

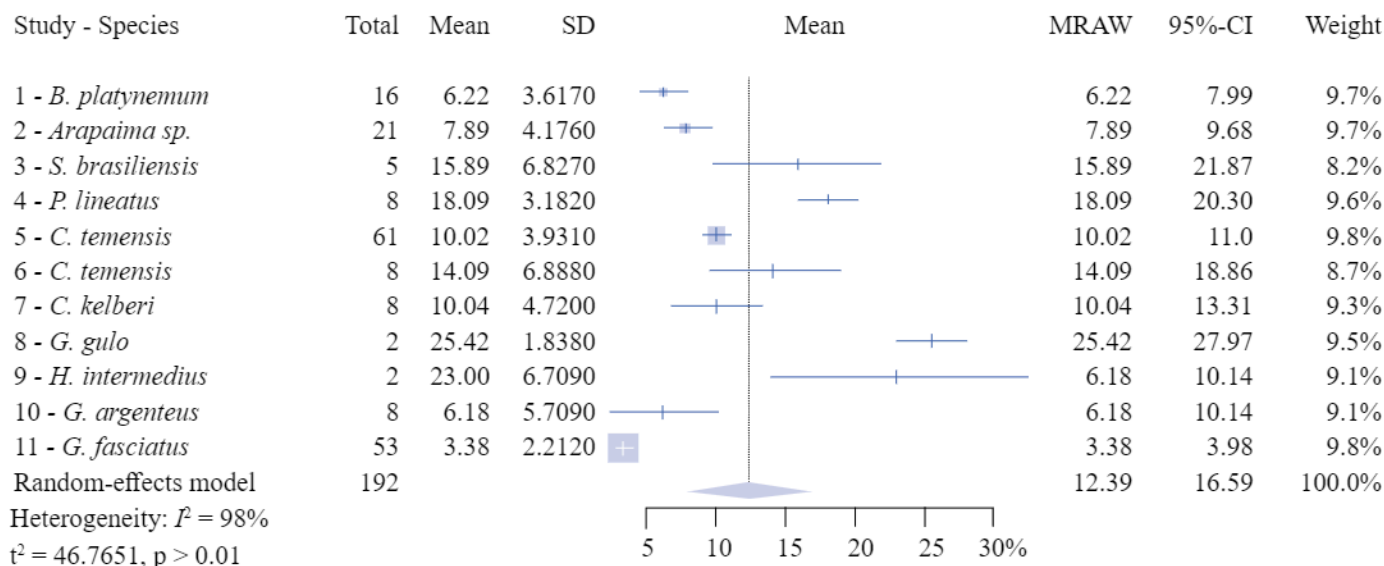
The logistic model indicated a significant correlation ($p < 0.0001$, adjusted $R^2 = 0.703$) between the probability of classifying fish as a mover and an increase in POEVSr. Using logistic regression as a discrete classification tool could correctly predict up to 93.8% of the individuals as either movers or sedentary, based on only the POEVSr value. However, the aim of this study was not to replace the multivariate life-history classification with a simple dichotomy based on POEVSr. Consequently, the best-fit logistic curve also contains (as the result of a function) a continuum of "hat probabilities" ($p^{\wedge}$, from 0 to 1, the Y-axis itself in Fig. 3), in relation to an increase in POEVSr. The output of this logistic function shows a full spectrum of sedentary and mover probabilities for an individual fish in relation to a given POEVSr value. This continuum of probabilities can be applied to formulate life-history hypotheses or even as *a priori* probability for Bayesian inference. The output of the logistic function is available as the Supplementary Material 1.

For a fish with only 8% (recorded in its otolith) of the measured $^{87}\text{Sr}/^{86}\text{Sr}$ environmental variation (POEVSr), the *a priori* probability of being a mover is only 5% ($p^{\wedge} = 0.05$, Fig. 3). When the POEVSr $\approx 20\%$, an equal probability of being either a mover or sedentary individual is expected ($p^{\wedge} = 0.5$), while values of POEVSr $\approx 32\%$ and $\approx 36\%$ give, respectively, 95 ($p^{\wedge} = 0.95$) and 98% ($p^{\wedge} = 0.98$) *a priori* probability of being a mover (Fig. 3).

