

# Ichthyofauna on the move: fish colonization and spread through the São Francisco Interbasin Water Transfer Project



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Projects on river basin integration are keen social-economical drivers in dry regions like the Brazilian semiarid, however, there are concerning ecological impacts implied in those projects. In a long-term analysis, ichthyofauna colonization and spread through the East Axis of the São Francisco River Integration Project (SFIP) was monitored to assess possible impacts on the receiving Paraíba River basin. The fish were collected semiannually (2012 to 2021) from 19 sites in the São Francisco (SF) and Paraíba (PB) basins. A total of 69 fish species were recorded, with distinct fish assemblages between SF (n = 50), PB (n = 35), and the SFIP artificial reservoirs (n = 25). The SFIP reservoirs were colonized by species from the donor basin (SF). In a pioneer finding, *Anchoviella vaillanti* was recorded for the first time in the receiving basin and it is in the process of establishment. The two SF species that reached PB through the SFIP canals (*A. vaillanti* and *Moenkhausia costae*) may be using their year-round reproduction and wide diet to successful spread and colonize the new environment. Since we detected species with potential to reach the receiving basin and became invasives, the implementation of barriers to contain their spread are recommended.

**Keywords:** *Anchoviella vaillanti*, Brazilian Semiarid, Paraíba do Norte River basin, Rivers Interlinking Project, Species introduction.

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Projetos de integração de bacias hidrográficas são socialmente importantes em regiões como o semiárido brasileiro, porém há impactos ecológicos preocupantes implícitos nesses grandes projetos de infraestrutura. A colonização e dispersão da ictiofauna pelo Eixo Leste do Projeto de Integração do Rio São Francisco (PISF) foi monitorada para avaliar possíveis impactos na bacia receptora do rio Paraíba do Norte. Os peixes foram coletados semestralmente (2012 a 2021) em 19 locais das bacias do São Francisco (SF) e Paraíba (PB). Foram registradas 69 espécies de peixes, sendo 50 nos pontos do SF, 25 nos reservatórios artificiais ao longo do PISF e 35 nos pontos do PB. As assembleias de peixes das bacias do SF, PB e dos reservatórios do PISF foram significativamente distintas. Os reservatórios do PISF foram colonizados por espécies provenientes da bacia doadora (SF). *Anchoviella vaillanti* foi registrada pela primeira vez na bacia receptora do PB e está em processo de estabelecimento. As duas espécies do SF que chegaram ao PB pelos canais do PISF (*A. vaillanti* e *Moenkhausia costae*) apresentaram dieta e estratégias reprodutivas que permitem o sucesso na disseminação e colonização. Uma vez que foram detectadas espécies com potencial de atingir a bacia receptora, recomenda-se o monitoramento e manejo contínuos.

**Palavras-chave:** *Anchoviella vaillanti*, Bacia do rio Paraíba do Norte, Introdução de espécies, Projeto de Interligação de Rios, Semiárido Brasileiro.

## INTRODUCTION

River basin integration projects have been implemented worldwide to complement water supply for human and animal use, irrigation projects, and/or industrial activities (Davies *et al.*, 1992; Das, 2006; Qin *et al.*, 2019). In general, the goal is to redistribute water in order to alleviate the imbalance between supply and demand for water resources, especially in arid and semi-arid regions (Grant *et al.*, 2012; Zhuang, 2016). Regardless of the purpose for which the project was designed, there are two common universal characteristics: high structural and functional complexity, and generate questions about environmental sustainability (Das, 2006).

According to Lévêque *et al.* (2008), the Brazilian Northeast region is recognized for harboring one of the biggest gaps in terms of ichthyofauna knowledge and also faces strong environmental pressures that can lead to a decline in populations and communities (Collen *et al.*, 2013). The pressures involve, for example, rainfall scarcity, habitat loss, the introduction of non-native species (Langeani *et al.*, 2009), the construction of artificial reservoirs (Rebouças, 1997), and more recently, the construction of the São Francisco Interbasin Water Transfer (SF-IWT) system that transfers part of the waters from the São Francisco River to different receiving basins in the semiarid region.

During inter-basin water transfer projects, one of the major concerns is to continuously assess the environmental impacts, especially the interchange of aquatic organisms between the donor and the receiving basins (Meador, 1992; Rahel, 2007). Species introduction and the integration of watersheds are among the factors that most threaten the conservation of ichthyofauna in the world (Dudgeon *et al.*, 2006; Pittock *et*

*al.*, 2009; Pelicice *et al.*, 2017; Dudgeon, 2019; Albert *et al.*, 2020) and, more specifically, in the Brazilian Northeast semi-arid region (Albuquerque *et al.*, 2012). The ecological consequences of introducing non-native species into a river basin are, among others, the loss of native biodiversity and fishery resources, the spread of pathogens, trophic alterations, and biotic homogenization (Davies *et al.*, 1992; Arismendi *et al.*, 2009; Gozlan *et al.*, 2010; Grant *et al.*, 2012; Vitule, Prodocimo, 2012; Simberloff, Vitule, 2014; Vitule *et al.*, 2019; Geller *et al.*, 2021).

According to Berbel-Filho *et al.* (2016), the biotic homogenization of the ichthyofauna is one of the probable environmental impacts of the São Francisco River Integration Project and may also pose a danger to rare and/or threatened species in the receiving basins. Brito *et al.* (2020) discuss that the homogenization of ichthyofauna, sometimes caused by the introduction of non-native species, has been an obstacle to the maintenance of native fish species, especially in semiarid regions. Currently, the São Francisco and Paraíba do Norte River basins share less than 25% of native species among themselves (Silva *et al.*, 2020), and the interchange of non-native cosmopolitan species may cause additional pressure on native and endangered species (Misra *et al.*, 2007; Gallardo, Aldridge, 2018). Therefore, it is essential to conduct ecological studies to assess possible impacts on native fishes in water transfer projects, in addition to measuring homogenization, invasion capacity (Blackburn *et al.*, 2011; Hui *et al.*, 2016; Pereyra, 2016), and environmental invasibility (Ricciardi, Cohen, 2007).

The Study of Environmental Impacts (SEI - Brasil, 2004), a mandatory document presented before the implementation of mega infrastructure projects in Brazil, predicted the mixing of fish communities between the donor (São Francisco) and the receiving (Paraíba do Norte) basins as a consequence of the SF-IWT implementation. Moreover, in the SEI it was reported the possible depletion of native fish populations in receiving hydrographic basins (Andrade *et al.*, 2011). Studies that could fill up the gaps in species diversity, ecology, and niche occupation are important and necessary in the Brazilian Northeast, not only to supplement the ichthyofauna community data but also to assess the possible impacts of the ecological changes during the SF-IWT project. Specifically, long-term studies that evaluate the changes in fish assemblages on the integrated basins, the species interchange, and describe the temporal events occurring in a water transfer system. Those studies are yet scarce, even though they are fundamental tools to improve management, conservation, and impact mitigation on ichthyofauna.

To detect the possible changes in the fish communities caused by the integration of the São Francisco and Paraíba do Norte River basins, this study presents the results of a decade of ichthyofauna monitoring in the SF-IWT East Axis. We present data to supplement the species list of the São Francisco and Paraíba do Norte Rivers, report the fish colonization in the artificial SF-IWT canals, investigate the fish dispersion from the donor to the receiving basin through the canals, and the occurrence of São Francisco basin endemic species in the Paraíba do Norte basin. The status of the species translocated by SF-IWT is analyzed, as well as the risk of introducing other fish species from the São Francisco River into the receiving basin. Finally, the feeding and reproduction behavior of two translocated species are described to characterize the species' invasiveness.

