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Hydroelectric Dams Affect Hyporheic Copepod Diversity

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ABSTRACT

This study investigates the ecological impact of a small hydroelectric power plant (SHPP) on the hyporheic zone of the venacquaro stream (VEN), a low-order groundwater-fed stream in Central Italy. The hyporheic zone, a critical ecological interface where groundwater and surface water interact, plays a pivotal role in nutrient cycling, pollutant retention, and supporting aquatic biodiversity. However, hydrological alterations from activities such as damming pose significant threats to this zone. The research employs a three-pronged approach to assess the effect of a SHPP on hyporheic copepod communities. Copepods were selected as the focal group due to their dominance in this habitat. Initially, a generalized estimating equation (GEE) model was used to evaluate changes in copepod diversity, specifically alpha and beta diversity. The study then examines environmental shifts caused by the SHPP using permutational analysis of variance (PERMANOVA) and principal component analysis (PCA). Lastly, a multivariate species distribution model (mSDM) explores correlations between environmental variables and copepod abundances. Results reveal significant alterations in copepod assemblage structure and environmental variables downstream of the SHPP. The GEE model indicates a notable shift in beta diversity, primarily driven by disruptions in hyporheic connectivity rather than environmental changes alone. This disruption favours stygobitic species downstream, suggesting the influence of groundwater upwelling. Environmental analysis shows several differences between upstream and downstream sites, with changes in parameters such as pH, temperature, and dissolved organic carbon. The study highlights the need for effective management strategies to mitigate sediment accumulation and maintain habitat quality in SHPP-affected streams. Techniques like sediment bypass tunnels (SBTs) are recommended to preserve both economic and ecological values. This research contributes to the still limited understanding of SHPP impacts on hyporheic ecosystems, emphasizing the importance of considering these effects in hydropower development and riverine ecosystem conservation.

1 | Introduction

Based on a recent review by Boyer et al. (2024), the definition of the hyporheic zone slightly varies across different disciplines within environmental sciences. However, it is generally described as a critical ecological interface (i.e., an ecotone), located beneath and adjacent to streambeds, and serving as a nexus where shallow groundwater and surface water mix and interact within the voids of the porous medium. The hyporheic zone is influenced by a combination of physical, biological and biogeochemical factors, showing wide variations across different spatial and temporal scales (Gooseff 2010). This zone plays a significant role in stream ecosystems by modulating chemical and biological processes, which result in precious ecosystem services encompassing temperature and flood regulation (O'Sullivan et al. 2019), along with the cycling, retention and transformation of nutrients (Merill and Tonjes 2014) and pollutants, including microplastics (Lewandowski et al. 2019). Drawing from the river continuum concept, the hyporheic zone is also pivotal in maintaining vertical, longitudinal, and lateral connectivity in stream ecosystems (Doretto, Piano, and Larson 2020). Further, it serves as refuge and nursery for different life stages of various aquatic organisms (Mugnai, Messana, and Di Lorenzo 2015) and, importantly, supports a unique biodiversity exclusive of this ecotone. Indeed, being a triple ecotone between surface water, shallow groundwater and terrestrial environments, the hyporheic zone represents a complex mosaic of microhabitats for both stygobitic (i.e., obligate groundwater dwellers) and non-stygobitic species (Iepure et al. 2022). Within the aquatic invertebrate fauna, copepods (Crustacea: Copepoda) are the dominant group, closely matched by Ostracoda, Nematoda, and Oligochaeta (Malard et al. 2003; Galassi, Huys, and Reid 2009; Ranga Reddy 2014; Di Lorenzo, Stoch, and Galassi 2013; Mugnai, Messana, and Di Lorenzo 2015).

Hydrological alteration is one of the major threats to the hyporheic zone. Activities such as damming, channelization, and water extraction trigger changes in habitat conditions and nutrient fluxes that can potentially impact the survival of aquatic communities (Boulton et al. 2010). Numerous studies have detailed the impacts of flow alteration on the abiotic compartment of the hyporheic zone, including changes in flow dynamics (Arntzen, Geist, and Dresel 2006), oxygen concentration (Hancock and Boulton 2005; Nyberg, Calles, and Greenberg 2008), heat transport (Brookfield and Sudicky 2013), water chemistry (Siergieiev et al. 2014), and sediment deposition (Mcconchie, Toleman, and Hawke 2005; Quinlan et al. 2015). However, the specific effects of these environmental changes on hyporheic assemblages are still inadequately explored.

