Ichthyoplankton in a regulated river: community structure and distribution patterns in a run-of-river dam cascade system in the Neotropics

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Run-of-river (ROR) hydroelectric systems drastically reduce discharge in the reduced flow stretch (RFS). We evaluated the influence of RFS formation and environmental variables on the species composition and spatio-temporal distribution of fish eggs and larvae in a ROR system. Samples were collected fortnightly (Oct 2016 to Jan 2017) at the Rio das Antas Energy Complex. A total of 5,681 eggs and 2,124 larvae were collected. The study confirmed ichthyoplankton structure is shaped by strong spatio-temporal variations; species composition and egg and larval densities differed significantly among sites and months, primarily influenced by flow, temperature, dissolved oxygen, and transparency. However, the expected longitudinal progression of larval stages from upstream spawning grounds was absent, indicating the natural drift process is disrupted by the dam cascade. This disruption is confirmed by distinct ichthyoplankton densities and compositions between the upstream (S1) and downstream (S4) sections of the Complex. Furthermore, no reproductive evidence was found for migratory species historically present in the basin, corroborating our initial predictions. These findings demonstrate that cascaded ROR systems modify natural drift dynamics and species distribution, challenging their sustainable image and highlighting the importance of preserving free-flowing river stretches to maintain ichthyofauna reproductive processes.

Keywords: Fish eggs and larvae, Fragmentation, Freshwater fish, Hydropower, Reduced flow stretch.

Submitted May 6, 2025
Accepted October 30, 2025
Epub February 2, 2026

Associate Editor Franco Teixeira de Mello
Section Editor Fernando Pelicice
Editor-in-chief José Birindelli

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 23, no. 4, Maringá 2025

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Sistemas hidrelétricos a fio d'água (ROR) regulam o fluxo no trecho de vazão reduzida (TVR). Avaliamos a influência da formação do TVR e das variáveis ambientais na composição de espécies e distribuição espaço-temporal de ovos e larvas de peixes de um sistema ROR. As amostras foram coletadas quinzenalmente (Out 2016 a Jan 2017) no Complexo Energético Rio das Antas. Coletamos 5.681 ovos e 2.124 larvas. O estudo confirmou que a estrutura do ictioplâncton é moldada por variações espaço-temporais; a composição de espécies e as densidades de ovos e larvas diferiram significativamente entre os locais e meses, influenciadas pela vazão, temperatura, oxigênio dissolvido e transparência. A esperada progressão longitudinal dos estágios larvais a partir de áreas de desova a montante esteve ausente, indicando que o processo de deriva natural foi interrompido; ruptura confirmada pelas distintas densidades e composição do ictioplâncton entre os ambientes a montante (S1) e jusante (S4). Não foram encontradas evidências reprodutivas de espécies migradoras historicamente presentes na bacia, corroborando nossas predições iniciais. Esses resultados demonstram que sistemas ROR em cascata modificam a dinâmica natural de deriva e a distribuição das espécies, questionando sua imagem sustentável e ressaltando a importância da preservação de trechos de rios livre para a manutenção dos processos reprodutivos da ictiofauna.

Palavras-chave: Fragmentação, Hidrelétrica, Ovos e larvas de peixes, Peixes de água doce, Trecho de vazão reduzida.

INTRODUCTION

The construction of dams, as one of the main anthropogenic impacts on natural systems, results in habitat fragmentation, affecting longitudinal patterns and serial continuity (Ward, Stanford, 1983; Dudley, Platania, 2007; Grill *et al*., 2019), beyond ecological connectivity (Crook *et al*., 2015), and flow regime (Finer, Jenkins, 2012; McManamay *et al*., 2015). The disruption of ecological processes in lotic systems can have even more pronounced consequences when they are derived from multiple dams in cascade (Miranda *et al*., 2008; Pelicice *et al*., 2015; Agostinho *et al*., 2016). In this context, the magnitude of longitudinal changes in ecological processes is mainly determined by the position of damming along the lotic continuum (Ward, Stanford, 1983; Santos *et al*., 2017) and the type of operation of the hydropower system (Cella-Ribeiro *et al*., 2017).

One of the most used types of hydropower dam designs is run-of-river (ROR), where water is removed from the river upstream of the dams and moved to a downstream power facility a variable distance before being returned to the river channel (Anderson *et al*., 2015). The ROR results in the formation of a reduced flow stretch (RFS), which occurs between a section formed by the original bed of the river between the upstream dam and the point where water returns flow of the water to the river channel downstream (Kubecka *et al*., 1997). It suggested these systems are less damaging than traditional main-stem hydropower dams, because they reduce the risk of fish passing through the turbines and facilitate the installation of transposition mechanisms (Paish, 2002). However, the reduction of discharges in the RFS can be pronounced (Singh, Agarwal, 2017), often insufficient to support fish communities (Kubecka *et al*., 1997). Therefore, a more comprehensive understanding of the effects of ROR dams on aquatic ecosystems is needed (Anderson *et al*., 2015), especially when these dams are planned in cascading projects. In such a case, the impact factors are probably multiplicative rather than merely additive (Roberts, 1995).

The construction of dams in rivers leads to significant alterations in the aquatic environment, directly impacting local biota, especially fish populations. By disrupting the natural flow of water, the dams fragment essential habitats and hinder the migration of species that rely on these movements for reproduction and feeding, resulting in drastic declines in fish populations and, in extreme cases, leading to the local extinction of certain species (Chen *et al*., 2023). Additionally, the alteration of flow regimes restricts spawning and larval development areas, further compromising fish recruitment (Gogola *et al*., 2013; Silva *et al*., 2017a). Thus, given its sensitivity to changes in flow regulation, ichthyoplankton has been widely used as an indicator for assessing the effects of dam cascades on fish assemblages (*e.g*., Sanches *et al*., 2006; Dudley, Platania, 2007; Gogola *et al*., 2010; Reynalte-Tataje *et al*., 2012a). However, studies specifically addressing the effects of a dam cascade combined with an RFS remain scarce. In the current policy environment, which promotes the expansion of hydroelectric projects (Pelicice *et al*., 2017), understanding these effects is crucial, as many new and proposed projects include dam cascades whose potential impacts may be neglected because of the complexity and multiplicity of synergistic factors.

The length of uninterrupted lotic stretches (Sanches *et al*., 2006; Dudley, Platania, 2007; Silva *et al*., 2017b) and the percent of natural discharge downstream of the dams (Gogola *et al*., 2010; Reynalte-Tataje *et al*., 2013) have consistently been identified as key factors determining fish reproductive success in many systems. In this context, the fragmentation and reduced flow caused by the ROR system primarily affect the accessibility of non-sedentary species, as well as those with higher requirements for spawning.

Thus, this study was conducted to investigate variations in the structure of the ichthyoplankton community in a cascade of reservoirs in southern Brazil. Our objective was to evaluate the spatial and temporal distribution of fish eggs and larvae, larval developmental stages, and fish larvae assemblages, as well as their relationship with the environmental characteristics of areas influenced by hydropower plants. To achieve this, we have tested the following hypotheses: (i) the ichthyoplankton along the longitudinal gradient is influenced by seasonal and spatial environmental variations; (ii) the early larval development stages (yolk-sac and preflexion) are more abundant in upstream areas, closer to spawning grounds, while later stages (flexion and postflexion) tend to occur in downstream areas. Given historical evidence that the study area was part of established breeding routes for at least three migratory species in the basin (Alves, Fontoura, 2009; Becker *et al*., 2013; Luz-Agostinho *et al*., 2010), we predict the absence of reproductive evidence for migratory fish, thus attesting the effects of the fragmentation imposed by dam cascade.

MATERIAL AND METHODS

Study area. The study was conducted at the Rio das Antas Energy Complex (CERAN), located in the Taquari-Antas River basin (26,428 km²), an important tributary of the Jacuí River, which drains to the Laguna dos Patos system in southern Brazil (Fig. 1). The Taquari-Antas River presents a high average slope and is characterized by torrential rainfall regimes, rapid surface runoff, and abrupt discharge variations throughout the year (FEPAM, 2009; FEOW, 2015).