## MATERIAL AND METHODS

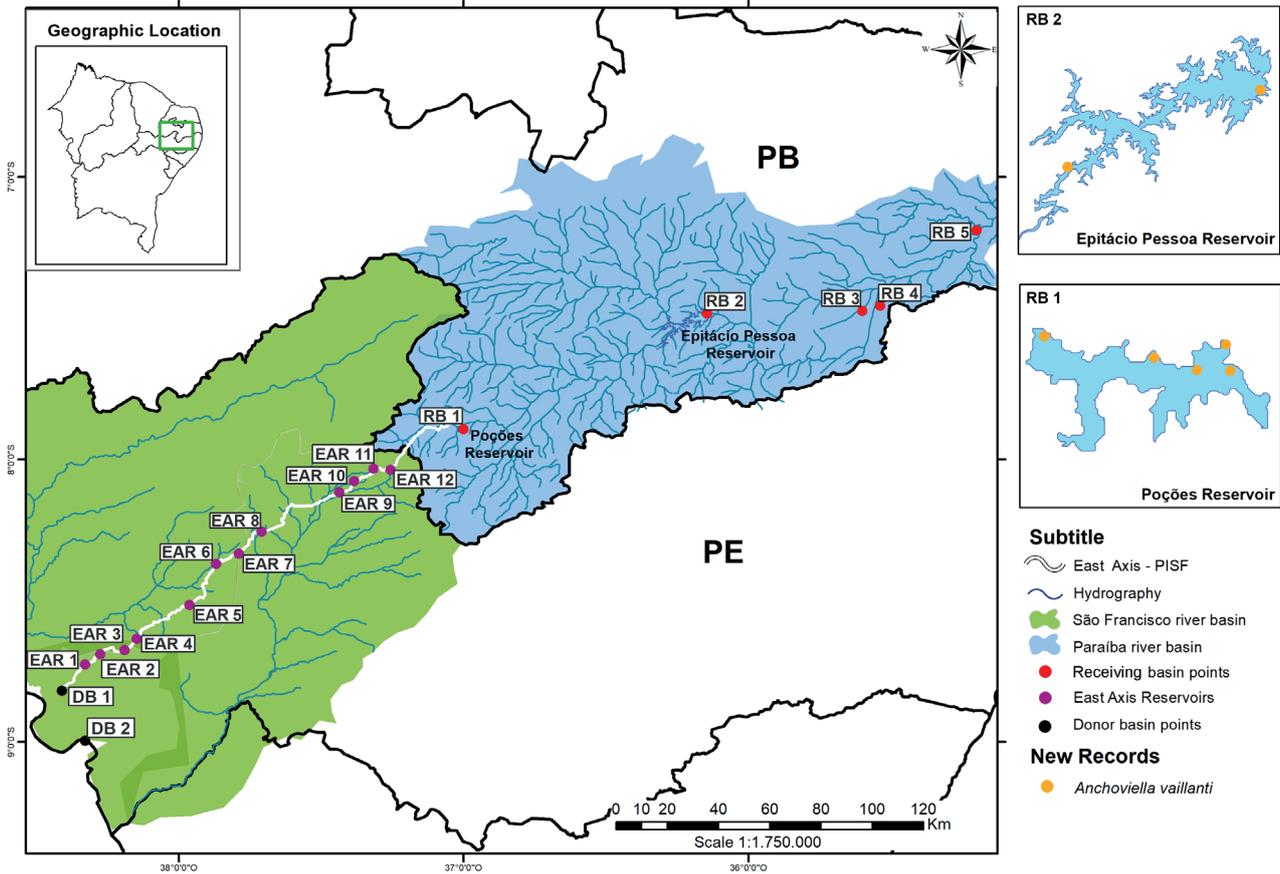
**Study area.** The São Francisco Interbasin Water Transfer (SF-IWT) to the Northeastern Hydrographic Basins Project is the largest water infrastructure project in Brazil. The enterprise is divided into two main axes (North and East Axis) that aim to guarantee the water security of 12 million people in 390 municipalities in the Caatinga biome, covering the states of Pernambuco, Ceará, Rio Grande do Norte, and Paraíba (Brasil, 2004). The operationalization of the system is intended to result in the improvement of the Jaguaribe (Ceará), Apodi-Mossoró (Rio Grande do Norte), Piranhas-Açu (Paraíba and Rio Grande do Norte), Pajeú, Moxotó, Brígida, and Terra Nova (Pernambuco) River basins (Brasil, 2004).

The Caatinga region of Northeastern Brazil, where SF-IWT is located, has semiarid climate, with average temperatures ranging from 25° to 30°C, and reaching higher temperatures during the dry season (Brasil, 2004; Albuquerque *et al.*, 2012). The short rain periods are concentrated from January to May (rainy season). The average rainfall of 600 mm annually in this region is very low compared to 1,900 mm in the Southeastern Brazil, for example. As a result, rivers of the Caatinga biome are, for the most part, intermittent, as they can be completely dry for several months or even years (Brasil, 2004). As geographical reference, we use the freshwater ecoregions proposed by Abell *et al.* (2008).

The fish specimens were caught from 19 sampling sites between August 2012 and December 2021, during the SF-IWT East Axis Installation (between 2012 and 2017) and Operation (2018–currently; Brasil, 2018) phases, within the limits of the São Francisco (SF) and Paraíba do Norte (PB) basins (Fig. 1; Tab. S1). The monitoring campaigns were conducted every six months (once in the dry and once in the rainy period) in two locations of the Itaparica Reservoir (donor basin – DB – São Francisco River; Fig. S2 A–B) and five locations in the Paraíba do Norte River basin (receiving basin – RB; Fig. S2 G–J). In addition to these, all the 12 artificial reservoirs along the East Axis (EAR) were monitored after their filling (Fig. S2 C–F). The first reservoir in the East Axis (Areias Reservoir – EAR 1; Fig. S2 C) was sampled for the first time in March 2015, while the last reservoir (Barro Branco Reservoir – EAR 12; Fig. S2 F) was sampled for the first time in December 2017.

A three-days-sampling effort was conducted on all analyzed sites. For sites located in the donor basin, there was a total of 16 three-days-sampling. On the receiving basin, 12 three-days-sampling were conducted in each of the five sites monitored, five samplings occurred before the water input from the SF-IWT and seven after. For all 12 artificial reservoirs, there were different sampling sizes because the filling date of each reservoir varied, meaning that the SF-IWT waters reached those reservoirs at different dates. The sampling effort employed in the 12 artificial reservoirs ranged from five to 12 three-days-sampling, depending on the filling date. Eight reservoirs had five samplings (EARs 2, 3, 4, 6, 7, 9, 10, 11), three reservoirs had eight samplings (EARs 5, 8, 12), and 12 samplings were conducted at oldest reservoir, Areias (EAR 1).

**Capture, processing, and preservation of biological material.** Six fishing methods were applied, including five actives: trawl (10 m long, 5 mm mesh), sieve (60 cm diameter, 5 mm mesh), cast nets (mesh sizes of 15 and 30 mm between adjacent knots), hand net



**FIGURE 1** | Schematic representation containing the monitored sites along the East Axis of the São Francisco River Integration Project (SF-IWT) and the exact location of the new records of *Anchoiella vaillanti* in the Poções and Epitácio Pessoa Reservoirs. DB = Donor basin, EAR = East Axis Reservoirs, RB = Receiving basin. Detailed location list of the sampling sites in Tab. S1.

(40 mm/side rectangular base, 5 mm mesh), and ichthyoplankton conical net (300 µm mesh); and one passive method: gill nets (10 or 50 m long with mesh sizes of 20, 30, 40, 50, 60, and 80 mm between adjacent knots). For each site, it was established a minimum of active capture attempts for the four active methods, except ichthyoplankton: three times per day, totalizing at least nine times per site (three days per site). Additional attempts were added if different species kept being caught. For ichthyoplankton, sampling occurred once during the daytime (around 8 am) and once at night-time (around 6 pm), for 10 min per period in each site. The net was positioned in areas of higher river flow or dragged by the boat at low speed (in reservoirs), and kept both in the surface water and around 3 m deep for 10 minutes each. Total ichthyoplankton effort was 40 min per site. Gill nets were kept overnight (12–14 h). Photographic records of specimens collected by local fishermen were also taken into consideration (Tab. 1). Collected specimens were euthanized by overexposure to 1 g/mL clove oil (based on MCTI – CONCEA, 2018), fixed in a 10% formaldehyde solution and preserved in 70° GL alcohol. Vouchers were deposited in the Ichthyological Collection of the Museu de Fauna da Caatinga (MFCI), Universidade Federal do Vale do São Francisco (UNIVASF).

**Reproductive and dietary analysis of non-native species.** Supplementary analyzes were conducted for the SF translocated species *Anchoviella vaillanti* (Steindachner, 1908) and *Moenkhausia costae* (Steindachner, 1907), both captured in the receiving basin, to assess the ecological niche. Diet data were analyzed using the Alimentary Index - IAI (Kawakami, Vazzoler, 1980), while reproduction data was evaluated through macroscopic visualization of the gonads and Gonadosomatic Index - GSI (Vazzoler, 1996). Sixty individuals of *M. costae* were analyzed in RB 1 (15 in the dry season and 45 in the rainy season) and 60 individuals of *A. vaillanti* in RB 1 (15 in the dry season) and RB 2 (45 in the dry and rainy seasons). There were not enough specimens of *A. vaillanti* to be analyzed in RB 1 during the rainy seasons. All dissected specimens were used in both reproductive and dietary analyses.

**Terminology, taxonomic classification, and conservation status.** The species were identified according to Britski *et al.* (1988) and Ramos *et al.* (2018), complemented by reviews of some taxonomic groups. Larvae specimens were identified according to Nakatani *et al.* (2001) and Silva *et al.* (2010). The nomenclature and systematic classification of species were based on Betancur-R *et al.* (2017) and Fricke *et al.* (2022). The definition of endemic species was based on Reis *et al.* (2003), Rosa *et al.* (2003), Barbosa *et al.* (2017), Lima *et al.* (2017), and Silva *et al.* (2020).

The geographical distribution data and historical records of the species were obtained from SpeciesLink (<https://specieslink.net/>), SiBBR (Sistema de Informação sobre a Biodiversidade Brasileira, <https://www.sibbr.gov.br>), Portal da Biodiversidade (<https://portaldabiodiversidade.icmbio.gov.br/>), and GBIF (Global Biodiversity Information Facility, <https://www.gbif.org>). The endangered species were assessed using the Livro Vermelho da Fauna Brasileira Ameaçada de Extinção updated list (MMA, 2022).