Dams, built on 60% of the world's rivers, are key anthropogenic factors causing hydrological alterations. Their presence and operation constitute a substantial risk to global freshwater aquatic ecosystems (Bednarek 2001; Friedl and Wüest 2002; Liew, Tan, and Yeo 2016; Santos et al. 2017; Benjankar et al. 2018; Wang et al. 2019; Maavara et al. 2020; Xie et al. 2021; Zhang et al. 2022; Guo et al. 2023; Chen et al. 2023). Dam construction across rivers serves multiple objectives, encompassing flood mitigation, enhancement of river navigability, recreational development, and production of hydroelectric power. The energy derived from hydropower stands as a dominant contribution to the renewable energy sector, accounting for approximately two-thirds of the world's electricity production from renewable sources (Ocko and Hamburg 2019). Although hydropower plants play a pivotal role in mitigating climate change effects, their infrastructures are increasingly recognized as potential disruptors of riverine ecosystems (Bejarano, Jansson, and Nilsson 2018; Hecht et al. 2019). Hydropower plants are typically categorized into large hydropower plants (LHPPs) and small hydroelectric power plant (SHPPs). The distinction between the two often revolves around their electricity generation capacity (Breeze 2014; Elbatran et al. 2015). LHPPs are usually defined as having a capacity of more than 10 MW (MW), while SHPPs typically have a capacity of up to 10 MW.

Although SHPPs are significant contributors to renewable energy, they are also associated with well-documented ecological impacts on surface water ecosystems like habitat fragmentation and biodiversity loss (Benejam et al. 2016; Lange et al. 2018; Kuriqi et al. 2021; Šarauskienė et al. 2021). In contrast, research on the impacts of SHPPs on the hyporheic zone remains scant. Apart from a single study by Bruno et al. (2009), this ecotone has largely been overlooked, suggesting a research gap in our understanding of the full ecological effects of SHPPs on riverine ecosystems as a whole.

The present study addresses this research gap by investigating, using a three-tiered approach, the impacts of SHPP on hyporheic invertebrates of a low-order, groundwater-fed stream in Central Italy. Given their abovementioned dominance in the hyporheic zone, copepods were selected as the target group for this analysis. Initially, through a generalized estimating equation (GEE) model we evaluated the influence of the SHPP on copepod diversity, specifically examining changes in alpha diversity (species richness) and beta diversity (species turnover). Further investigations delved into the environmental shifts prompted by the SHPP. Lastly, by employing a multivariate species distribution model (mSDM), we explored the correlations between environmental variables and copepod abundances.

2 | Study Area

The venacquaro stream (VEN) is an Apennine low-order stream which originates on the northwestern slope of Pizzo d'Intermesoli mountain (Abruzzo, Central Italy). In its upper section, the stream bifurcates into two tributaries. The western branch emerges as a significant contributor to the overall streamflow, with an average discharge of ~50 $L s^{-1}$, while the eastern one generally provides a minimal contribution, seldom exceeding 5 $L s^{-1}$ over the hydrological year. Previous findings (Petitta 2016) suggest that the western branch, unlike its eastern counterpart, is predominantly fed by groundwater from the Gran Sasso aquifer (recharge area ~1600 m asl). Conversely, the eastern branch relies predominantly on the replenishment derived from localized precipitation. The SHPP is located at 1000 m asl and about 150 m downstream of the intersection of the two tributaries.

3 | Material and Methods

3.1 | Sampling Survey

A stratified random sampling procedure was adopted for sampling both the U and D, with respect to the SHPP location, hyporheic zones of VEN (Figure 1). In total, 12 sites were sampled: 6 located in the U dam section (from VEN_1_U to VEN_6_U), hereafter referred as U stretch, and 6 from the downstream dam section (from VEN_1_D to VEN_6_D), hereafter referred as downstream stretch. We sampled each site twice a year, in winter (in December 2014 and January 2015) and in spring/summer (in May and June 2015). For each sample, 2–3 spatial replicates were taken. The hyporheic habitats were sampled using a Bou-Rouch pump. For each sample, 10 L of water was pumped at 50 cm depth and filtered through a hand net (mesh size 60 μm). The exhaustiveness of the sampling effort was assessed through species richness estimators. To evaluate how larger the total number of species in both systems can get through repeated sampling we used one parametric estimator (Michaelis–Menten; MM) and five non-parametric ones (Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap). Each estimator calculates the potential species richness (S) in relation to the sample size (Sobs). For