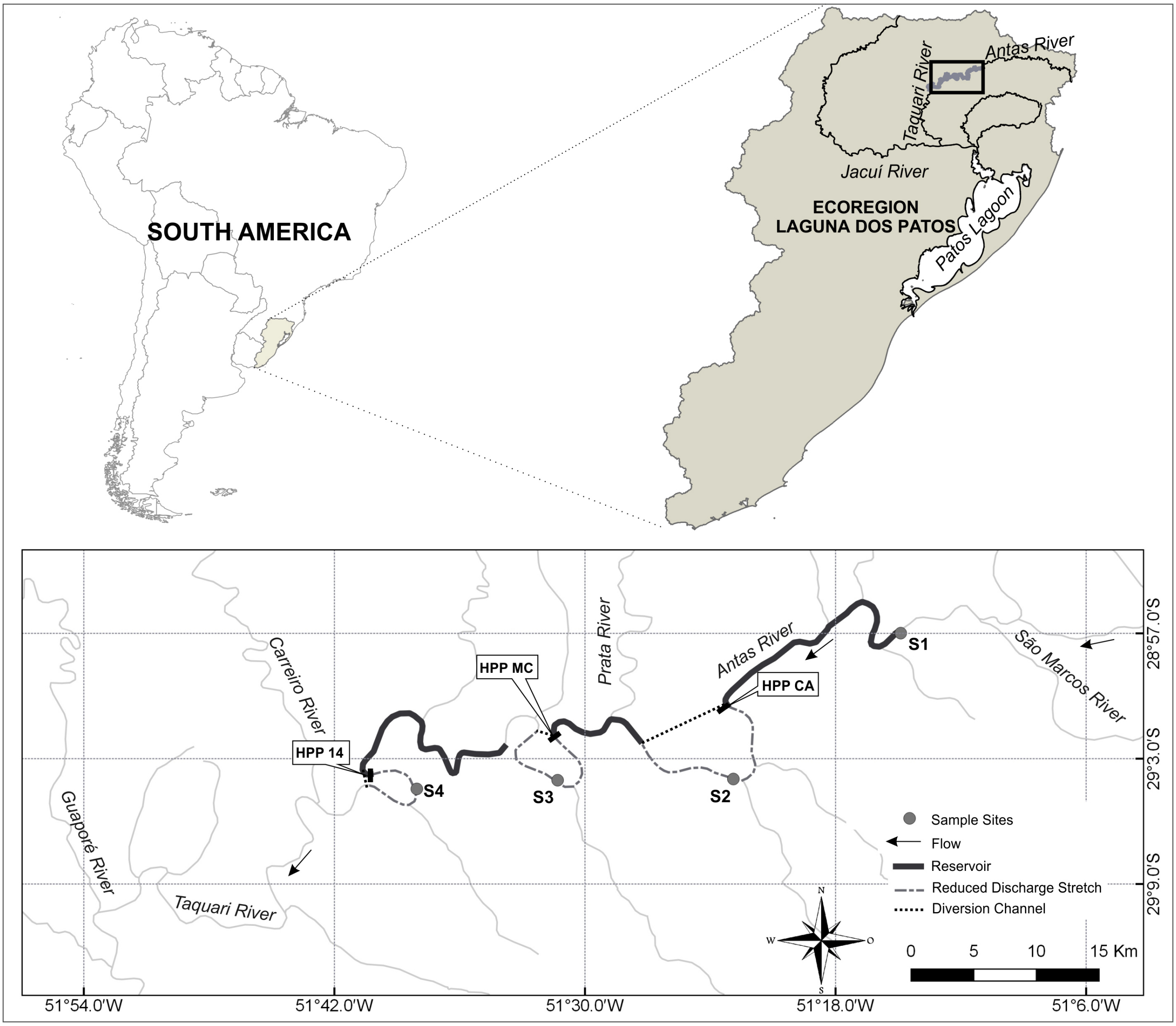

FIGURE 1 | Distribution of the ichthyoplankton sampling network in the Rio das Antas Energy Complex, Brazil, within the context of the Lagoa dos Patos ecoregion, South America. Sampling sites Hydroelectric plants (S): 14 de Julho Hydroelectric Power Plant (HPP 14), Monte Claro Hydroelectric Power Plant (HPP MC), Castro Alves Hydroelectric Power Plant (HPP CA).

The CERAN complex is composed of three Hydropower Plants (HPPs): Castro Alves (HPP CA), Monte Claro (HPP MC), and 14 de Julho (HPP 14). The reservoirs are storage, but with an uncontrolled spillway, that is, without a discharge control device (floodgates) and relatively low residence time. All of them, without a mechanism of fish passage, and use the river deviation technique, where a channel (penstock) conducts the water retained from the dam to the powerhouse, as a result a reduced flow stretches (RFS), in which a minimum discharge is maintained. Additional characteristics of hydroelectric plants can be accessed in Tab. **S1**.

The area directly influenced by the CERAN complex comprises approximately 100 km of longitudinal extension (Fig. 1). This range is located approximately 200 km upstream of the confluence of the Taquari River with the Jacuí River (Scopel *et al*., 2005). In this study area all tributaries are of small proportions in length and volume, except for the Prata River, which has an average width of approximately 60 m at its confluence with the Antas River. This tributary flows into the reservoir HPP MC but is also dammed by a hydroelectric dam about 10 km upstream of its mouth.

Four sampling sites were established in CERAN (Fig. 1): site S1 is located in a free-flowing reach upstream of the entire complex, near the transition section of the HPP CA; the other three sites are lotic remnants situated within the RFSs of the three respective HPPs (S2, S3, and S4). However, the roles concerning habitat fragmentation differ critically between S4 and other RFSs. Sites S2 and S3 are located in isolated inter-dam reaches, each trapped between an upstream dam and a downstream reservoir; therefore, they are separated from the rest of the basin. In contrast, although S4 is also within an RFS, it is positioned below the most downstream dam of the complex (HPP 14). This positioning means it is fully integrated with the broader downstream river basin ecosystem. Therefore, while hydrologically altered, S4 functionally represents the downstream section of the complex from a connectivity viewpoint, marking the end of the artificially fragmented segment.

Sampling. Ichthyoplankton was collected fortnightly from October 2016 to January 2017, during the reproductive period of fish from the region (Luz-Agostinho *et al.,* 2010). Sampling was performed in each site using conical-cylindrical plankton nets (500-µm mesh) equipped with a mechanical flow meter to measure the volume of filtered water (Nakatani *et al*., 2001). All samples were taken from the subsurface and during 10 min at four times: 9:00 p.m., 1:00 a.m., 5:00 a.m., and 9:00 a.m. At places with lower water flow speed, horizontal trawling was used for sample collection. Otherwise, stationary nets were installed in the middle and the margin with greater flow, in sections transverse to the water course (Reynalte-Tataje *et al*., 2013). The sampled biological material was fixed in 4% formaldehyde buffered with calcium carbonate.

To complement the species composition results, a light trap was installed at the margin of each site at nightfall (9:00 p.m.) and removed before sunrise (5:00 a.m.). The trap model followed that of Ávila-Simas *et al*. (2014), adapted from Reynalte-Tataje *et al.* (2012b).

The sampling procedures followed the specifications of the monitoring project approved by the current environmental agency (Fundação Estadual de Proteção Ambiental Henrique Luiz Roessler), according to the following licenses: 1353/2015-DL (HPP CA), 02844/2016-DL (HPP MC) and 1264/2015-DL (HPP 14).

Simultaneously with ichthyoplankton sampling, the following environmental variables were measured: water temperature (°C), dissolved oxygen (mg/L), pH, conductivity (μS/cm-1), transparency (m) and width (m). Transparency was measured with Secchi disk during daytime sampling (9:00 a.m.). Daily flow data (m^3/s) (discharge) of each site were provided by CERAN. These variables were used in statistical analyses to determine the influence of environmental characteristics on the dynamics of ichthyoplankton. Additionally, to measure the influence of longitudinal fragmentation, the distance of the dam-free river (km) was measured, considering the sum of free stretches upstream and downstream of each site, using Google Earth Pro software (http://www.google.com/earth). The stretch of the channel centerline was used as base (Dudley, Platania, 2007). This variable was presented only to improve understanding of the compartmentalization of environments and was not used in statistical analyses.