**Data analysis.** A Venn diagram was generated to illustrate the species' data logical relationships between the three regions (SF, EAR, PB) (<https://bioinformatics.psb.ugent.be/webtools/Venn/>). The seriated ordination of species based on appearance events consists of a presence/absence matrix, with sampling sites in columns and taxa in rows. This analysis was performed using PAST 3 software (Hammer *et al.*, 2001). To indicate the groups affected by the SF-IWT project, the conservation status, origin, adaptability, habitat usage, and trophic ecology data were considered.

Changes in the fish community across studied regions (DB-SF, RB-PB, and EAR) were evaluated using the Bray-Curtis similarity index, observing matrices of dissimilarity. Abundance data was log-transformed to mitigate high-abundance species bias. Analysis of Similarity (ANOSIM) was used to compare the dissimilarity matrices, evaluating whether there were differences in fish communities between regions for richness and abundance. The ANOSIM analyses the variance and multivariate differences in groups through permutations (Clarke, Gorley, 2006).

Spatial beta diversity was analyzed by partitioning diversity into LCBD (Local Contribution to Beta Diversity) and Species Contribution to Beta Diversity (SCBD) components of species richness difference and species replacement (Legendre, 2014), using Podani's family indices. This analysis allows us to assess species and sites that contribute to beta diversity (Legendre, Caceres, 2013). Presence-absence data determined the composition of species in the basin, while abundance data provided insights on the degree of occupation of each location. The data was previously Hellinger transformed

to limit the relevance of rare species. High LCBD values indicate strong differences in species composition from the mean sites. LCBD is partitioned into components of Replacement and Abundance/Richness Difference. Meanwhile, SCBD indicates important species for overall local diversity.

Richness, abundance, and Shannon diversity were included as variables to find the best explanatory model for fish assemblage. Modeling was conducted via stepwise selection by the Akaike information criterion (AIC) until the minimum adequate model was obtained (Crawley, 2013). The explanatory variables ‘abundance’ and ‘Shannon diversity’ were excluded from analysis due to collinearity issues, leaving ‘richness’ as the only explanatory variable in the final model. Data was analyzed using a Canonical Analysis of Principal coordinates (CAP). The CAP allows the detection of linear relationships on (dis)similarities matrices, highlighting the relative contribution of predictor variables to the fish assemblages (Legendre, Anderson, 1999). The dissimilarity based on the matrix obtained by Bray–Curtis distance was tested using PERMANOVA for explanatory variables, with 999 permutations.

To verify the stabilization trends of non-native species populations in the receiving basin, the G test was used to assess whether there is a significant difference ( $\alpha = 0.05$ ) between the sampling abundances of the species transposed to stretches of the Paraíba do Norte River.

The main statistical analysis were performed in R software 4.1.2 (R Development Core Team, 2021) using functions available in the package Vegan (Oksanen *et al.*, 2013). For beta diversity analysis, the Adespatial package (Dray, 2021) was used. Models were run using the MASS package (Ripley *et al.*, 2013). The plots and map (Fig. 5) came from package ggplot2 (Wickham, 2006).

To compare the diet of the non-native species on PB (*Anchoviella vaillanti* and *Moenkhausia costae*) over the seasons (rainy and dry), fish stomach volume was analyzed. Data were log-transformed prior to the analysis. Species diet and season groups were sorted by Non-metrical Multidimensional Scaling analysis (NMDS) using the Bray–Curtis similarity index and compared by the similarity analysis test (ANOSIM). The similarity percentage analysis (SIMPER) was used to evaluate which food item contributed most to the differentiation of the groups. The NMDS, ANOSIM, and SIMPER tests were performed on Primer 6 & Permanova software (Clarke, Gorley, 2006). The average GSI for each gonadal stage was compared using analysis of variance (ANOVA; Tukey’s post hoc), with a significance level of  $\alpha < 0.05$ .

## RESULTS

A total of 89,372 specimens, distributed in 69 species, 24 families, and eight orders were recorded. At the two sites on the São Francisco River, 50 species were recorded, 25 in the artificial reservoirs along the East Axis, and 35 in the Paraíba do Norte River basin (Tab. 1). Characidae was the most representative family, with 16 species, followed by Cichlidae with seven species, and Loricariidae represented by six species. The majority of small-sized fish were captured with trawls, sieves, and cast nets, while medium- and large-sized individuals were caught with gill nets.

**TABLE 1** | List and respective occurrences and abundances of species recorded during the SF-IWT Ichthyofauna Monitoring. The Origin column indicates native (N), endemic (E) and non-native species (NN) considering the hydrographic ecoregions of São Francisco (SF) and Northeastern Caatinga and Coastal Drainages (NCCD). SL = standard length (mm).

Taxa	Origin	São Francisco basin	East Axis Reservoirs	Paraíba do Norte basin	SL (min–max)	Voucher	Abundance (Adults / Juveniles)
<b>CLUPEIFORMES</b>							
<b>Engraulidae</b>							
<i>Anchoviella vaillanti</i> (Steindachner, 1908)	E (SF)	X	X	X (NN)	24–78	MFCI 3317 MFCI 6196 MFCI 8280	8783
<b>CHARACIFORMES</b>							
<b>Crenuchidae</b>							
<i>Characidium bimaculatum</i> Fowler, 1941	N			X	19–35	MFCI 2336	1012
<b>Erythrinidae</b>							
<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	N			X	216	MFCI 8287	1
<i>Hoplias intermedius</i> (Günther, 1864)	N	X			325	MFCI 2148	2
<i>Hoplias gr. malabaricus</i> (Bloch, 1794)	N	X	X	X	23–330	MFCI 3279 MFCI 6660 MFCI 7012	449
<b>Parodontidae</b>							
<i>Apareiodon davisi</i> Fowler, 1941	E (NCCD)			X	16–72	MFCI 1287	198
<b>Serrasalminidae</b>							
<i>Metynnis lippincottianus</i> (Cope, 1870)	NN	X	X		11–137	MFCI 3282 MFCI 7827	644
<i>Myleus micans</i> (Lütken, 1875)	E (SF)		X		75	Not Deposited	1
<i>Piaractus mesopotamicus</i> (Holmberg, 1887)	NN	X			592	Not Deposited	1
<i>Pygocentrus piraya</i> (Cuvier, 1819)	E (SF)	X			30–340	MFCI 3211	21
<i>Serrasalmus brandtii</i> Lütken, 1875	N	X	X		11–230	MFCI 1566 MFCI 7868	967
<i>Serrasalmus cf. rhombeus</i> (Linnaeus, 1766)	N	X			200–220	MFCI 1568	6
<b>Anostomidae</b>							
<i>Leporinus piau</i> Fowler, 1941	N			X	14–186	MFCI 1143	321
<i>Leporinus taeniatus</i> Lütken, 1875	N	X	X		180–190	MFCI 6142	2
<i>Megaleporinus reinhardti</i> (Lütken, 1875)	N	X			225	MFCI 9334	2



TABLE 1 | (Continued)

Taxa	Origin	São Francisco basin	East Axis Reservoirs	Paraíba do Norte basin	SL (min-max)	Voucher	Abundance (Adults / Juveniles)
<b>Curimatidae</b>							
<i>Curimatella lepidura</i> (Eigenmann & Eigenmann, 1889)	N	X			135–140	Not Deposited	4
<i>Psectrogaster rhomboides</i> Eigenmann & Eigenmann, 1889	N			X	175–182	Not Deposited	40
<i>Steindachnerina notonota</i> (Miranda Ribeiro, 1937)	N			X	77–112	MFCI 2140	517
<b>Prochilodontidae</b>							
<i>Prochilodus argenteus</i> Spix & Agassiz, 1829	E (SF)	X			500–635	Not Deposited	2
<i>Prochilodus brevis</i> Steindachner, 1875	N			X	21–275	MFCI 8730	42
<i>Prochilodus costatus</i> Valenciennes, 1850	E (SF)	X			360	MFCI 3348	1
<b>Triporthidae</b>							
<i>Triporthus guentheri</i> (Garman, 1890)	E (SF)	X	X		26–37	MFCI 3360 MFCI 7149	7
<i>Triporthus signatus</i> (Garman, 1890)	N			X	142–170	MFCI 5795	133
<b>Iguanodectidae</b>							
<i>Bryconops cf. affinis</i> (Günther, 1864)	N	X	X		52–103	MFCI 3296 MFCI 8658	1102
<b>Acestrorhynchidae</b>							
<i>Acestrorhynchus britskii</i> Menezes, 1969	E (SF)	X			72–115	MFCI 3188	4
<i>Acestrorhynchus lacustris</i> (Lütken, 1875)	N	X	X		18–100	MFCI 6855	5
<b>Characidae</b>							
<i>Astyanax bimaculatus</i> (Linnaeus, 1758)	N			X	14–72	MFCI 1290	4048
<i>Astyanax lacustris</i> (Lütken, 1875)	N	X	X		23–58	MFCI 3316 MFCI 6179	9993
<i>Compsura heterura</i> Eigenmann, 1915	N	X		X	23–32	MFCI 3383 MFCI 2151	729
<i>Hemigrammus brevis</i> Ellis, 1911	E (SF)	X	X		12–22	MFCI 8929	4048
<i>Hemigrammus gracilis</i> (Lütken, 1875)	N	X			14–24	MFCI 1506	783
<i>Hemigrammus marginatus</i> Ellis, 1911	N	X	X	X	28–36	MFCI 0185 MFCI 8750 MFCI 1238	20329
<i>Hemigrammus rodwayi</i> Durbin, 1909	N			X	17–29	MFCI 8529	661
<i>Hyphessobrycon cf. parvulus</i> Ellis, 1911	N			X	17–32	MFCI 8339	661