DISCUSSION

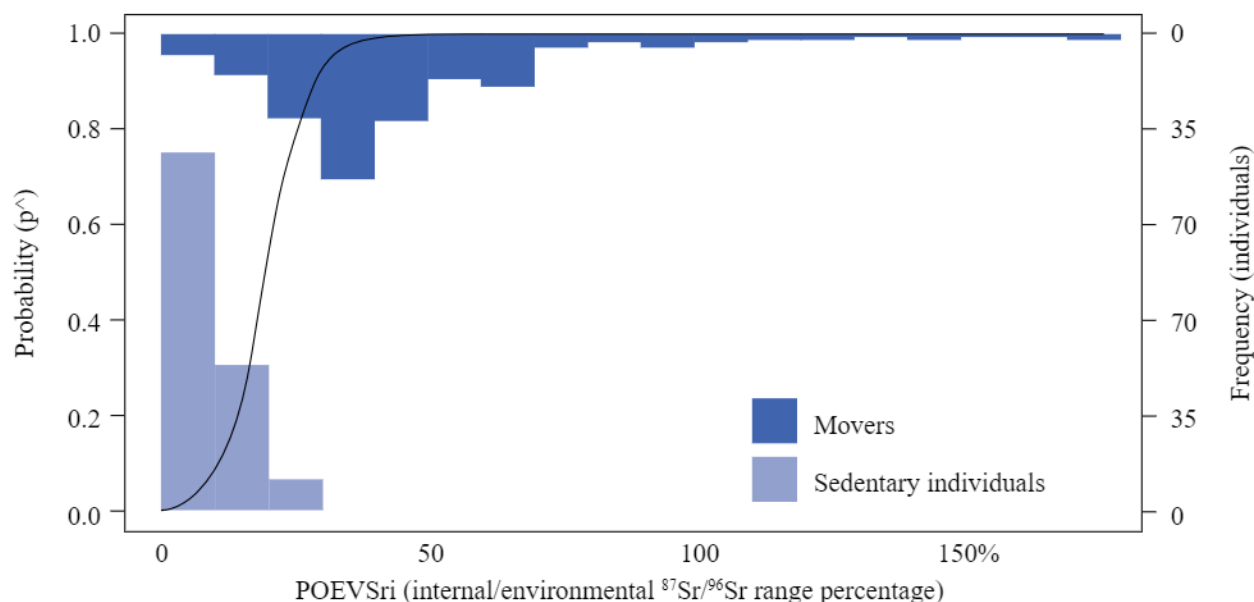
Meta-analyses rely on many criteria, including a balance between published and unpublished data (Fleiss, 1993) to prevent the "file-drawer problem" (Rosenthal, 1979) or the "publication bias" (Field and Gillett, 2010), which refer to a tendency to show and analyze only significant findings and archiving small and inconclusive datasets. This criterion justifies the inclusion of four unpublished datasets in our meta-analysis to approximate the distribution of the real-life data.

It is important to point out that a certain difficulty was encountered in obtaining the raw data for otoliths and environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, or even in getting an answer from most of the contacted researchers. This restricted the amount of data to run our models.



POEVsri: percentage of the otolith/environmental variability of Strontium isotopes.

Figure 2. Forest plot and meta-analysis parameters to represent the pooled random effects of the different datasets, exclusively for sedentary fish. The vertical dashed line shows the pooled mean random-effects POEVsri among the study's means. The rhombus demarcates the confidence interval (95%) of the random-effects pooled mean for sedentary fish. Dataset authors: 1) Hauser et al. (2019); 2) Pereira et al. (2019); 3 and 4) Avigliano et al. (2021); 5) Barroco (2019); 6) Sousa et al. (2016); 7, 8, and 9) Sousa et al. (unpublished); 10 and 11) David et al. (2019).



POEVsri: percentage of the otolith/environmental variability of Strontium isotopes.

Figure 3. Distribution of movers and sedentary fish in relation to the internal/environmental $^{87}\text{Sr}/^{86}\text{Sr}$ range percentage. According to the logistic model for the dataset, the S-shaped grey line shows the probabilities of classifying an individual as a mover.

The resulting dataset provided adequate data to apply diverse approaches, from the classic meta-analysis to logistic models. More importantly, it represents different views on establishing habitat areas, as well as classifying individual fish as either movers or sedentary individuals.