Laboratory analysis. The larvae were identified using the development regressive sequence (Ahlstrom, Moser, 1976; Nakatani *et al*., 2001) and classified into the following developmental stages: yolk-sac larvae, preflexion, flexion and postflexion (Ahlstrom *et al*., 1976, modified by Nakatani *et al*., 2001). Larvae that could not be identified at least to the level of order were classified as "unidentified" (newly hatched larvae), whereas those that were damaged in some physical aspects were classified as "unidentifiable".

To evaluate the reproductive strategy, the larvae identified at least at the genus level were classified according to the reproductive guild to which they belong, indicating if some type of migration and parental care is present (Balon, 1975; Vazzoler, 1996; Luz-Agostinho *et al*., 2010). Vouchers were deposited in the Ichthyology Collection of Nupélia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura), Universidade Estadual de Maringá (from NUP 23270 to 23294).

Data analysis. The abundance of the organisms captured was standardized to a volume of 10 m^3 of filtered water, according to Tanaka (1973) and modified by Nakatani *et al.* (2001). In addition, the frequency of occurrence of each taxonomic group (including larvae caught in the light trap) was calculated at each site. The total abundance (number) and proportional composition (%) were used only as complementary information in the species composition table (Tab. 1), whereas the density (ind./10m^3) was used in the exploratory statistical analyses.

Spatial differences in total egg and larval densities, as well as the influence of categorical factors (sampling sites and months), their interactions, and environmental variables on this abundance, were evaluated using Generalized Linear Models (GLMs) with a negative binomial distribution to minimize overdispersion, implemented via a function from the *MASS* package (Ripley *et al*., 2020). The modeling began with a full model including all predictors and their interactions, followed by a backward stepwise selection based on the Akaike Information Criterion (AIC) using the *stepAIC* function, supported by likelihood ratio tests to assess improvements in fit. In the final model, only statistically significant variables and interactions were retained to ensure parsimony and avoid overfitting. When results indicated significant effects, *post-hoc* tests were performed using the *emmeans* package to conduct pairwise comparisons.

The same analytical procedures were applied to assess differences in larval density across each developmental stage (response variable) between sampling sites and collection months (fixed factors), as well as their interaction. In cases where a significant interaction was detected, pairwise comparisons were conducted to examine differences in larval densities across sampling sites and months. The identification of preferential areas for spawning and growth was based on the premise that high concentrations of eggs and larvae in early developmental stages (yolk-sac and preflexion) indicate potential spawning sites, while sites with larvae in advanced developmental stages (flexion and postflexion) are considered growth areas, as proposed by Bialetzki *et al.* (2004).

To represent the interactions between sampling sites and the different developmental stages of fish larvae, a bipartite plot was constructed using the *bipartite* package (Dormann *et al*., 2020). The interaction matrix was generated using the *frame2webs* function (Dormann *et al*., 2020). Based on the resulting matrix, the specialization index H_2 was calculated. This standardized metric quantifies the degree of specialization in the network, with values ranging from 0 (minimal specialization) to 1 (maximum specialization) (Blüthgen *et al*., 2006).

To verify if larval density (response variable) differs between reproductive guilds (sedentary without parental care - non-guarder/SNG; sedentary with parental care - guarder/SG; and partial migrator/PM), and sampling sites, as well as the interaction between these two fixed factors, an analysis of GLM was used. If the interaction was verified, differences in the densities of each guild among the sampling sites were evaluated. Additionally, pairwise comparisons were performed using the *emmeans* package with Tukey's adjustment for multiple testing (Lenth, 2018). These comparisons were performed for each guild separately, assessing differences in larval density among all sampling sites within that guild.

To visualize the multivariate patterns, we performed NMDS (non-metric multidimensional scaling) using the *metaMDS* function from the *vegan* package, based on the Bray-Curtis dissimilarity matrix. The resulting ordination was plotted to illustrate the spatial distribution of samples and to identify potential groupings or gradients in species composition. To assess whether species composition differed among sampling sites, we performed a permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis dissimilarity index with 999 random permutations (Anderson, 2001). Following significant PERMANOVA results, we conducted *post-hoc* pairwise comparisons.

To summarize the influence of environmental conditions on the composition of fish larvae, we used dbRDA (distance-based redundancy analysis), a multivariate ordination technique that combines principal component analysis (PCA) with redundancy analysis (RDA), allowing the use of non-Euclidean dissimilarity indices, such as the Bray-Curtis index. This approach is particularly useful for ecological data, such as species abundance matrices, where the relationships between variables may not be linear (Legendre, Legendre, 1998), in which we consider the densities of taxonomic groups as the response variable to local conditions (Hammer *et al*., 2001). For this analysis, both the biotic and abiotic matrix data were composed of the mean values of the replicates obtained at each site. Axes 1 and 2 were also subjected to the permutation test (Permutest, 999 permutations) to verify their significance.

All analyses were performed using R software v. 4.5.0 (R Development Core Team, 2025) (Oksanen *et al*., 2007; Lenth, 2018; Dormann *et al*., 2020; Ripley *et al*., 2020).

RESULTS

Spatio-temporal distribution and development stages. A total of 5,681 eggs and 2,124 larvae were collected during the sampling period. Egg density varied significantly among sites (GLM: $p < 0.001$) and sampling months (GLM: $p < 0.001$) (Fig. 2A). Additionally, the interaction between month and sites was highly significant, although no clear pattern was observed, indicating that the effect of the month depends on the sites (GLM: $p < 0.001$). Overall, Site S3 presented the highest estimated egg density (GLM: Est = 1.44, $p < 0.0001$), followed by S4 (GLM: Est = 1.03, $p < 0.0001$). Among the sampled months, December exhibited the highest egg density (GLM: Est = 2.02, $p < 0.001$), followed by November (GLM: Est = 0.22, $p < 0.001$). (Fig. 2A). Considering the interaction of factors, the highest egg densities were recorded in November at S3 (GLM: Est = 1.38, $p = 0.005$). *Post-hoc* tests indicated significant differences between sites S1–S3 (GLM: Est = –1.28; $p < 0.001$), S1–S4 (GLM: Est = –0.87; $p = 0.03$) and S2–S3 (GLM: Est= 0.94; $p = 0.008$).

Larval density varied significantly among sampling sites (GLM: $p < 0.001$) and across sampling months (GLM: $p < 0.001$) (Fig. 2B). The interaction between these factors was also significant (GLM: $p < 0.001$), suggesting that the effect of the month depends on the sampling sites. Site S1 exhibited the highest estimated larval density (GLM: Est = 0.36, $p = 0.03$) (Fig. 2B). Among the months, November showed the highest larval density (GLM: Est = 1.86, $p < 0.001$). Considering the sampling × month interaction,