TABLE 1 | (Continued)

Taxa	Origin	São Francisco basin	East Axis Reservoirs	Paraíba do Norte basin	SL (min–max)	Voucher	Abundance (Adults / Juveniles)
<i>Moenkhausia costae</i> (Steindachner, 1907)	N	X	X	X (NN)	20–50	MFCI 3433 MFCI 6143 MFCI 7656	4696
<i>Phenacogaster franciscoensis</i> Eigenmann, 1911	E (SF)	X			20–28	MFCI 8706	36
<i>Psalidodon fasciatus</i> (Cuvier, 1819)	N	X		X	19–105	MFCI 2147	4203
<i>Psellogrammus kennedyi</i> (Eigenmann, 1903)	N	X			24–47	MFCI 8427	3
<i>Roeboides xenodon</i> (Reinhardt, 1851)	E (SF)	X	X		36–63	MFCI 3267 MFCI 7823	260
<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	N			X	23–46	MFCI 2218	2430
<i>Serrapinnus piaba</i> (Lütken, 1875)	N	X		X	13–31	MFCI 0172 MFCI 6485	326
<i>Tetragonopterus franciscoensis</i> Silva, Melo, Oliveira & Benine, 2016	E (SF)	X			100–110	MFCI 1627	7
<b>GYMNOTIFORMES</b>							
<b>Sternopygidae</b>							
<i>Eigenmannia microstomus</i> (Reinhardt, 1852)	N	X			142–290	MFCI 3407	2
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	N	X			490	MFCI 3358	4
<b>Gymnotidae</b>							
<i>Gymnotus</i> gr. <i>carapo</i> Linnaeus, 1758	N	X			110–285	MFCI 0181	3
<b>SILURIFORMES</b>							
<b>Callichthyidae</b>							
<i>Hoplosternum littorale</i> (Hancock, 1828)	NN	X			186	MFCI 8164	3
<b>Loricariidae</b>							
<i>Hypostomus pusarum</i> Starks, 1913	N	X	X	X	14–250	MFCI 3488 MFCI 6141 MFCI 2180	70
<i>Hypostomus</i> cf. <i>margaritifer</i> (Regan, 1908)	N	X			330	MFCI 3366	3
<i>Parotocinclus jumbo</i> Britski & Garavello, 2002	N			X	26–43	MFCI 1065	73
<i>Parotocinclus</i> sp.	N	X			29	MFCI 0168	3
<i>Parotocinclus spilosoma</i> (Fowler, 1941)	E (NCCD)			X		MFCI 001267	9
<i>Rhinelepis aspera</i> Spix & Agassiz, 1829	N	X			220–383	MFCI 3290	3
<b>Auchenipteridae</b>							



TABLE 1 | (Continued)

Taxa	Origin	São Francisco basin	East Axis Reservoirs	Paraíba do Norte basin	SL (min–max)	Voucher	Abundance (Adults / Juveniles)
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	N	X	X	X	25–140	MFCI 3359 MFCI 6148 MFCI 5359	375
<b>Doradidae</b>							
<i>Franciscodoras marmoratus</i> (Lütken, 1874)	E (SF)	X			160–350	MFCI 3408	10
<b>Heptapteridae</b>							
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	N			X	183	Not Deposited	2
<b>GOBIIFORMES</b>							
<b>Gobiidae</b>							
<i>Awaous tajasica</i> (Lichtenstein, 1822)	N			X	72–111	MFCI 2163	3
<b>SYNBRANCHIFORMES</b>							
<b>Synbranchidae</b>							
<i>Synbranchus marmoratus</i> Bloch, 1795	N	X		X	83–580	MFCI 8169 MFCI 1088	25
<b>CICHLIFORMES</b>							
<b>Cichlidae</b>							
<i>Astronotus ocellatus</i> (Agassiz, 1831)	NN	X		X	25–212	MFCI 1575 MFCI 5452	141
<i>Cichla monoculus</i> Spix & Agassiz, 1831	NN	X	X	X	68–292	MFCI 1582 MFCI 7873 MFCI 1101	848
<i>Cichlasoma orientale</i> Kullander, 1983	N			X	28–130	MFCI 2188	483
<i>Cichlasoma sanctifranciscense</i> Kullander, 1983	N	X	X		15–140	MFCI 3192 MFCI 6659	634
<i>Crenicichla brasiliensis</i> (Bloch, 1792)	N	X	X	X	40–191	MFCI 1502 MFCI 9495 MFCI 8335	316
<i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)	N			X	10–135	MFCI 2221	704
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	NN	X	X	X	8–240	MFCI 0155 MFCI 6163 MFCI 5793	7369



TABLE 1 | (Continued)

Taxa	Origin	São Francisco basin	East Axis Reservoirs	Paraíba do Norte basin	SL (min–max)	Voucher	Abundance (Adults / Juveniles)
<b>CYPRINODONTIFORMES</b>							
<b>Poeciliidae</b>							
<i>Poecilia hollandi</i> (Henn, 1916)	N	X	X		13–24	MFCI 8393 MFCI 7822	1708
<i>Poecilia reticulata</i> Peters, 1859	NN	X	X	X	12–23	MFCI 1546 MFCI 8029 MFCI 8344	1920
<i>Poecilia vivipara</i> Bloch & Schneider, 1801	N	X	X	X	11–52	MFCI 0170 MFCI 6751 MFCI 1074	6942
<b>ACANTHURIFORMES</b>							
<b>Sciaenidae</b>							
<i>Pachyurus francisci</i> (Cuvier, 1830)	E (SF)	X			390	MFCI 3371	1
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	NN	X	X	X	66–380	MFCI 1545 MFCI 8753 MFCI 7617	248
<b>TOTAL OF SPECIES</b>		<b>50</b>	<b>25</b>	<b>35</b>			<b>89,372</b>

**Species composition and distribution.** Among the 50 species recorded in the SF basin, 24% (n = 12) are endemic to this ecoregion, four of those were registered at least in one of the EARs, and one was recorded at two sites in the PB basin (*Anchoviella vaillanti*) (Tab. 1). Of the 25 species recorded in the East Axis artificial reservoirs, only one was not recorded at the locations on the SF basin: *Myleus micans* (Lütken, 1875). For the Paraíba do Norte River basin, only two of the 35 captured species are considered endemic to the Northeastern Caatinga and Coastal Drainage ecoregion: *Parotocinclus spilosoma* (Fowler, 1941) and *Apareiodon davisii* Fowler, 1941. The only threatened species recorded was *A. davisii* (Endangered species (EN) according to MMA (2022)). This species was registered at two out of the five sites in the PB basin (RB 3 – Acauã Reservoir and RB 5 – Gurinhém River). The seriated ordination analysis graph (Fig. 2) revealed species with restricted distribution its extremes or species with shared occurrence among the two basins at its center. The only species recorded in all 19 locations sampled was the exotic *Oreochromis niloticus* (Linnaeus, 1758).

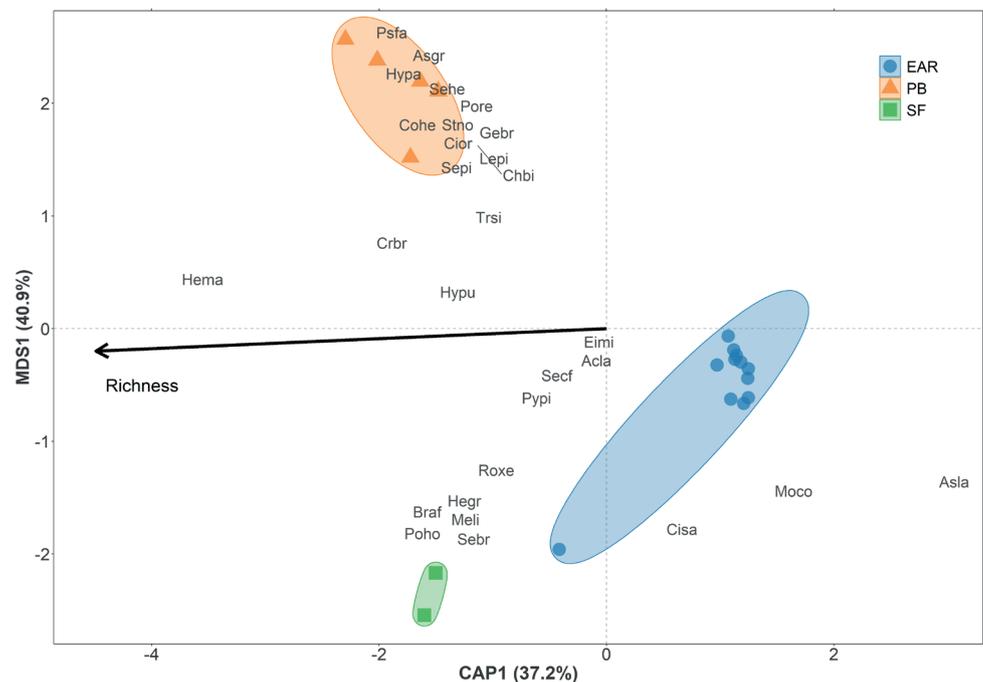
No fish eggs were found in our samplings. Meanwhile, the great majority of larvae (n = 2,045) was from *Anchoviella vaillanti*. Moreover, there were three larvae of *Characidium bimaculatum* Fowler, 1941 and three *Oreochromis niloticus*. The larvae not possible to identify at species level were: *Hypostomus* sp. (n = 1), Sciaenidae (n = 1), and not identified (n = 15). Most of the larvae were in pre-flexion stage (45%), followed by yolk sac (27%), flexion (15%), and post-flexion (12%).