Most of the conclusions about fish habitat areas are often based on multiparameter, evidence-based criteria, such as different isotopes (David et al., 2019; Hauser et al., 2020), salinity (Gillanders, 2005), and genetic markers (Barnett-Johnson et al., 2010; Barroco, 2019). Some studies have used more simple and pragmatic criteria to formulate conclusions, such as Kennedy et al. (2000), who proposed considering “movers as individuals whose $^{87}\text{Sr}/^{86}\text{Sr}$ value was 2 SD from the mean value at a site”. Barroco (2019) considered “active” any individuals whose $^{87}\text{Sr}/^{86}\text{Sr}$ range was greater than 0.005, and all the remaining individuals were classed as sedentary. Sousa et al. (2016) considered an individual sedentary only if its $^{87}\text{Sr}/^{86}\text{Sr}$ variability was lower than 0.01. Although each study used different criteria to distinguish between resident areas and migration/dispersal markers, when the isotopic variability across the otolith rasters was calculated proportionally to the POEVSri, all the datasets showed surprisingly similar distributions.

In this synthesis, it was assumed that all fish incorporate strontium isotopes into the otolith in the same way, irrespective of the species and hydrographic basin. Most studies indicate that the water itself is the primary source of strontium (Farrell and Campana, 1996; Walther and Thorrold, 2006). Therefore, this satisfies the statistical assumption of common causality for the pooled effect meta-analysis (Fleiss, 1993), thereby allowing aggregation of all the data as a single statistical population to run the logistic model.

Meta-analytic pooled random effect versus the logistic model approach

Since significant heterogeneity among the studies may reflect fundamental differences among populations, it was decided to focus on the random-effects model, as indicated by Hedges and Olkin (1983) and Hedges and Vevea (1998).

The logistic distribution model resulted in a more conservative estimation of the minimum POEVSri value (32%) to indicate a high probability of an individual being a mover. Thus, between the two models, it is more reliable to use the logistic prediction, knowing that it has a buffer margin when compared to the low probability of an individual being deemed sedentary by the random-effects model (POEVSri value of 28.95%). This relative consistency indicates that enough samples were grouped to

represent the expected frequentist distribution, even with the variance among the studies.

To apply the POEVSri logistic model in future studies, some practical criteria need to be satisfied, which are discussed in the following topics.

Representative sampling for adequate characterization of environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratio variability in the watersheds

The availability of information on $^{87}\text{Sr}/^{86}\text{Sr}$ values in the study areas varied considerably among the different studies included in this meta-analysis. Avigliano et al. (2021) had bi-seasonal strontium isotopic measurements from 43 different aquatic environments in the La Plata watershed, while Hauser et al. (2019) gathered data from 34 localities in the Amazon basin. Conversely, Barroco (2019) obtained $^{87}\text{Sr}/^{86}\text{Sr}$ results from only four of a total of 14 environmental samples, while Sousa et al. (2016) were unable to obtain any strontium ratio results from water samples that were collected.

Sousa et al. (2016) bypassed the lack of site-based data by using the strontium isotopic ratio in the otoliths of sedentary “young-of-the-year” to represent the local aquatic geochemical signatures from sites where juvenile *C. temensis* were inhabiting. Similarly, Barrow et al. (2021) used otoliths with little isotopic variation to characterize typical $^{87}\text{Sr}/^{86}\text{Sr}$ signatures for each section of the Murray and Darling rivers, which were then compared with otoliths showing more raster variability, indicating migration.

From the studies included in the meta-analysis, strontium isotopic data was obtained at an average of 23 sites per study. Furthermore, it appears that this data was adequately representative of the different study areas to be able to potentially identify the species’ living areas. For instance, in the development of Barroco’s (2019) thesis, the only four environmental strontium isotope data points were very representative of the different stretches of the watershed and were therefore enough to raise hypotheses of home ranges that were confirmed *a posteriori* by population genetics.

Each of the studies used previous knowledge of the geological heterogeneity of the study area, species’ auto-ecology, and natural history to predict routes and important sites to be included in the environmental strontium isotope sampling. For large watersheds, such as the Amazon, La Plata, or the Mekong rivers, obtaining a representative sampling of all possible environmental isotopic variability is almost impossible. Therefore, prior knowledge of the species’ life histories is relied upon to corroborate the data.