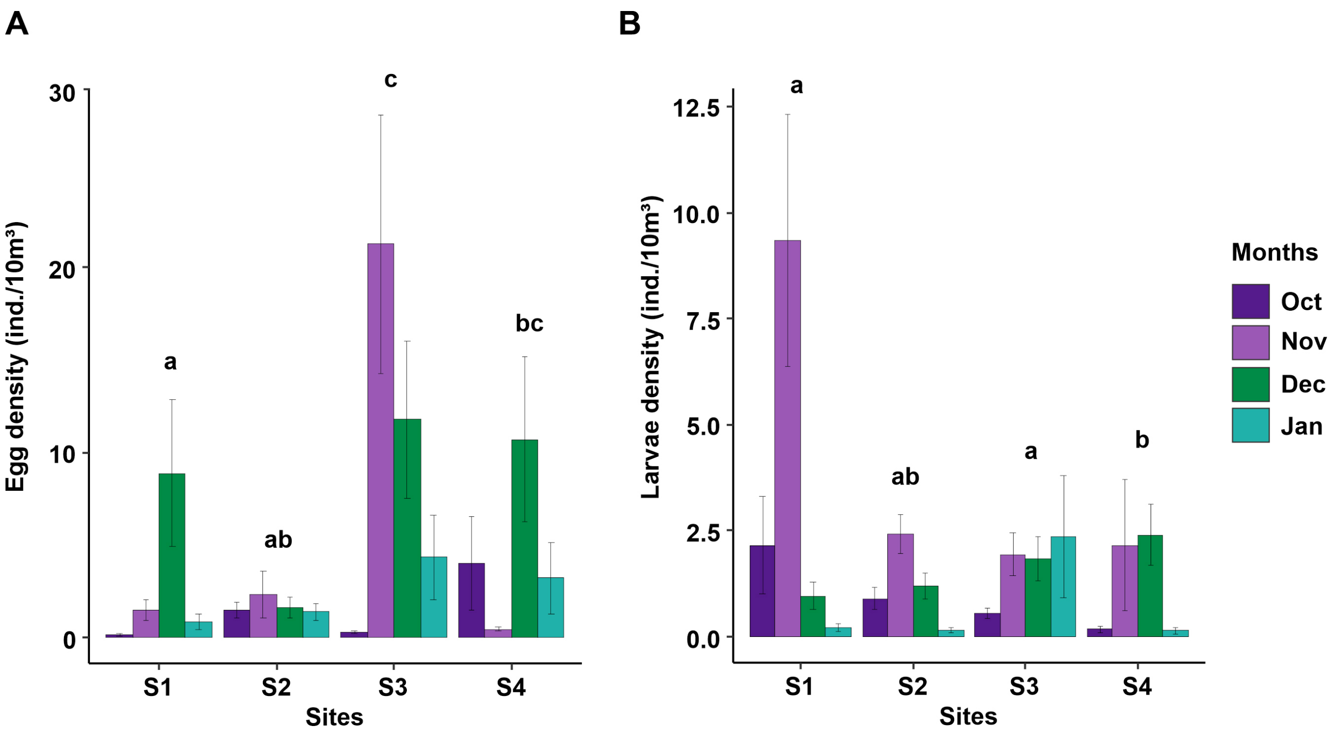

FIGURE 2 | Spatio-temporal distribution of ichthyoplankton density (individuals/10 m³) at sampling sites between October 2016 and January 2017 in the Rio das Antas Energy Complex (CERAN), Brazil. **A.** Fish eggs. **B.** Fish larvae. Months: October (Oct), November (Nov), December (Dec) and January (Jan).

the highest larval densities were observed at S1 in November (GLM: Est = 2.24, $p < 0.0001$). Significant differences were observed between sites S1 and S4 (GLM: Est = 0.85; $p = 0.01$) and S3 and S4 (GLM: Est = –0.86; $p = 0.007$) (Fig. 2B).

Regarding developmental stages, distinct patterns were observed along the longitudinal gradient among the sampling sites (Fig. 3A). For the yolk-sac stage, a significant difference was detected at S3 in November (GLM: Est = 2.38; $p < 0.001$), indicating an increase in larval density at this site during that month compared to the others. Mean yolk-sac densities were highest at S3 (0.97 ind./10 m^3), while preflexion reached its highest value at S1 (2.39 ind./10 m^3), both substantially exceeding the values recorded at the other sites (Fig. 3A). Advanced stages, flexion and postflexion, presented low densities at all sites, with a slight trend of increasing postflexion at S4 (0.04 ind./10 m^3) (Fig. 3A). Pairwise comparisons indicated that S1 and S2 were statistically different from S3 and S4 (Fig. 3A). Temporally, this spatial pattern was accompanied by an increase in mean densities in November, particularly for preflexion (2.71 ind./10 m^3), which was higher than the mean recorded in December (0.99 ind./10 m^3) (Fig. 3B). Flexion and postflexion larvae remained at low densities throughout the sampling period (< 0.25 ind./10 m^3) (Fig. 3B).

The bipartite plot represented in Fig. 4 illustrates the interaction between sampling sites along the cascade of dams and the different larval developmental stages, considering the frequency of occurrence of each stage. It is observed that the early developmental stages (yolk-sac and preflexion) are more frequently observed at sites S1, S2, and S3. In contrast, postflexion larvae were more frequently at sites S4. Despite

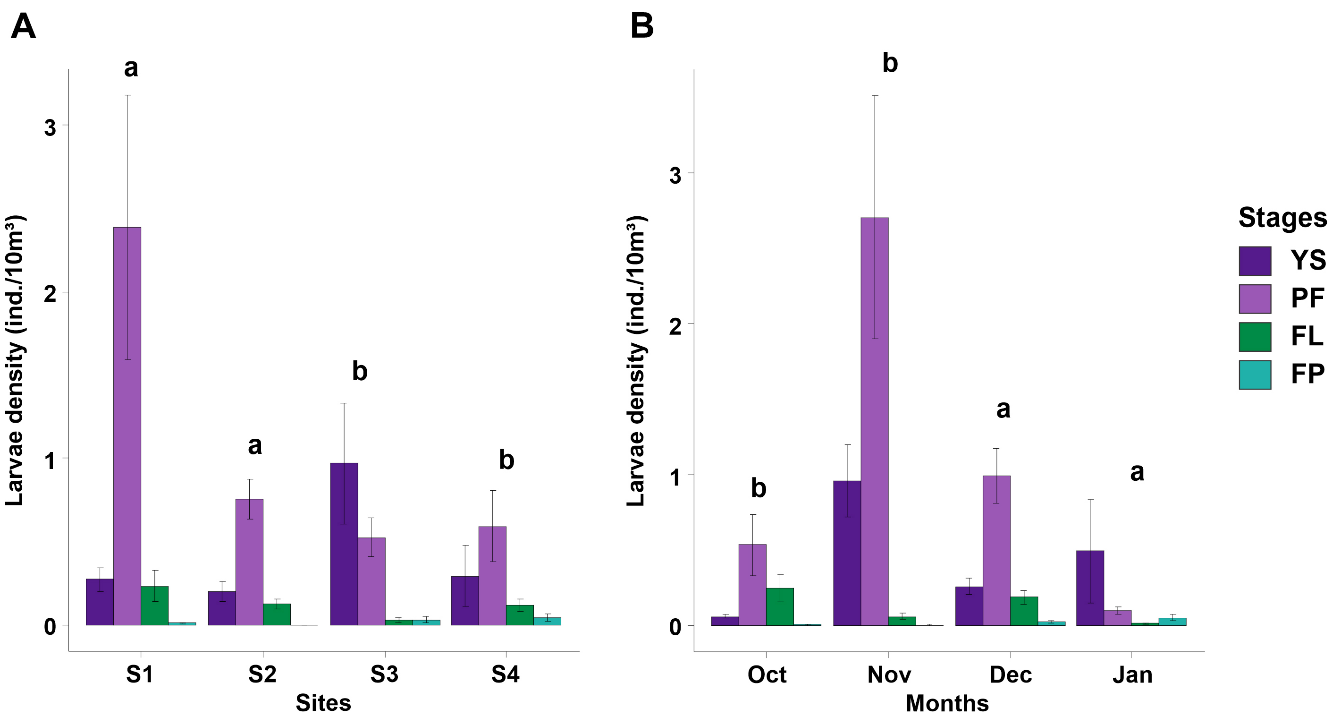

FIGURE 3 | Larval density (individuals/10 m^3) at the Rio das Antas Energy Complex (CERAN), Brazil. **A.** Sampling sites (S1–S4); **B.** Months (October 2016 to January 2017). Larvae developmental stages: YS (yolk-sac), PF (preflexion), FL (flexion), and FP (postflexion). Months: October (Oct), November (Nov), December (Dec) and January (Jan).