**FIGURE 2 |** Seriated ordination of the species presence/absence at the sampling sites of the East Axis of the São Francisco River Integration Project (SF-IWT). Black cells represent the presence of the species at a particular location. The species written in bold represents the new occurrence record in the receiving basin. In the upper right corner, Venn diagram showing species richness interactions between groups of sites. SF = São Francisco River basin, PB = Paraíba do Norte River basin, EAR = East Axis Reservoirs.

**Species diversity and community patterns.** The total beta diversity index for the study was 0.39 out of the maximum possible value of 1 (when all sites contain different species). At DB-SF, beta diversity was 0.34, at RB-PB was 0.36 and at EAR was 0.29. The contribution of individual samples to beta diversity (LCBD), ranged from 0.024 to 0.095, with EAR sites having the lowest values (<0.044), and PB and SF the highest (>0.075). The p-values for the significantly higher beta diversity samples ranged from 0.001 to 0.039. These ecologically unique samples were at SF and PB sites.

The ANOSIM analysis showed that the sites and species within a region (SF, EAR, or PB) are more similar to each other and dissimilar to the sites and species from a different region ( $r = 0.9773$ ). Likewise,  $p < 0.05$  indicated a significant difference between regions (Fig. 3). The effect of richness was highly significant (PERMANOVA marginal significance test,  $p < 0.001$ ) in structuring fish communities across the basins. The first horizontal axis (CAP1,  $p < 0.001$ ), represented by richness difference across regions, accounted for 37% of the model explanation. Sites on the right side of the horizontal axis, represented by EAR, had a minimal influence of richness when compared to sites on the left represented by SF and PB basins. Meanwhile, axis 2 (MDS1) of unconstrained data reflecting the regions' separation, had SF more closely related to EAR, and PB as an isolated group.



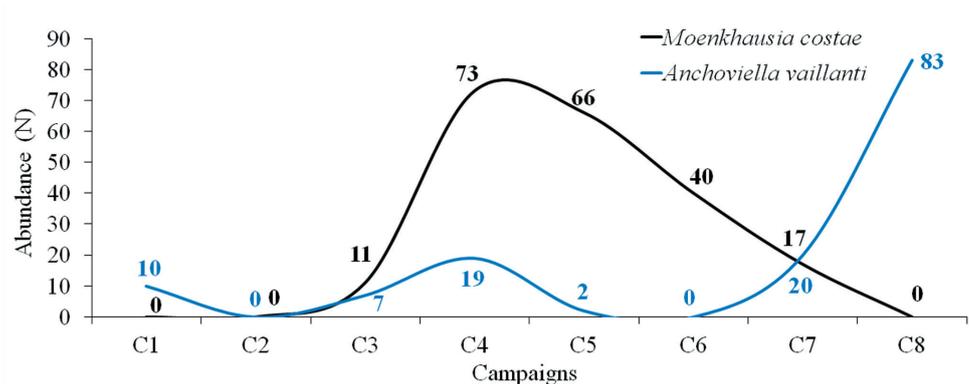
**FIGURE 3 |** Canonical analysis of principal coordinates (CAP) for the species and sites that contributed to the differences between basins and reservoirs (SF = São Francisco River basin, PB = Paraíba do Norte River basin, EAR = East Axis Reservoirs). Fitted site scores are colored and shaped according to the basin or EAR designation. A subset of species that explain at least 70% of the variation among sites is represented by species name abbreviation (two first letters of genus and the two first of the epithet). The only predictor significant for the linear model was richness.

Species that explained at least 70% of the variation among sites were selected to be shown in Fig. 3. Of those species, ten were also pointed by SCBD as indicator species (varied the most): *Anchoiella vaillanti*, *Astyanax lacustris* (Lütken, 1875), *Bryconops* cf. *affinis*, *Hemigrammus marginatus* Ellis, 1911, *Hyphessobrycon* cf. *parvellus*, *Moenkhausia costae*, *Poecilia hollandi* (Henn, 1916), *Psalidodon fasciatus* (Cuvier, 1819), *Serrapinnus heterodon* (Eigenmann, 1915), and *Serrasalmus brandtii* Lütken, 1875 (Fig. S3H).

**Non-native species.** Eight non-native species (11.6% of the total number of species) were documented (Tab. 1). Three of those species, *Hoplosternum littorale* (Hancock, 1828), *Metynnis lippincottianus* (Cope, 1870), and *Piaractus mesopotamicus* (Holmberg, 1887) (Fig. S3E), were sampled exclusively in the SF basin. The five others were registered in both sampled basins (Tab. 1).

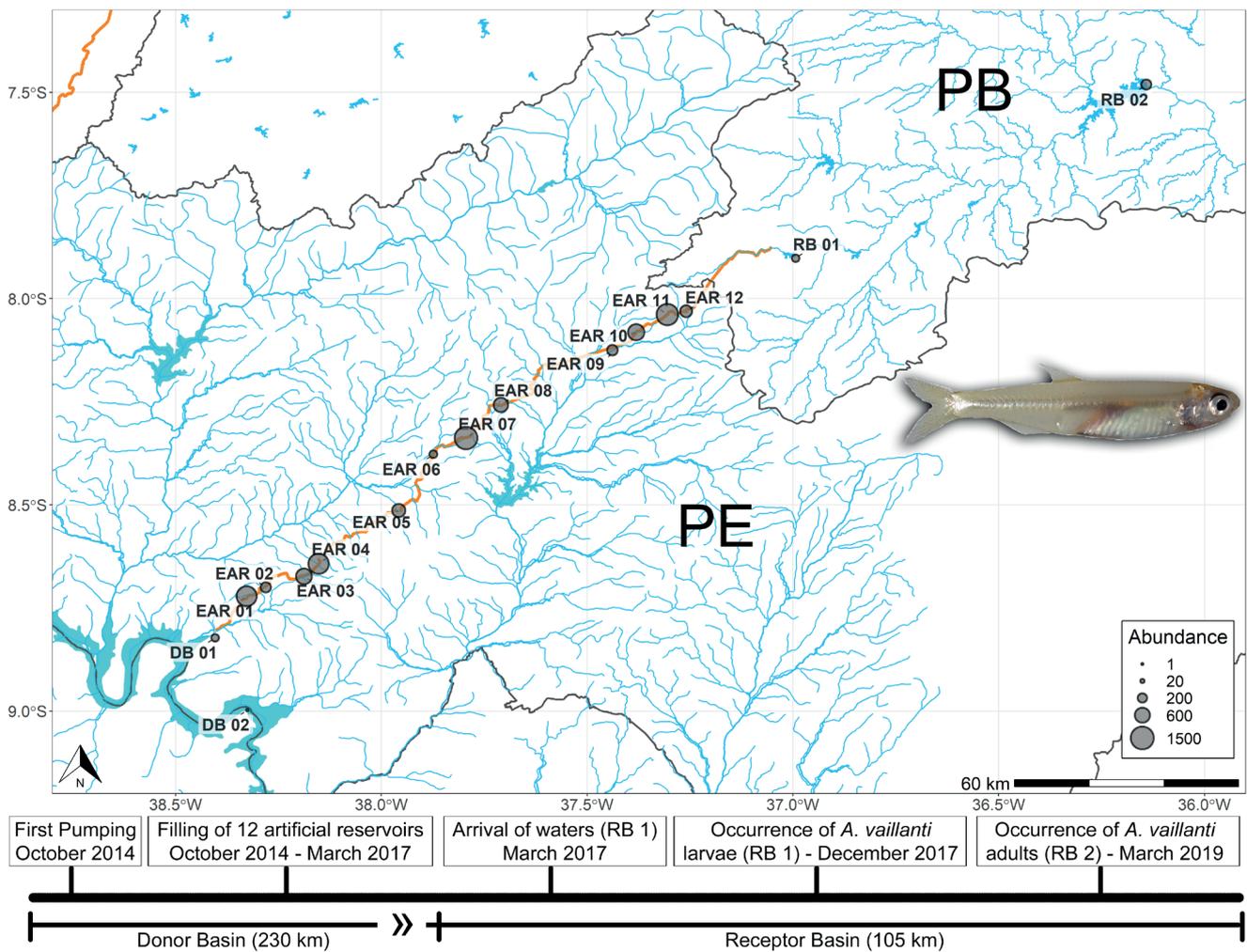
Ten of the 25 species (40%) that inhabit the EAR have no recorded occurrence in the PB basin (Tab. 1) and may become introduced species in this receiving basin: *Acestrorhynchus lacustris* (Lütken, 1875), *Astyanax lacustris*, *Bryconops* cf. *affinis*, *Cichlasoma sanctifranciscense* Kullander, 1983, *Hemigrammus brevis* Ellis, 1911, *Myleus micans*, *Poecilia hollandi*, *Roebooides xenodon* (Reinhardt, 1851), *Serrasalmus brandtii*, and *Triportheus guentheri* (Garman, 1890). Two species (*Anchoiella vaillanti* and *Moenkhausia costae*) were proven to be translocated from SF to the PB basin.