Sampling needs to fully represent any spatial-temporal variability, including the geological heterogeneity of the study

area and seasonal differences. In addition, the choice of sampling sites should consider the hydrology and morphology of the basins, as well as the auto-ecology of each species investigated. This will establish the direct correlation between the size of the basin and the required number of samples to generate a representative isotopic map. For example, Brennan et al. (2015) reported seven different chemical signatures in a relatively small basin in Alaska (total area less than 35,000 km²), while Avigliano et al. (2021) reported relatively isotopic signatures with little variability in areas of the La Plata Basin (total area = 3,100,000 km²) that exceeded 45,000 km². Sampling also needs to provide considerable degrees of freedom for univariate or even multivariate analyses, allow for the inclusion of several strategic points in the network of aquatic environments, and maintain a budget for seasonal repetitions of these samplings.

Few studies have recorded intense seasonal or temporal variations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios at given points of a watershed (e.g., Eastin and Faure, 1970; Wei et al., 2013; Santos et al., 2015; Crook et al., 2017). However, when seasonal or temporal variability occurs, it becomes difficult “disentangling the influence of temporal water chemistry variation versus fish movement.” Therefore, “temporally and spatially replicated water samples should be a general requirement for studies that analyze otolith Sr ($^{87}\text{Sr}/^{86}\text{Sr}$, Sr/Ca, Sr/Ba) to make inferences about fish movement and migration” (Crook et al., 2017).

For the Amazon watershed, Santos et al. (2015) collected isotope data over several decades at many stations along the Amazon watershed. They found that the Béni River, in the Amazon Basin, showed significant seasonal variability of strontium isotopes, while other sub-basins varied little between seasons and years. This diverged from the findings of Crook et al. (2017) in Australia, which indicates that site-specific approaches need to be applied to each basin to best characterize seasonal isotopic variability.

Among the studies directly included in this meta-analysis, Duponchelle et al. (2016), Hauser et al. (2019), and Pereira et al. (2019) used and extended the decades of data from Santos et al. (2015), which resulted in the most extensive temporal sampling. In another approach, David et al. (2019) conducted four campaigns from 2014 to 2017 in the lower/middle Waikato River Basin, including one in summer and three in winter. A common strategy utilized in some of the studies included here (Barroco, 2019; Avigliano et al., 2021; Sousa et al., unpublished) is to conduct at least two water collections in contrasting seasons throughout the annual hydrological cycle and to compare the isotopic signatures obtained at each location.

If significant differences are recorded, then it would be necessary to collect more temporal samples to validate this effect.

Crook et al. (2017) stated that as the size and complexity of a watershed increase, temporal $^{87}\text{Sr}/^{86}\text{Sr}$ variability likely increases as well, due to the existence of tributaries with different isotopic values that converge together in the main river. Furthermore, if there are significant variations in the flow of each tributary, temporal $^{87}\text{Sr}/^{86}\text{Sr}$ variability could occur within the scale of magnitude of the tributaries' flow differences. If these biogeochemical changes remain long enough in the aquatic environment for absorption into a fish otolith, they become recorded and indistinguishable from spatial displacements of the fish (Crook et al., 2017), at least without a multivariate approach for the final models.

Due to localized rainfall in only part of the basin, this can result in temporary biogeochemical changes downstream that are difficult to measure or even detect. These fluctuations are likely part of the “noise” that we find along the raster when reading the otolith rings, even in sedentary specimens. Therefore, when formulating hypotheses about the life history of specimens, it is essential to consider that the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of a given river basin is not a fixed or a weighted average of its tributaries, but a mixture of varying flows that change seasonally.

Species' age when considering migration and dispersal

Different studies included in this meta-analysis have considered the minimum age criteria for either migration or dispersal in respective fish species. Some species may migrate very early between the larval and juvenile stages (David et al., 2019), while others remain in a river sub-basin for most of their lives. However, the latter may still move significant distances upstream upon reaching reproductive age (called “homing”), with the offspring then migrating back downstream (Duponchelle et al., 2016).

The POEVSri, as presented here, considered only the total isotopic variability found in an otolith, which is the difference between the highest and lowest $^{87}\text{Sr}/^{86}\text{Sr}$ values. However, for species' otoliths showing demarcations between distinct living areas for different life phases (such as post-larvae and juvenile), applying a different POEVSri to each phase or comparing them in a single index is possible. In this approach, it would be possible to differentiate the behavior in each phase, finding a low POEVSri within each life phase, notably when there is no significant migration, and a high POEVSri between phases, especially if accompanied by migration.