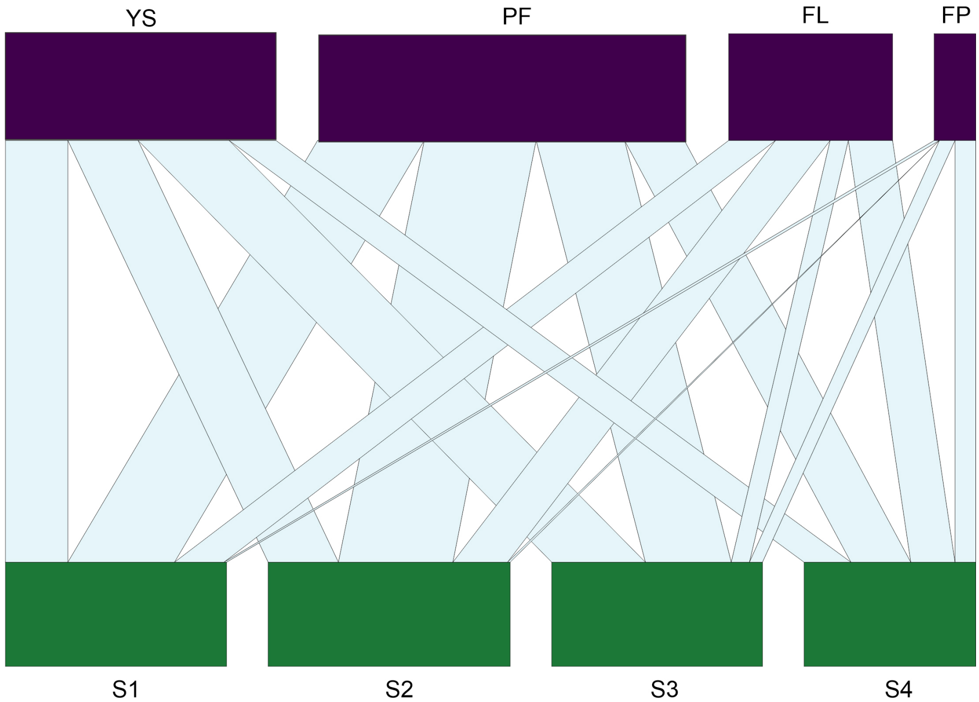

FIGURE 4 | Bipartite plot demonstrating the relationship between larval development stages (purple) and sampling sites (green) at the Rio das Antas Energy Complex (CERAN), Brazil. The width of the bars is proportional to the occurrence of larvae. The bands (light blue) and lines (gray) represent the stage-location connection, wider bands indicating stronger interactions. Larvae developmental stages: YS (yolk-sac), PF (preflexion), FL (flexion) and FP (postflexion).

this, the specialization index value was H_2 = 0.045, demonstrating low specialization of interactions. This means that the distribution is relatively homogeneous across the stages and sampling points. Thus, there is no clear upstream–downstream progression trend of spawning.

Ichthyoplankton density x Environmental variables. Regarding the environmental variables, water temperature ranged from 18.63 to 26.15°C at the sampling sites. Transparency varied from 0.53 to 1.42 cm, while dissolved oxygen levels ranged from 5.30 to 9.98 mg/L. pH varied from 7.02 to 8.15, and electrical conductivity ranged from 19.63 to 39.13 μS/cm. Precipitation during the sampling months ranged from 0 to 6.89 mm, with notable differences in rainfall distribution between the sampling sites. Finally, the flow rate varied from 18.67 to 1528.4 m^3 (Tab. **S2**).

For the eggs, the GLM results indicated that the variables dissolved oxygen (GLM: Est = –0.61; $p < 0.01$) and water transparency (GLM: Est = –1.09; $p < 0.01$) had significantly negative effects on the eggs density (Fig. 5A). This indicates that increasing these variables decreases the probability of egg occurrence. Furthermore, dissolved oxygen had the strongest effect, indicating that higher concentrations are associated with lower egg density. Similarly, water transparency also had a significant negative effect, suggesting that clearer waters are correlated with lower egg density. Furthermore, pH had a significant positive effect on egg density (GLM: Est = 0.64; p = 0.05), while

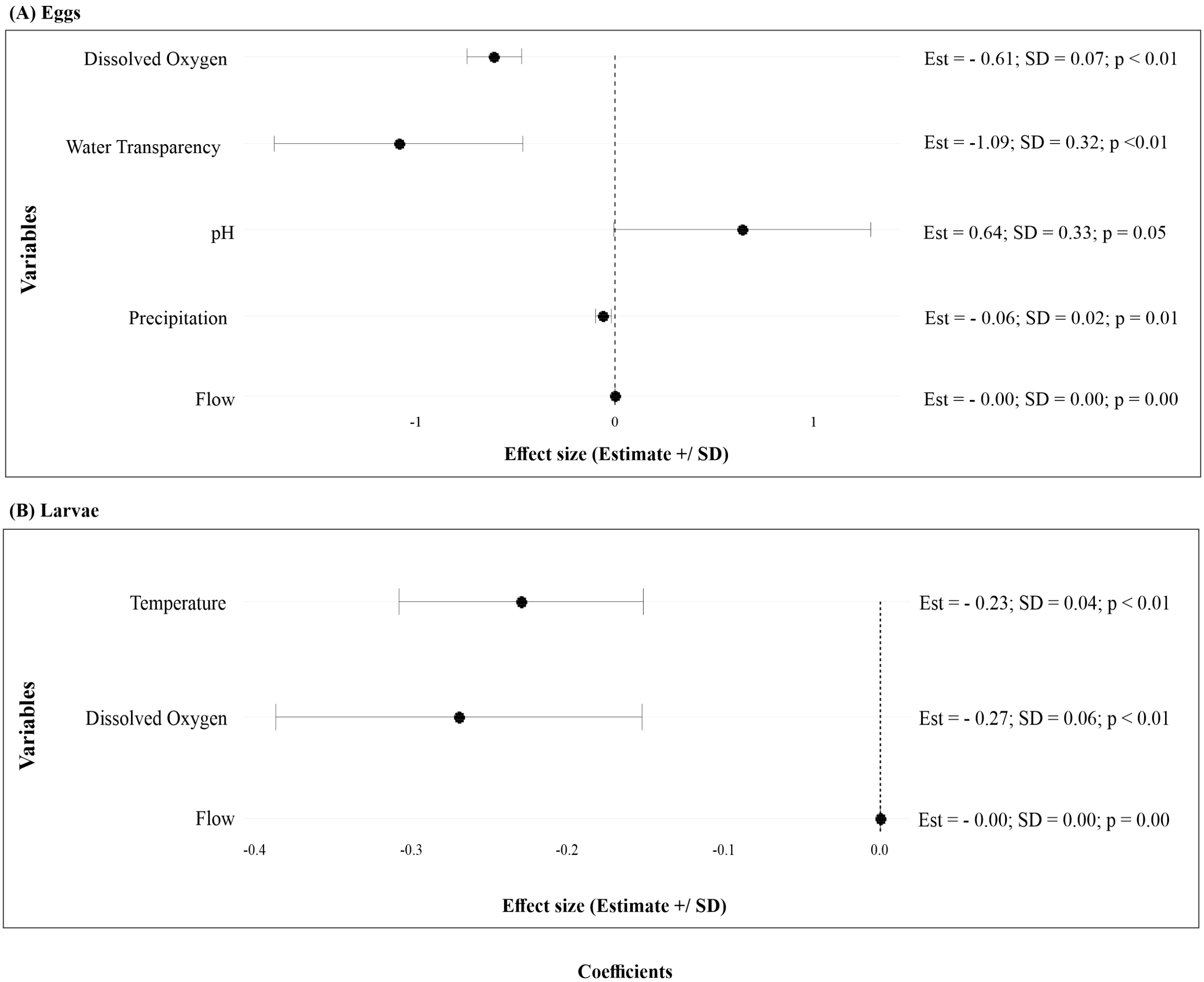

FIGURE 5 | Forest plot representing the Generalized Linear Models (GLM) to explain the relationship between environmental variables and ichthyoplankton densities. **A** | Fish eggs. **B** | Fish larvae. Estimates (Est) and Standard deviation (SD).

precipitation (GLM: Est = –0.06; $p = 0.01$) and flow (GLM: Est = –0.002; $p = 0.00$) had significant negative effects (Fig. 5A). These results indicate that higher pH levels positively influence egg density, while increased precipitation and flow have negative effects, meaning that higher values of these variables reduce egg density. On the other hand, temperature and conductivity did not show significant relationships with egg distribution (GLM: $p > 0.05$).

For larvae, temperature had a significant negative effect on abundance (GLM: Est = –0.23; $p < 0.01$), indicating that higher temperatures were associated with lower larval densities (Fig. 5B). In addition, dissolved oxygen (GLM: Est = –0.27; $p < 0.01$) and flow (GLM: Est = –0.00; $p < 0.01$) also showed significant negative effects on larval distribution (Fig. 5B). Other environmental variables (water transparency, pH, conductivity, precipitation), did not show significant effects (GLM: $p > 0.05$).