**Non-native species dispersed to the receiving basin.** *Moenkhausia costae* showed variations in abundance in RB 1 with a gradual decrease from its first occurrence, in August 2018, until the last sampling, performed in December 2021 (Fig. 4). Statistical analysis revealed that variations in abundance between the campaigns in which *M. costae* was captured in RB 1 are still significant (G test = 276.7; df = 7; p < 0.001). In contrast to *M. costae*, the abundance of *A. vaillanti* has been increasing since the first records (Fig. 4). The species presented the second highest abundance in site RB 2 (n = 124), only after *H. marginatus* (n = 165). A significant variation was also detected between its abundances in RB 1 (G test = 232.2; df = 7; p < 0.001) and RB 2 (G test = 681.9; df = 7; p < 0.001).



**FIGURE 4** | Variation in the abundance of non-native species *Anchoiella vaillanti* and *Moenkhausia costae* in the Poçoões Reservoir (RB 1) in the campaigns conducted after the arrival of the SF-IWT waters.

**New distribution record.** An endemic species from the donor basin (São Francisco) – *Anchoviella vaillanti* (Clupeiformes, Engraulidae; Fig. S3 A) – was recorded in the receiving basin for the first time after the beginning of the operation of the East Axis. The graphic variation in *A. vaillanti* abundance at all sampling sites is represented in Fig. 5. All records are from Brazil, Paraíba State, Paraíba do Norte River basin: MFCI 7633, 5, 41–56 mm SL, Poçoões Reservoir (RB 1), Monteiro, 07° 53'19.67"S 36° 59'56.96"W, 28 Aug 2018, A. L. B. Silva. MFCI 8280, 19, 32–52 mm SL, Epitácio Pessoa Reservoir (RB 2), Boqueirão, 07° 33'26.3"S 36° 16'29.2"W, 14 Mar 2019, A. L. B. Silva & G. R. dos Santos. Another 326 individuals were caught at larval stages (32 in RB 1 and 294 in RB 2) with the ichthyoplankton net.



**FIGURE 5** | Spatial distribution of *Anchoviella vaillanti*. The size of the circles represents juveniles/adults' abundance at each sampling site. The species went from the São Francisco donor basin through the SF-IWT East Axis artificial canals and reservoirs, reaching the receiving Paraíba do Norte basin sites, in the states of Pernambuco (PE) and Paraíba (PB), Brazil. DB = Donor basin, EAR = East Axis Reservoirs, RB = Receiving basin. Detailed location list of the sampling sites in Tab. S1.

**Feeding and reproductive analysis of dispersed non-native species.** The *Moenkhausia costae* diet was based on six food items (Tab. 2). The most important items were Ostracoda and Zooplankton. Only three of the 60 analyzed stomachs of *M. costae* were empty. The *Anchoviella vaillanti* diet was composed of eleven food items. Copepoda and Organic Matter represented the majority of items ingested (Tab. 2). All analyzed *A. vaillanti* stomachs contained at least one item. Both species presented mainly zooplanktivorous feeding habits in the receiving basin, although *A. vaillanti* had also an opportunistic insectivorous feeding (due to the high Chironomidae abundance).

The NMDS followed by ANOSIM indicated no differences between species diet ( $R = 0.44$ ;  $p > 0.05$ ), nor between rainy and dry seasons ( $R = 0.12$ ;  $p > 0.05$ ). The items Organic matter, Ostracoda, and Zooplankton (NI) accounted for 43% of the season dissimilarity (81% total), while Organic matter, Zooplankton (NI), and Copepoda accounted for 45% of the dissimilarity between species (77% total).

**TABLE 2 |** Alimentary Index (IAi) of the items consumed by non-native species of the Paraíba do Norte River basin (RB), *Moenkhausia costae* and *Anchoviella vaillanti*. N = number of non-empty stomachs analyzed; NI = not identified.

Site	<i>M. costae</i>				<i>A. vaillanti</i>			
	RB 1		RB 2		RB 1		RB 2	
Season	Rainy	Dry	Rainy	Rainy	Dry	Dry	Rainy	Rainy
N	15	12	15	14	15	15	15	15
<b>AQUATIC INSECTS</b>								
Chironomidae (Diptera)	2.72		0.03		81.16	1.58		2.23
Corixidae (Hemiptera)					0.01	3.24		
Insect fragments								4.87
Odonata								1.38
<b>CRUSTACEA</b>								
Cladocera	5.98						0.86	
Conchostraca							1.28	
Copepoda		0.88					92.51	
Ostracoda	91.30	78.81					5.35	
Zooplankton (NI)				99.90	18.83	3.63		2.81
<b>OTHERS</b>								
Sediment		4.42						0.01
Organic Matter			99.97	0.10		91.55		88.7
<b>VEGETAL</b>								
Filamentous algae		15.89						

The standard length of *Moenkhausia costae* ranged from 20 to 56 mm in RB 1, with the lowest values obtained in the dry season (ANOVA;  $F = 91.25$ ;  $df = 1$ ;  $p < 0.0001$ ). The smallest breeding female was 38 mm, and the male was 32 mm. In the dry season, *M. costae* had three gonadal stages: immature (53.3%), maturing (40% of the individuals analyzed), and mature (6.7%). The mean GSI was  $0.98 \pm 0.74$  for males and  $1.42 \pm 1.26$  for females. In the rainy season, three gonadal stages were observed: mature (64.45%), maturing (33.33%), and partially emptied (2.22%). The mean GSI ( $GSI_m$ ) obtained was  $6.34 \pm 5.47$  for females and  $2.28 \pm 0.64$  for males. In the rainy season, mature females had the highest  $GSI_m$  values (ANOVA;  $F = 70.03$ ;  $df = 1$ ;  $p < 0.0001$ ). Juvenile specimens were observed only in the dry season (Tab. 3).

For *Anchoviella vaillanti*, the standard length varied between 32 and 56 mm, with the smallest lengths recorded in the rainy season of RB 2 and the largest in the dry season of RB 1. Considering the specimens from both seasons, it was observed that fish in RB 1 are larger than those of RB 2 (ANOVA;  $F = 49.42$ ;  $df = 1$ ;  $p < 0.001$ ). The smallest breeding female was 44 mm, and the male was 32 mm. For the *A. vaillanti* three gonadal stages were observed: maturing (66.67%), mature (30%), and partially emptied (3.33%). The average GSI obtained was  $5.05 \pm 1.08$  for females and  $2.76 \pm 0.93$  for males. When comparing the  $GSI_m$  values between the gonadal stages, it was detected that the male indices in stage III were significantly higher than in stage II (ANOVA;  $F = 14.57$ ;  $df = 1$ ,  $p < 0.05$ ). In RB 1, 14 of 15 analyzed specimens were maturing females (Tab. 3).

**TABLE 3** | Abundance and mean values of the gonadosomatic index ( $GSI_m$ ) by gonadal stages obtained for *Moenkhausia costae* (RB 1) and *Anchoviella vaillanti* (RB 1 and RB 2). RB = Paraíba do Norte River basin; SL = standard length; N = abundance; M = males; F = females; I = indeterminate. Different bold letters (a, b, c) in the columns indicate statistical differences (ANOVA;  $p < 0.05$ ) between gonadal stages of each sample.