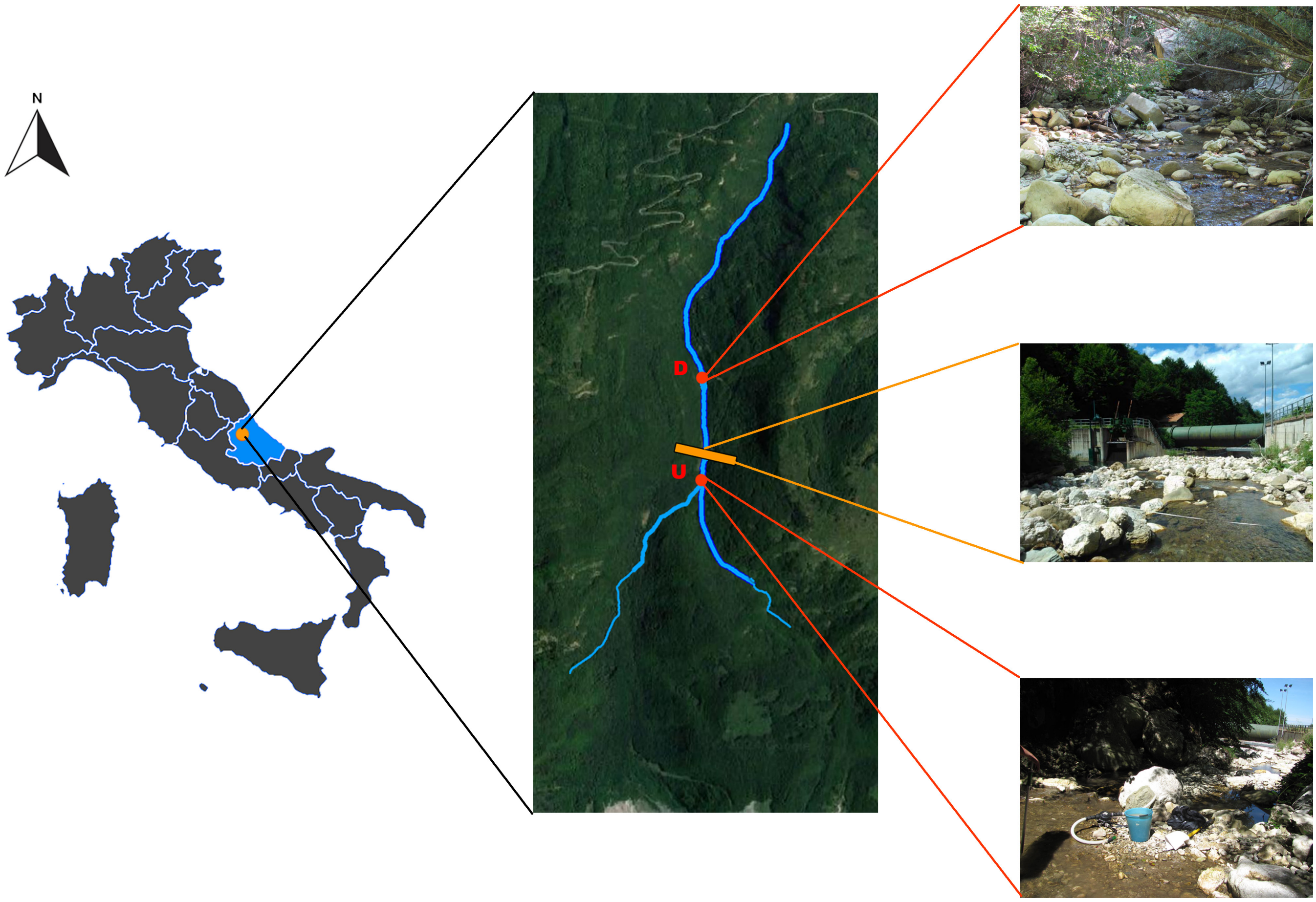

FIGURE 1 | Study area along the venacquaro stream (VEN) in the Apennine region of Abruzzo, Central Italy. Left: The location of VEN at national scale. Center: Hydrographic profile of VEN; red dots represent upstream (U) and downstream (D) sites, and the orange line indicates the location of the small hydroelctric power plant (SHPP), situated at 1000 m asl, approximately 150 m downstream from the confluence of the two tributaries of VEN. Right: Photographs of the SHPP, and downstream and upstream sampling locations. [Color figure can be viewed at wileyonlinelibrary.com]

each estimator, a curve showing the evolution of the predicted S was obtained by gradually increasing Sobs. Values were estimated with the E-PRIMER software (Clarke and Gorley 2015) by means of 999 randomizations without replacement.