Taxonomic composition × Environmental and reproductive guild variables. A total of 20 taxa were identified at the lowest possible taxonomic level, encompassing four orders – Atheriniformes, Characiformes, Cichliformes, and Siluriformes. Characiformes was the most abundant group, followed by Siluriformes (Tab. 1). Among the identified taxa, 10 were determined at the species level, six at the genus level, and four at the family level. The assemblage was dominated by small-sized species, particularly those from the genera *Astyanax*, *Psalidodon* and *Bryconamericus*, which contributed the most to overall abundance and larval density. In relation to the guilds there was a predominance of sedentary species with no parental care (Tab. 1).

The NMDS analysis revealed variations in the positioning of species along the axes (Fig. 6). The samples were evenly distributed positioned along axis 1 and 2. On axis 1, sites S1 and S2 exhibited a positive clustering, whereas sites S3 and S4 were dispersed along this axis (Fig. 6). The final solution obtained a stress of 0.17. The PERMANOVA test showed that the site factor (sampling location) has a significant effect on species composition ($p = 0.001$). The *post-hoc* test indicated significant differences between S1 and S3 ($p = 0.02$), S1 and S4 ($p = 0.01$), and S2 and S4 ($p = 0.02$). Sites S2 and S3, within the complex, have similar composition, with no significant differences between them.

The results of the db-RDA show that the environmental variables included in the model explain a significant portion of the variation in species composition (db-RDA: $F = 3.28$, $p = 0.001$) (Fig. 7). The *post-hoc* test revealed significant influences of transparency ($F = 6.24$; $p = 0.001$), pH ($F = 5.63$; $p = 0.001$), flow ($F = 3.50$; $p = 0.001$), temperature ($F = 2.29$; $p = 0.014$), dissolved oxygen ($F = 2.28$; $p = 0.019$), and conductivity ($F = 0.776$; $p = 0.036$) on community structure, whereas precipitation showed no significant differences ($F = 1.060$; $p = 0.366$). These results emphasize the strong influence of abiotic factors on species distribution and composition along the studied stretch.

The GLM indicated significant effects of reproductive guild (GLM: Est = 283.97; $p < 0.0001$) and sampling site (GLM: Est = 23.76; $p < 0.0001$) on larval density, as well as a significant interaction between these factors (GLM: Est = 51.35; $p < 0.0001$). Multiple comparisons revealed that, overall, the SNG guild exhibited higher densities than the other guilds at most sampling sites, except in S3, where PM exceeded SG ($p < 0.0001$) (Fig.8). These results indicate that differences among guilds vary according to position, reinforcing the importance of the interaction between these factors. Pairwise comparisons within each guild showed that for PM, densities in S3 were significantly higher than at all other sites ($p < 0.01$) (Fig. 8). For SG, no significant differences were detected among sites ($p > 0.85$) (Fig. 8). For SNG, densities in S1 were significantly higher than in S2, S3, and S4 ($p < 0.001$), while no significant differences were observed among the latter three sites (Fig. 8).

TABLE 1 | Taxonomic groups, reproductive strategy (RS), abundance (Ab) and total density of larvae, as well as frequency of occurrence of each taxa and development stages of the fish recorded in the Rio das Antas Energy Complex, during the period October 2016 to January 2017. The taxonomy classification followed Betancur-R *et al.* (2013), and Fricke *et al.* (2025). Sampling site (S). Reproductive strategy: PM – Partial Migrator; S – Sedentary; G – Guarder; NG – Not Guarder. Larvae development stages: YS (yolk-sac), PF (preflexion), FL (flexion) and FP (postflexion). * indicates capture in the light trap. Density scales: a: 0.01–1.00; b: 1.01–5.00; c: 5.01–26.00 (%).

Taxa	RS	Ab (nº)	Density (ind./10m³)	S1				S2				S3				S4			
				YS	PF	FL	FP	YS	PF	FL	FP	YS	PF	FL	FP	YS	PF	FL	FP
CHARACIFORMES																			
Crenuchidae																			
Characidium orientale Buckup & Reis, 1997	S; NG	39	9.36		a								a				b*	a	a
Erythrinidae																			
Hoplias sp.	S; G	16	3.69		a	a*											a*	a*	
Stevardiidae																			
Bryconamericus iheringii (Boulenger, 1887)	S; NG	366	111.18	b	b*		a*	b	b*	a	a*	b*	b*	a*	a*	b*	b*	a*	a*
Bryconamericus sp.	S; NG	19	4.65		a*				a*				a				a*		
Diapoma alburnus (Hensel, 1870)	S; NG	3	1.01												a				a
Characidae																			
Charax stenopterus (Cope, 1894)	S; NG	1	0.36											a					
Acestrorhamphidae											a								
Oligosarcus jenynsii (Gunther, 1964)	S; NG	1	0.13								a								
Oligosarcus sp.	S; NG	5	1.68						a	a									
Astyanax sp.	S; NG	7	1.27				a*										a*		a
Psalidodon aff. *fasciatus* (Cuvier, 1819)	S; NG	1031	322.36		c	a			b*	b*			b*	a*		a	b*	a*	
Acestrorhamphidae morphotype 1		1	0.47		a														
SILURIFORMES																			
Auchenipteridae																			
Glanidium sp.	S; G	7	3.65												a				a
Heptapteridae																			
Rhamdia aff. *quelen* (Quoy & Gaimard, 1824)	S; NG	15	4.27	a	a	a				a			a	a				a	a
Heptapteridae morphotype 1		60	20.97		a	b	a			a								a	
Heptapteridae morphotype 2		2	0.51																a
Loricariidae																			
Loricariichthys anus (Valenciennes, 1836)	S; G	2	0.27																a
Pimelodidae																			
Pimelodus pintado Azpelicueta, Lundberg & Loureiro, 2008	PM; NG	202	99.60	a				a	a	a		c	a			a	a	b	a
Pimelodidae morphotype 1	PM; NG	133	46.40	b	a	a		b	b			a	a			a			
ATHERINIFORMES																			
Atherinopsidae																			
Odontesthes sp.	S; NG	27	0.93										a*				b*	a	
CICHLIFORMES																			
Cichlidae																			
Crenicichla punctata Hensel, 1870	S; G	1	0.57																a
Unidentified		4	1.30						a			a							
Unidentifiable		182	53.80	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
Total		2124	688.44	b	c	b	a	b	c	b	a	c	c	a	a	b	c	b	a

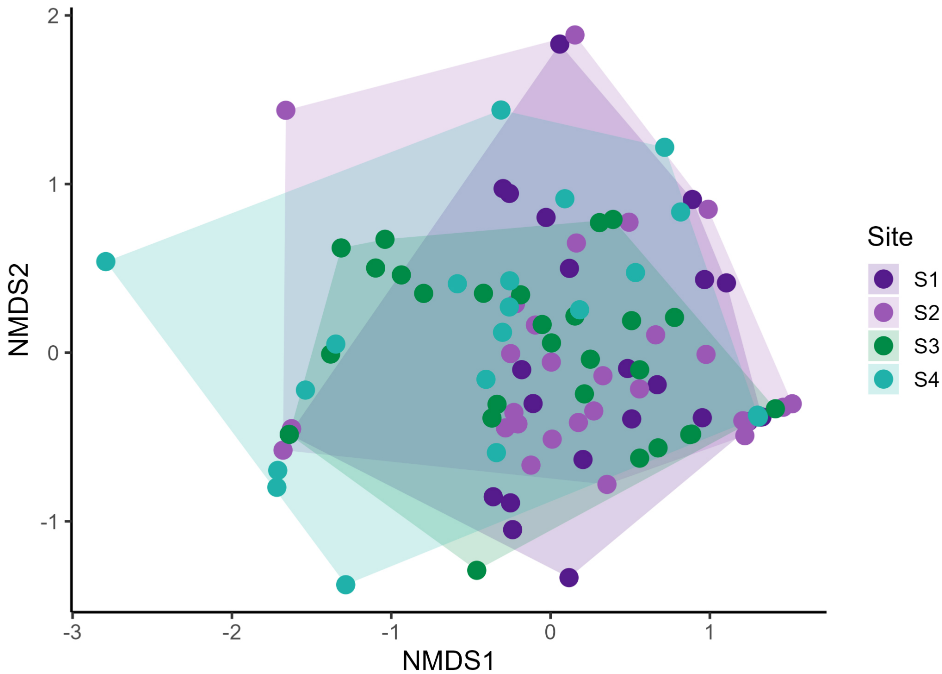

FIGURE 6 | Representation of Nonmetric Multidimensional Scaling (NMDS) among sampling sites (S1–S4) based on species composition between October 2016 and January 2017 in the Rio das Antas Energy Complex (CERAN), Brazil.