Species	Site	Season	SL range (mm)	Gonadal development stages							
				I (immature)		II (maturing)		III (mature)		IV (spent/spawned)	
				N (M/F/I)	$GSI_m$ (M/F)	N (M/F/I)	$GSI_m$ (M/F)	N (M/F/I)	$GSI_m$ (M/F)	N (M/F/I)	$GSI_m$ (M/F)
<i>M. costae</i> (n = 60)	RB 1	Dry	20–39	0 / 2 / 6	0 / <0.01	1 / 5 / 0	0.45a / 1.42 ± 1.13b	1 / 0 / 0	1.51a / 0	0 / 0 / 0	0 / 0
		Rainy	39–50	0 / 0 / 0	0 / 0	0 / 2 / 0	0 / 5.43 ± 1.58b	12 / 1 / 0	2.09 ± 1.36a / 10.9c	0 / 0 / 0	0 / 0
		Rainy	31–45	0 / 0 / 0	0 / 0	3 / 7 / 0	1.78 ± 1.55a / 0.99 ± 4.36b	2 / 2 / 0	2.61 ± 0.81a / 13.5 ± 0.51c	0 / 1 / 0	0 / 5.77
		Rainy	41–56	0 / 0 / 0	0 / 0	2 / 1 / 0	1.83 ± 0.66a / 4.33b	8 / 4 / 0	2.78 ± 1.79a / 12.06 ± 5.04c	0 / 0 / 0	0 / 0
<i>A. vaillanti</i> (n = 60)	RB 1	Dry	41–56	0 / 0 / 0	0 / 0	0 / 14 / 0	0 / 4.48 ± 1.25a	0 / 1 / 0	0 / 6.67a	0 / 0 / 0	0 / 0
		Dry	33–40	0 / 0 / 0	0 / 0	9 / 6 / 0	1.81 ± 1.96a / 1.99 ± 1.68a	0 / 0 / 0	0 / 0	0 / 0 / 0	0 / 0
	RB 2	Rainy	32–48	0 / 0 / 0	0 / 0	1 / 6 / 0	3.26a / 6.18 ± 1.54b	7 / 0 / 0	4.14 ± 1.48b / 0	1 / 0 / 0	3.78 / 0
		Rainy	32–52	0 / 0 / 0	0 / 0	3 / 10 / 0	1.04 ± 1.4a / 3.85 ± 1.41c	1 / 1 / 0	2.94b / 4.62c	0 / 0 / 0	0 / 0

## DISCUSSION

In almost a decade of samplings, the SF-IWT East Axis ichthyofauna monitoring registered 69 fish species and more than 89,000 individuals. The fish assemblages' composition was different when comparing the donor basin SF, the receiving basin PB, and the EAR. As expected, the fish composition from the EAR was closely related to the donor basin (SF). Four species first colonized the EAR after their initial operation (*Anchoviella vaillanti*, *Astyanax lacustris*, *Moenkhausia costae*, and *Oreochromis niloticus*). Nowadays, 25 species compose the fauna of the SF-IWT reservoirs and canals. It was recorded eight non-native species in both basins and reservoirs. Two of those, *M. costae* and *A. vaillanti*, used the SF-IWT artificial canals to go from the donor to the receiving basin. However, only *A. vaillanti* populations seem to be spreading and increasing in numbers. *Moenkhausia costae* and *A. vaillanti* diets consisted basically of zooplankton and they presented fractionated-type spawning.

**Ichthyofauna monitoring.** Since the Environmental Impact Study (Brasil, 2004) was performed to assess the SF-IWT impacts, progress has been made to fulfill the knowledge gaps on Caatinga ichthyofauna due to our continuous monitoring. Ichthyofauna studies have been carried out since the 19<sup>th</sup> century for the São Francisco River Basin and the more recent species lists were published by Britski *et al.* (1988), Alves *et al.* (2011), Santos *et al.* (2015), and Barbosa *et al.* (2017), in which 244 species were identified. Lima *et al.* (2017) listed 386 fish species for the Caatinga domain, of which 121 are registered for the hydrographic basins involved in the SF-IWT (Silva *et al.*, 2020). Silva *et al.* (2020) obtained 86 species for the SF basin by considering primary and secondary data from 117 sites located in lentic and lotic stretches of the river. Our results show nine different fish species (out of 50) for the SF basin, supplementing the list provided by Silva *et al.* (2020): *Acestrorhynchus britskii* Menezes, 1969 (Fig. S3B), *Franciscodoras marmoratus* (Lütken, 1874), *Hemigrammus gracilis* (Lütken, 1875), *Hoplias intermedius* (Günther, 1864), *Hypostomus* cf. *margaritifera*, *Pachyurus francisci* (Cuvier, 1830) (Fig. S3D), *Piaractus mesopotamicus*, *Rhinelepis aspera* Spix & Agassiz, 1829, and *Serrasalmus* cf. *rhombus* Linnaeus, 1766. Regarding the PB basin, Ramos *et al.* (2018) listed 47 species, whereas Silva *et al.* (2020) registered 44 species. We registered a new species for the PB basin, the SF translocated species *A. vaillanti*. The other 34 fish species recorded by us represented over 70% of the species listed by Ramos *et al.* (2018) and Silva *et al.* (2020).

In our study, all the species found in EAR were translocated from two sites inserted in a lentic stretch of the São Francisco River (popularly known as Itaparica Reservoir). The water transposed from the donor to the receiving basin is captured from the Itaparica Reservoir. As the East Axis reservoirs were filled, the first species recorded were the same for all of the 12 EARs: *Anchoviella vaillanti*, *Astyanax lacustris*, *Moenkhausia costae*, and *Oreochromis niloticus*. Thus, we characterized them as pioneer species in the EAR, with a high colonization capacity and successful dispersion in new environments (Agostinho *et al.*, 1999). The SF and PB basins, despite having compositional differences, presented higher richness when compared to EAR. The result was expected, since the EAR and the canals are artificially created very recent new environments (Agostinho *et al.*, 1999). It not only takes time for fish to colonize these new environments, but the structural

characteristics of the SF-IWT project represent many different barriers to be transposed by the fish (e.g., dams and pumping stations). Our results represent the first record of ichthyofauna composition and colonization in the SF-IWT East Axis Reservoirs. We are presenting the first decade of data, so this can be used as a base for future studies aiming to detect and understand all steps for fish species colonization in transposition systems.

**Introduction of non-native species.** According to the Project's characteristics of pumping water to overcome major geographical obstacles and hydrographic basin barriers, water travels only one way, starting exclusively from the donor basin towards the receiving basin (Andrade *et al.*, 2011). Thus, it is physically not possible to transfer species in the opposite direction. So far, we have only detected small-sized species (*Anchoviella vaillanti* and *Moenkhausia costae*) that were able to travel along the transposition canals and reservoirs, transpose all the SF-IWT East Axis barriers, and reach the receiving basin. The arrival of these small-sized species was only possible after the passage of larval, juvenile, and adult forms through the six pumping stations and 12 reservoirs.

Downstream the pumping stations, it was possible to observe that some adult individuals of larger species (e.g., *Acestrorhynchus lacustris*, *Hoplias* spp., and *Oreochromis niloticus*) were also able to overcome these barriers without major damage. However, eggs and juveniles of fish species could also spread through the system. We did occasionally detect *A. vaillanti* larvae in RB 1 six months before the adults, so it might be that for other species the larvae and eggs could also be detected in advance when a specific protocol is used. Due to this concerning possibility, we recommend further studies focusing specifically on tracking eggs and larvae to help management actions.

Some non-natives found in the SF basin and/or the EAR, are already spread in the receiving PB basin as well: *Astronotus ocellatus* (Agassiz, 1831), *Cichla monoculus* Spix & Agassiz, 1831, *Oreochromis niloticus*, and *Poecilia reticulata* (Ramos *et al.*, 2018; Silva *et al.*, 2020). However, there are species from the SF basin occupying the EAR that do not occur in the receiving basin. Among the 10 species that we recorded in the East Axis Reservoirs and that do not occur in the receiving basin, there are representatives of several trophic guilds (i.e., omnivorous – *Astyanax lacustris* (Vidotto-Magnoni *et al.*, 2021); insectivorous – *Triporthus guentheri* (Pinto *et al.*, 2011); piscivorous – *Acestrorhynchus lacustris* (Rocha *et al.*, 2011), and *Serrasalmus brandtii* (Pompeu, 1999). Those species may overcome the SF-IWT barriers and colonize the PB basin environment causing impacts on the native ichthyofauna through competition and predation if they manage to establish themselves.

From the SF species present in EAR with the potential to spread to the receiving basin, we wanted to highlight *Serrasalmus brandtii*. This species represents an imminent danger in the event of colonizing the PB basin. The species belongs to a genus with a voracious predatory feeding habit and can benefit reproductively from altered environments (Silva *et al.*, 2015; Andrade *et al.*, 2018; Bazzoli *et al.*, 2019). In addition, according to Teixeira *et al.* (2020), the introduction of *S. brandtii* can be considered an ecological risk, as this species can reproduce more quickly in the initial stages of invasion. Characteristics such as tolerance to adverse environmental conditions, predatory habits, and high reproductive plasticity give the introduced species high success rates in the invasion

processes (Garcia *et al.*, 2021). Despite not yet occurring in the PB basin, *S. brandtii* was already found in the first three EAR, reaching one reservoir at a time, indicating a gradual spread through the EAR system. Moreover, only continuous monitoring will help detect future spread and the development of containment methods.

The installation of barriers would help containing the dispersion of non-native fish to the receiving basin. Studies have suggested, for example, the use of physical, acoustical, and/or electrical barriers on large infrastructure projects to avoid fish passage (Hillyard *et al.*, 2010; Burger *et al.*, 2015). A trial installation of 25 mm high anti-shoal metal gratings upstream of the first pumping station and downstream of the first reservoir in the East Axis (EAR 1) happened to test effectiveness in the SF-IWT. The main objective of these grids was to minimize and delay the translocation of medium and large species, in number and biomass, from the donor basin to the receiving basin. The grids did not prevent the colonization of new species that exceeded the barriers in the forms of eggs, larvae, juveniles, and small-sized fish. Therefore, the combination of physical and electrical methods would be ideal. The best placement for those containment barriers would be right before the first pumping station (DB 1), to avoid SF species from reaching the artificial reservoirs and canals. Moreover, barriers on the last reservoir output area (EAR 12), right before the first site on the receiving basin (RB 1), would help containing species that managed to disperse through the EAR from reaching receiving basin.