For each biological sample, a set of chemical and physical parameters (temperature, pH, O_2 expressed both in mg L^{-1} and percentage of saturation, and electrical conductivity (E.C.) in µS cm^{-1}) was measured in the field with a WTW 3430 SET G multiparameter probe. Further, laboratory analyses were performed for 110 chemical compounds, namely: sulphates, phosphates (method: APAT CNR IRSA 4020 Man 292,003), nitrates, nitrites, ionized ammonium (method: 135 APAT CNR IRSA 4020 Man 292,003), metals (method: EPA 3005A 1992 + EPA 6010C/APAT CNR IRSA 3150C Man 29), pesticides (method: EPA 3510C 1996 + EPA 8270D 2007), volatile organic compounds (method: EPA 5030C 2003 + EPA 8260C 2006; EPA 8260 C 2006), hydrocarbons (method: EPA 3510C 1996 + EPA 8270D 2007) and dissolved organic carbon (DOC) and total organic carbon (method: ISO 8245: 1999). Particulate organic matter (POM) was estimated as weight loss on ignition: after removal of all the collected fauna, samples were dehydrated at 105°C (24 h) and weighed; the dry-weight samples were burnt at 540°C (4 h) in a muffle furnace and re-weighted to determine POM amount as the difference between dry and ashed mass (Fischer, Wanner, and Pusch 2002).

Biological samples were preserved in 80° ethyl alcohol and taken to the laboratory where the specimens were sorted under a Leica M205C stereomicroscope and identified to the species level taking advantage of taxonomic keys and other specialized literature (Borutzky 1952; Dussart 1967; Dussart 1969; Boxshall and Halsey 2004; Wells 2007).

3.2 | SHPP Dam Impacts on the Hyporheic Copepod Assemblage

We identified four ways in which the presence of the SHPP dam could affect the hyporheic copepod assemblage of VEN (Figure 2):

(a) The dam may not act as a disturbance factor, thus leaving the hyporheic copepod assemblage unaltered.

(b) The dam may lead to alterations in physicochemical parameters. As a result, a potential indirect impact of the dam on the hyporheic copepod assemblage could occur if the dwelling species demonstrate a strong dependence upon these specific parameters.

(c) The dam may result in downstream community alterations by serving as a physical barrier, thus disrupting the