A minimal level of knowledge of each species' biology is required to apply the present model (and any other model)

when determining habitat areas based on isotopic signatures. Conducting a radio or acoustic telemetry study in conjunction with isotopic studies to validate understanding about their life cycles would be very useful. This approach to individual specimens could provide more detail on their respective home ranges and habitats than population genetic studies.

Size of study areas and watersheds

In the meta-analysis, it was decided to simply use the maximum linear length of each study area in order to describe its size. Other correlated parameters, such as drainage area, river discharge, and maximum connectivity distance (as presented in Avigliano et al., 2021) are affected by variables such as topography, rainfall, and sinuosity, which add unnecessary complexity to fit into the model.

No significant correlation was found between the model and the size of study areas, which varied from hundreds to thousands of kilometers in length (Table 1, Fig. 1). Although it is expected that variability in watershed size would correlate well with isotopic environmental heterogeneity, it appears that other factors influence as well.

If a study area involves a mixing gradient of water from tributaries with different geochemistry parameters, which also might vary seasonally, some fish would acquire most of the different $^{87}\text{Sr}/^{86}\text{Sr}$ signatures, even if they were sedentary. Consequently, their rasters would show signatures analogous to migration, even if their movements are limited.

For example, when considering the mixing of sediment-laden and black waters in the Amazon Basin, Bouchez et al. (2010) found poor mixing of the Purús (blackwater) and Solimões (sediment-laden) rivers extending up to 100 kilometers downstream of their confluence, even after turbulence, islands, and bends. However, for long-range migratory fish species, which pass through many different mixing gradients and show substantial isotopic heterogeneity, it is possible to discern their life history amidst the “noise” in the otoliths’ rasters, as described in Duponchelle et al. (2016) and Hauser et al. (2019).

On a different scale, although river stretches of up to ten of kilometers may show some homogeneity in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, significant variation in fish isotopic signatures is still needed to correlate their home range to the environmental signature. Although the study area in David et al. (2019) involved a spatial scale of less than 100 km and showed relatively little $^{87}\text{Sr}/^{86}\text{Sr}$ variability, the use of multiparametric models, as well as considerable prior knowledge about the fish’s biology and natural history, was of enormous benefit. For these authors, knowing that *Galaxias* spp. become territorial between juvenile and adult stages

was very important when designing the home-range hypothesis. Nonetheless, while the authors developed the model using several trace elements, it was only validated using $^{87}\text{Sr}/^{86}\text{Sr}$.

The “caution bias”

In reviewing studies included in the meta-analysis, it was found that some authors have been overly cautious, classifying movers (including migrators) and sedentary individuals (or residents) only those individuals whose otoliths showed clear and explainable life histories. Therefore, some studies did not sort some individuals according to their models. For example, Hauser et al. (2019) identified only 49 individuals of 58 *Brachyplatystoma platynemum* as migrators or residents. Avigliano et al. (2021) classified only 25 of 30 *Prochilodus lineatus* individuals as migrators or residents. Although *B. rousseauxii* is known as a long-range migratory species, Duponchelle et al. (2016) only identified 19 of 37 individuals as migrators in the cases in which the only possible hypothesis to explain the life-history indicators contained in the otoliths were homing behavior, (or) inter-basin straying or inter-basin multiple runs.

While caution is entirely understandable when describing life histories using ecogeochemistry, it represents a bias within the metadata. Consequently, the generated model then retained this conservative bias, which classified fish individuals based on high confidence in their life histories. Without this “caution bias,” the cut-off probabilities to define a mover fish *a priori* would be subtly different, as we would see a little more overlap between movers or residents and a more considerable standard deviation of those categories. However, as most of the caution bias is based on the need to combine multivariate parameters, models, hypothesis definitions, and strontium isotopic analysis to confirm classification, the reticent approach is well justified.

CONCLUSIONS

The meta-analysis combining unpublished data and a literature review revealed patterns in classifying fish as movers or residents according to variability in strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios in their otoliths as a percentage of the isotopic environmental variability. This percentage (POEVsri index) indicates the intensity of a fish movement in each study area.