**Dispersion of donor basin species to the receiving basin.** *Moenkhausia costae* was classified by Ramos *et al.* (2021) as an introduced non-native species in the PB basin. The species present natural occurrences in the SF and the other SF-IWT basins – Jaguaribe, Piranhas-Açu, and Apodi-Mossoró basins (Silva *et al.*, 2020). The species colonized the EAR over time and reached RB 1 (Poções Reservoir) in the receiving basin. Our data showed that so far, *M. costae* has only been detected at a single site in the receiving basin – RB 1). After peaks of *M. costae* abundance in RB 1, a gradual specimens decrease was observed during the last samplings. Following the introduction, a species must go through three more phases before being considered invasive in a water body: establishment, dispersion and impact (Blackburn *et al.*, 2011; Garcia *et al.*, 2021). It seems that *M. costae* is still facing the establishment process in the receiving basin. The species' gradual abundance decrease may indicate that the ecological interactions (*e.g.*, presence and abundance of predators), and physical-chemical differences (Orsi, Britton, 2014) did not result in an optimal environment for species establishment after the initial introduction process. Only the continuous monitoring in all RB sites will verify if the species will keep declining or manage to disperse in the basin over time.

*Anchoviella vaillanti* was another SF species dispersed to the PB basin. This small-sized species is considered endemic to the São Francisco River basin and, until now, had no record of occurrence in the PB basin (Lima *et al.*, 2003; Reis *et al.*, 2003; Lustosa-Costa *et al.*, 2017; Ramos *et al.*, 2018; Silva *et al.*, 2020; Fricke *et al.*, 2022). *Anchoviella vaillanti* can be characterized by occupying basal trophic levels, being an important prey for larger fish (Rocha *et al.*, 2011, 2015). In contrast to *M. costae*, our data allowed us to assume that *A. vaillanti* has been establishing populations in the receiving basin since we kept capturing an abundant number of larvae, juveniles, and adults in reproductive stages (II and III) over time. The diffusion of *A. vaillanti* in the PB basin must be continuously monitored to detect possible impacts on local species that occupy the same trophic niche

(Daga *et al.*, 2020), and to track changes in the trophic web that could cause biotic homogenization (Bezerra *et al.*, 2018, 2019). Facing the arrival of a non-native species, native species may need to develop ecological adaptations, with changes in reproductive and food tactics (Sato *et al.*, 2003; Deacon *et al.*, 2011), aiming to increase the fitness of the fishes in the face of adverse environmental conditions (Sternberg, Kennard, 2014). Those changes are generally gradual and slow, therefore only time and specific studies will help detect any further spread and possible impacts caused by *A. vaillanti* in the receiving basin.

**Feeding and reproductive analysis.** The results of the food analysis allowed us to classify the feeding habits of the PB basin non-native species analyzed (*Moenkhausia costae* and *Anchoviella vaillanti*) as zooplanktivorous, since both ingested mainly microcrustaceans. Several studies have characterized the genus *Moenkhausia* Eigenmann, 1903 with zooplanktivorous feeding habits (Pouilly *et al.*, 2003; Rejas *et al.*, 2005; Silva, Hahn, 2009; Silva, 2019), insectivorous (Grant, Noakes, 1987; Casatti, 2002; Pouilly *et al.*, 2004; Tófoli *et al.*, 2010; Oliveira *et al.*, 2016) or still omnivorous (Esteves, Galetti Jr, 1994; Machado *et al.*, 2009), depending on the environment. The results presented here represent the first description of the diet of *M. costae* in the PB basin. For *A. vaillanti*, Pompeu, Godinho (2003) also defined that the species has zooplanktivorous and insectivorous feeding habits, in addition to having significant importance in the foraging of other species (Bazzoli *et al.*, 1997; Lizama, Ambrósio, 2003; Pompeu, Godinho, 2003; Rocha *et al.*, 2011, 2015). Likewise, we observed that during RB 1 the dry season, when resources were limited, *A. vaillanti* presented an opportunistic insectivorous feeding, since Chironomidae were highly available. The opportunistic feeding by zooplanktivorous species allows effective exploitation of patchily distributed food resources. This opportunistic habit is not incompatible with selective feeding, and may eventually be established as a common strategy to most zooplanktivorous species (Abelha *et al.*, 2001).

The food preference for microcrustaceans in RB 1 and RB 2 may be associated with their greater availability, ease of ingestion, and the morphological apparatus' characteristics that both *A. vaillanti* and *M. costae* present (Abelha *et al.*, 2001; Ximenes *et al.*, 2011). After RB 1 received water from the SF-IWT, its volume was maintained at high levels, promoting a homogenization of the environment and favoring the opportunistic character of these species for certain food resources (Machado-Evangelista *et al.*, 2015), such as aquatic microcrustaceans (autochthonous), organic matter, Chironomidae, and filamentous algae. In RB 2, it was observed that specimens of *A. vaillanti* were associated with places with more turbid waters (due to the inflow of water from the SF-IWT), smaller depths, muddy substrate and absence of aquatic macrophytes. According to Oliveira *et al.* (2016), in these shallower places, nutrients are better utilized, resulting in greater biological production. This shallow area with a great amount of nutrients and occurrence of aquatic macrophytes can be used by many species of fish as nurseries for spawning and refuge for juveniles (Casatti *et al.*, 2003; Winfield, 2004).

For reproductive biology, *M. costae* showed similar behavior to that described by Bazzoli *et al.* (1997), in which the species presented fractionated-type spawning, with prevalence of mature individuals in the rainy season. *Anchoviella vaillanti* presented fractionated-type as well. Mature individuals were found in both RB 1 and RB 2,

which may indicate that a part of the population was in reproductive activity at this site. The greater lengths of *A. vaillanti* in RB 1 may be associated with environmental conditions, such as lower concentration of predators, greater availability of resources and physicochemical characteristics of the water, which have changed (especially in RB 1) after the input of water from the SF-IWT (Barbosa *et al.*, 2021). The fractionated-type spawning presented in both species is an advantage for rapid spread and colonization of new environments, since they can reproduce year-round when conditions are favorable, not depending on seasonal changes. The observed small reproductive sizes and, consequently, early maturation was also an advantage for the fast colonization (Agostinho *et al.*, 1999).

Both feeding and reproductive characteristics found for *M. costae* and *A. vaillanti* reinforce trophic plasticity, fertility, and prolificity that facilitate their dispersion. Especially for *A. vaillanti*, which not only presented a wide range of diet items, but also had individuals in most of the reproductive stages in both seasons, with different sizes, and significantly high abundance. The species seems to have great adaptability and opportunism for trophic and reproductive characteristics.

The colonization and establishment of populations of *M. costae* and *A. vaillanti* may represent, in the medium and long term, a threat to native species, especially small-sized fish that present similar niches (*e.g.*, PB characids). The effects of competition caused by the arrival of these two species can only be well evaluated in long-term studies, as the intensity of competition varies according to the characteristics and distribution of resources in time and space (Ward *et al.*, 2006).

**Additional considerations.** An important consequence of the Integration Project will be the increase of rivers' water supply on the Northeastern Caatinga and Coastal Drainages ecoregions, including the four SF-IWT receiving basins (Brasil, 2004). A group of annual endangered fish, such as rivulids, may be directly affected by this regime change since they are highly adapted to the flooding and dry cycles in temporary puddles and rivers of the Brazilian semiarid region (Costa *et al.*, 2018; Abrantes *et al.*, 2020). The change in flow is a limiting factor for the establishment of fish populations dependent on well-established hydrological cycles, like those annual fish (Bunn, Arthington, 2002). On the other hand, Barbosa *et al.* (2021) reported improvement in some water quality parameters in the Poçoões reservoir (RB 1) after the arrival of water from the SF-IWT, and emphasized that this change may vary for other reservoirs in the basin.

Our work characterized the ichthyofauna in the donor and receiving basin surrounding the SF-IWT East Axis. We present the first occurrence of *Anchoviella vaillanti* in the PB basin. We draw attention to species that are colonizing the artificial reservoirs of the East Axis and can spread to the receiving basins. Finally, we presented preliminary results of food and reproductive aspects of the two species translocated by the integration canals and reservoirs. Despite being clearly defined as an impact arising from the operation of the SF-IWT Project, assessing the full magnitude or qualification of species new records are not possible yet, due to sample size and monitoring time. The first occurrence of *A. vaillanti* in PB basin and the additional fish species reported for SF, complements the list of fish fauna recently published by Ramos *et al.* (2018) and Silva *et al.* (2020).

Since we detected fish species from the donor basin being translocated or with potential to reach the receiving basin, future studies should address the impacts in the fish communities inhabiting the Paraíba River basin. We also suggest a more detailed monitoring of eggs and larvae dispersion, since it seems to be the pathway for fish to transpose the SF-IWT system and reach the receiving basin. Additionally, we suggest the implementation of physical and electrical barriers to contain the fish dispersion through the SF-IWT canals and reservoirs.

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