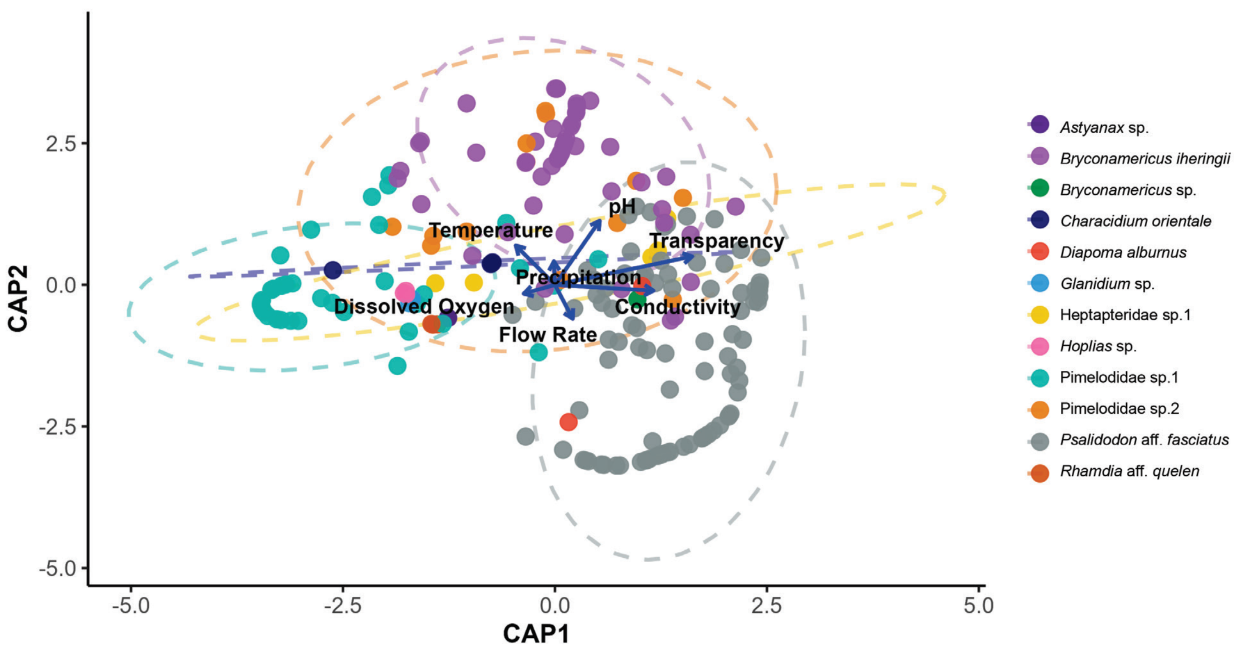

FIGURE 7 | Distance-Based Redundancy Analysis (db-RDA) of species composition in relation to environmental variables between October 2016 and January 2017 in the Rio das Antas Energy Complex (CERAN), Brazil.

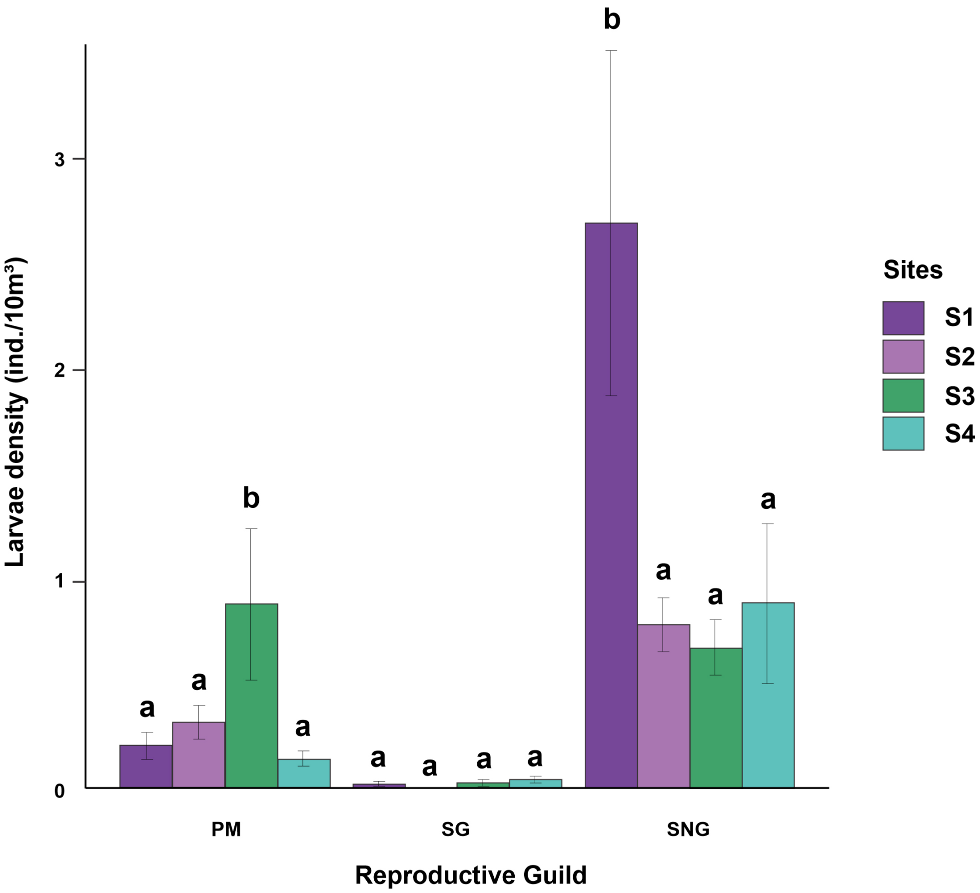

FIGURE 8 | Spatial distribution of reproductive guilds of fish larvae (individuals/10m^3) at sampling sites (S1–S4) between October 2016 and January 2017 in the Rio das Antas Energy Complex (CERAN), Brazil. Reproductive guilds: Partial Migrator (PM), Sedentary without parental care - non-guarder (SNG) and Sedentary with parental care - guarder (SG).

DISCUSSION

Our results demonstrated that the structure of ichthyoplankton was influenced by spatial and seasonal environmental variations, corroborating our first hypothesis. The presence of run-of-river (ROR) systems operating in cascade alters the hydrological regime and physical characteristics of the river, likely influencing the spatial and temporal distribution of eggs and larvae in the Rio das Antas Energy Complex (CERAN). Early larval stages (yolk-sac and preflexion) were indeed more abundant, especially in the upstream (S1) and intermediate (S3) reaches. Nevertheless, despite the tendency for more developed larvae in S4, the expected longitudinal progression to more advanced stages (flexion and postflexion) was not observed. The observed patterns diverge from those expected in a free-flowing and continuous river, refuting our second hypothesis. These findings suggest that reproduction is not restricted to specific sections of the river but occurs at multiple sites along the gradient, as expected in environments dominated by non-migratory species. Furthermore, the absence of reproductive records for migratory species historically present in this basin (Alves, Fontoura, 2009; Luz-

Agostinho *et al*., 2010; Becker *et al*., 2013), strongly supports our prediction that the fragmentation caused by the dam cascade disrupts larval drift and acts as an ecological filter, affecting species dispersal and recruitment. Hydraulic retention caused by dams, combined with changes in flow regime and sediment transport, can reduce longitudinal connectivity and disrupt the natural dispersion of eggs and larvae (Agostinho *et al*., 2007; Pompeu *et al*., 2012).