The spatial and temporal analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ variability in otoliths to determine fish movement has good application for fish conservation purposes, especially when the environmental signatures correlate well. However, studies require adequate sampling for spatial and temporal of environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratio variability in the watersheds, to differentiate the effects

of these dimensions. Researchers should also consider species biology and life history to utilize the whole information recorded in otoliths (as in this study) or select regions of interest to analyze a single life phase through application of the POEVSri. For each new study, all the causality and orthodox conceptual criteria still need to be addressed to test the life-history hypothesis.

Once these requirements are satisfied, an otolith containing more than 32% internal/environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratio variability (POEVSri) may be considered as prevenient from a mover fish until proven otherwise. In the same way, a fish showing POEVSri less than 8% may be considered as sedentary until proven otherwise. Between those values, the logistic model presented a gradient of probabilities of a given fish being a mover or sedentary, with equal odds when POEVSri is approximately 20%. The presented logistic progression of mover probabilities can spot most individuals as *a priori* movers or *a priori* residents for Bayesian and Popperian *a posteriori* approaches in future studies.

CONFLICT OF INTERESTS

Nothing to declare.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

ACKNOWLEDGEMENTS

We are thankful to Fibracón Consultoria Perícias e Projetos Ambientais LTD, who sampled fish, water and data for the unpublished dataset presented here. We are also very grateful to DSc. Bruno O. David, from Waikato Regional Council, for his complete dataset on fish in the Waikato River, as well as for checking the manuscript and providing criticism, which greatly enriched the discussion of this study.

FUNDING

R&D/Aneel Portfolio, Itiquira Energética S.A., Tangará Energética S.A. and Brookfield Renewables Partners L.P.

Grant No: PD-00700-0119/2019

AUTHORS' CONTRIBUTIONS

Conceptualization: Rosa FR, Sousa RGC; **Data curation:** Rosa FR; **Formal Analysis:** Rosa FR, Sousa RGC; **Investigation:** Rosa FR, Avigliano E, Sousa RGC; **Methodology:** Rosa FR, Duponchelle F, Pereira LA, Hauser M, Barroco LSA, Freitas CEC, Sousa RGC; **Funding acquisition:** Rosa FR, Sousa RGC;

Supervision: Rosa FR, Sousa RGC; **Project administration:** Rosa FR, Sousa RGC; **Writing – original draft:** Rosa FR, Avigliano E, Duponchelle F, Pereira LA, Hauser M, Barroco LSA, Freitas CEC, Sousa RGC; **Writing – review & editing:** Rosa FR, Avigliano E, Duponchelle F, Pereira LA, Hauser M, Barroco LSA, Freitas CEC, Sousa RGC; **Final approval:** Rosa FR.

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Table S1. Inputs (POEVsri) and outputs ($p^{\wedge}$) for the best-fit logistic function.

POEVsri (%)	mover $p^{\wedge}$ (p hat probabilities)	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers	POEVsri (%)	$p^{\wedge}$ for movers
0	0,007	0	0,007	10	0,081	20	0,512	30	0,926	40	0,993	50	0,999	60	0,100	70	0,100
1	0,009	1	0,009	11	0,101	21	0,574	31	0,941	41	0,995	51	0,100	61	0,100	71	0,100
2	0,012	2	0,012	12	0,126	22	0,633	32	0,954	42	0,996	52	0,100	62	0,100	72	0,100
3	0,015	3	0,015	13	0,156	23	0,688	33	0,963	43	0,997	53	0,100	63	0,100	73	0,100
4	0,020	4	0,020	14	0,192	24	0,739	34	0,971	44	0,998	54	0,100	64	0,100	74	0,100
5	0,025	5	0,025	15	0,233	25	0,784	35	0,977	45	0,998	55	0,100	65	0,100	75	0,100
6	0,032	6	0,032	16	0,280	26	0,823	36	0,982	46	0,998	56	0,100	66	0,100	76	0,100
7	0,040	7	0,040	17	0,333	27	0,856	37	0,986	47	0,999	57	0,100	67	0,100	77	0,100
8	0,051	8	0,051	18	0,390	28	0,884	38	0,989	48	0,999	58	0,100	68	0,100	78	0,100
9	0,064	9	0,064	19	0,450	29	0,907	39	0,991	49	0,999	59	0,100	69	0,100	79	1