The differences in density and species composition between the extreme sites of the complex (S1 and S4) and those of the intermediate sections highlight the tendency for connectivity to be disrupted along the river continuum. The highest densities of larvae in S1 (particularly at the early stage - preflexion), observed in November, may indicate a spawning pulse. This pattern is typical of opportunistic species with prolonged reproductive cycles, which are common in dam-impacted systems (Winemiller, 1989; Agostinho *et al*., 2004). The S1 is connected to the upstream basin and free of dams, reflecting the highest density of larvae, especially of the sedentary guild without parental care (SNG), suggesting that the larvae normally derive from upstream spawning sites.

Although hydrologically altered due to its location in a reduced flow section (RFS), S4 benefits from its direct connection to the downstream river network. The absence of physical barriers about 200 km downstream of the last dam of the complex (HPP 14) possibly enables a greater number of species to reach this RFS. This feature provides exclusive characteristics for this stretch and can help explain the distinct species composition found at this site. In addition, the tendency for more developed larvae in RFS environments may be related to the reduced water velocity in these environments, rather than the natural drift of the larvae. The formation of RFS modifies flow patterns (Singh, Agarwal, 2017) and, consequently, larval drift, promoting the formation of environments suitable for the development of fish stages, which reach more advanced stages in shorter river stretches. Although speculative, these findings suggest that, although reproduction occurs throughout the system, the changes imposed by dams may redefine key hydrological conditions, especially for the final stages, which may compromise the recruitment of juveniles and, consequently, the long-term maintenance of the population.

The high density of eggs and larvae in early stages at S3, a highly fragmented environment between two dams, was notably associated with *Pimelodus pintado*, a species with partial migration. The reproductive success of *P. pintado* at S3 is particularly interesting, as it corroborates the tendency of it not to be a migratory species (Alves, Fontoura, 2009; Luz-Agostinho *et al*., 2010; Becker *et al*., 2013), with continuous reproductive records in impacted environments (Hermes-Silva *et al*., 2009; Reynalte-Tataje, *et al*., 2012a). Although it is a species historically established along the studied stretch (Alves, Fontoura, 2009; Becker *et al*., 2013), our results suggest a remarkable adaptation of this species to the changes imposed by hydroelectric dams. This condition cannot be attested for the migratory species of the basin, previously distributed along the CERAN Complex (Alves, Fontoura, 2009; Luz-Agostinho *et al*., 2010; Becker *et al*., 2013), at least in the stretch corresponding to sampling sites S2, S3, and S4. Therefore, it is reiterated that the absence of reproductive evidence of migratory species, proven to be present in the section studied before the interventions caused by the dam cascade, represents strong evidence of a synergistic impact imposed by fragmentation. In this sense, it is important to note that the dispersion of ichthyofauna to the upper Antas

River was potentially already limited by the presence of a natural barrier named "Cachoeirão" (Luz-Agostinho *et al*., 2010; Becker *et al*., 2013), located upstream of S2. Thus, the differences in egg and larval densities, as well as in the species composition of S2 compared to the others, can be explained by the combination of the presence of the natural barrier and the impacts of the cascade of dams, given that this location is the most segmented and has the lowest remaining discharge of the dam upstream.

Associatedly, analyses indicated that environmental variables such as dissolved oxygen, water transparency, flow, and temperature significantly influence egg and larval abundance, highlighting the central role of physicochemical conditions on ichthyoplankton dynamics. These results support previous studies showing the sensitivity of early fish ontogenetic stages to environmental variation (Nakatani *et al*., 2001; Bialetzki *et al*., 2005). It is important to note that the oxygenation pattern may be related to its inverse correlation with temperature, since the reproductive period coincides with the hottest months and lower water oxygenation.

For eggs, density was negatively correlated with dissolved oxygen, water transparency, precipitation, and flow, important features for successful spawning (Sanches *et al*., 2006; Tondato *et al*., 2010; Ziober *et al*., 2012; Souza *et al*., 2024). These patterns suggest that more turbid, less oxygenated waters may be associated with higher egg deposition, possibly due to enhanced retention or reflecting zones of lower deep and hydrological turbulence, commonly observed in RFS sections during periods of lower rainfall. The influence of RFS formation on the ichthyoplankton can also be seen in the negative ordering of flow. Overall, it may also indicate that high-flow peaks promote egg dispersion or loss, hindering retention in sampling areas. For larvae, negative effects of temperature, dissolved oxygen, and flow suggest that more stable environments with lower thermal variation and reduced flow favor larval presence and maintenance. The low flow may facilitate larval retention in marginal or backwater zones, which have lower flow energy and greater food availability (Pavlov *et al*., 2008).

The pattern of influence of environmental variables on the composition of ichthyoplankton were also corroborated by the db-RDA, which showed that variables such as temperature, transparency, dissolved oxygen, pH, conductivity, and flow explain a significant portion of the variation in sample composition. These results suggest that even small differences in environmental attributes can shape the presence or absence of certain taxa, as also reported by Agostinho *et al*. (2004) and Baumgartner *et al*. (2008). The relevance of flow and transparency as explanatory vectors suggests that species with different ecological requirements may respond differently to flow intensity and light availability. For instance, pelagic species tend to occur in clearer water stretches, whereas demersal species or those associated with substrate structure may prefer more turbid environments, which offer better protection from predators (Reynalte-Tataje *et al*., 2013).

In summary, the cascade of dams in the run-of-river system acts as a modulator of the structure and dispersion of ichthyoplankton. The results indicate that the complex functions as a filter, preventing the natural drift of larvae and the establishment of migratory species historically present in the study area, favoring the reproduction of sedentary and generalist species. The distinct dynamics observed at sites S1 (connected upstream) and S4 (connected downstream) highlight the critical importance of longitudinal connectivity for maintaining ichthyofaunal diversity. In addition, the absence of a clear pattern of longitudinal progression in the larval stages suggests that connectivity between river sections may be limiting the dispersion of eggs and larvae. The negative association between variables such as dissolved oxygen, flow, temperature, and egg and larval densities reinforces the sensitivity of ichthyoplankton to environmental changes caused by the formation of RFS, a condition that requires special attention during critical periods, such as prolonged droughts during reproductive seasons. From a conservation perspective, this scenario of changes calls into question the sustainable image attributed to ROR systems, especially when implemented in cascades, and reinforces the need for public policies that consider the synergistic impacts of this type of project. Strategic measures that promote reproduction and early development, as well as continuous monitoring of ichthyofauna and the environmental variables that directly influence these ecological processes, are essential. Integrated management of the hydroelectric plants should prioritize not only energy generation but also the maintenance of mechanisms that support aquatic biodiversity.

ACKNOWLEDGMENTS

This work had the incentive and support of Energetic Company Rio das Antas. We are grateful to Luis F. Beux (*in memoriam*) and Fernanda F. Brol from the Aquática Consultoria e Assessoria Ltda., for technical support and data collection. We are indebted to Prof. Dr. David A. Reynalte-Tataje for the valuable contributions in identifying the larvae. We thank Gabriela Medeiros and Débora R. de Carvalho for their graphic contributions.

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AUTHORS' CONTRIBUTION

Douglas Ticiani: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Writing-original draft.
Andrea Bialetzki: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Visualization, Writing-review and editing.
Jislaine Cristina da Silva: Formal analysis, Methodology, Validation, Visualization, Writing-original draft.
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Rosilene Luciana Delariva: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Visualization, Writing-review and editing.

FUNDING INFORMATION

The authors did not receive funding for this research.

ETHICAL STATEMENT

The sampling procedures followed the specifications of the monitoring project approved by the current environmental agency (Fundação Estadual de Proteção Ambiental Henrique Luiz Roessler), according to the following licenses: FEPAM 1353/2015-DL (HPP CA), 02844/2016-DL (HPP MC), and 1264/2015-DL(HPP14).

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

SUPPLEMENTARY MATERIAL

Supplementary material **S1**
Supplementary material **S2**

AI STATEMENT

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Ticiani D, Bialetzki A, Silva JC, Souza MBV, Delariva RL.** Ichthyoplankton in a regulated river: community structure and distribution patterns in a run-of-river dam cascade system in the Neotropics. Neotrop Ichthyol. 2025; 23(4):e250083. https://doi.org/10.1590/1982-0224-2025-0083

Neotropical Ichthyology

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