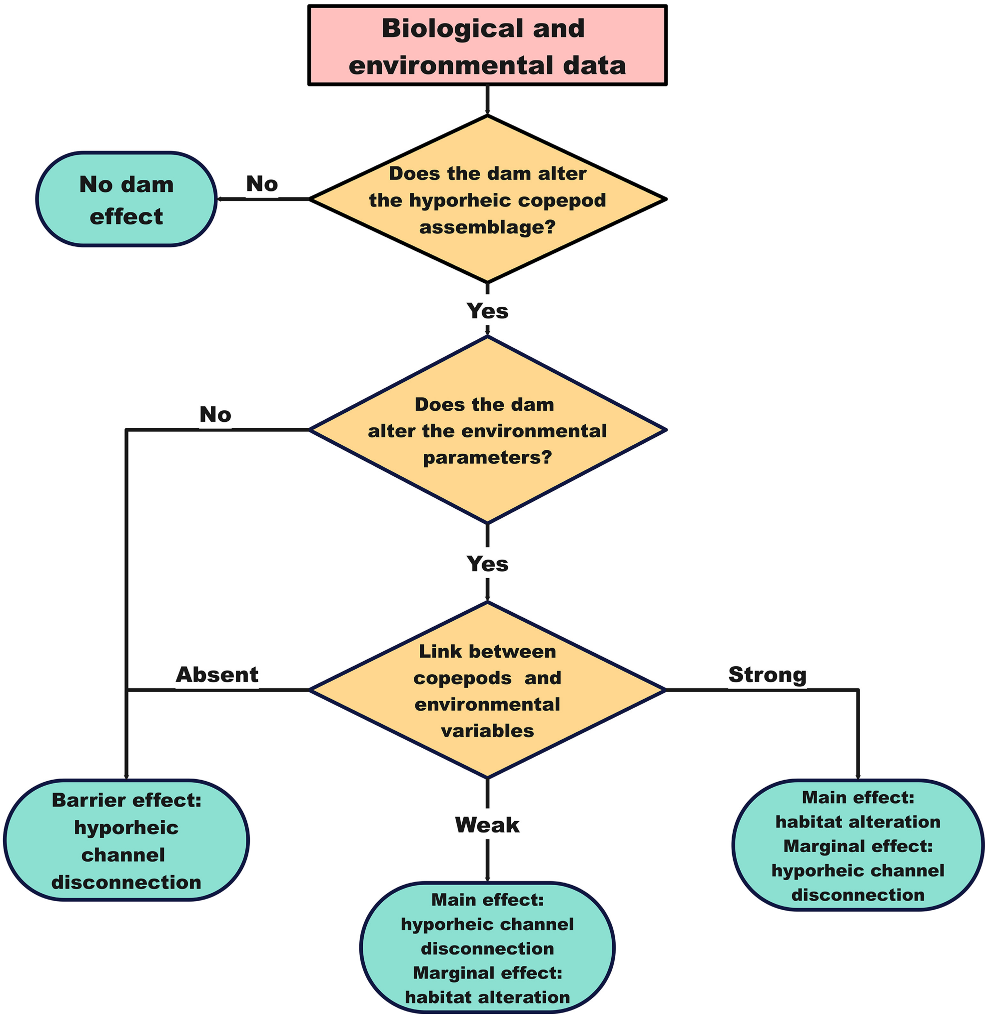

FIGURE 2 | Flowchart for the top-down decision-making process regarding the ecological impacts of venacquaro stream dam on the hyporheic-dwelling copepod community. [Color figure can be viewed at wileyonlinelibrary.com]

connectivity of the hyporheic channel. This possibility can manifest in two scenarios:

- The dam does not change the physicochemical parameters in the hyporheic zone, yet differences in the community are evident between the U and D sections.
- Changes between the U and D sections are noticeable both in physicochemical parameters and in the composition of the copepod assemblage, despite a strong dependence between copepod species and physic-chemical parameters being limited or totally absent.

(d) The dam alters the hyporheic copepod assemblage as a combination of the effects presented in point (b and c).

3.2.1 | Evaluating the SHPP Dam Effect on the Hyporheic Copepod Assemblage

To evaluate the effect of the dam on the hyporheic copepod assemblage of VEN, we fitted a GEE model after Warton (2022). GEE models are a good choice for design-based inference studies, also due to the straightforward interpretation of the model parameters. Briefly, GEE are an extension of the classical Generalized Linear Models (GLMs) which accounts both for the multivariate proprieties and the mean–variance relationships of the abundance data. The simplest GEE models for abundance at site *i* of species *j* is:

$$y_{ij} \sim F(\mu_{ij}, \phi_i) \text{ such that } \sigma^2_{y_{ij}} = V(\mu_{ij}, \phi_j)$$

$$g(\mu_{ij}) = \beta_{0j} + x_i' \beta_j$$

$$\text{cor}(r_{ij}, r_{ij'}) = \text{R}_{jj'} \text{ where } r_{ij} = \frac{y_{ij} - \mu_{ij}}{\sigma_{y_{ij}}}$$

In the equation:

– $y_{ij} \sim F(\mu_{ij}, \phi_i)$ is the probability distribution of the abundance data;

– $g(\mu_{ij})$ is the predicted abundance value of *j*-th species in the *i*-th site;

– β_{0j} is the model intercept for the *j*-th species;

– $x_i'\beta_j$ is the term which represents the effect of the included predictors (in our case, the segregation of U and D sites by the SHPP dam) on the response variables (in our case, species' abundances);

– $R_{jj'}$ is the correlation matrix which specifies how the abundances of the different species are associated with each other.

In the present study, we fitted a more complex GEE which was focused on understanding the effect of the dam also on the relative abundances. Within the GEE context, accounting for abundance variation across samples is a straightforward process since it is only needed to add another parameter (i.e., α) to the model:

$$y_{ij} \sim F(\mu_{ij}, \phi_i) \text{ such that } \mathrm{Var}(y_{ij}) = V(\mu_{ij}, \phi_j)$$

$$g(\mu_{ij}) = x_i'\alpha + \alpha_{0i} + \beta_{0j} + x_i'\beta_j$$

$$\mathrm{cor}(r_{ij}, r_{ij'}) = R_{jj'} \text{ where } r_{ij} = \frac{y_{ij} - \mu_{ij}}{\sigma_{y_{ij}}}$$

In this way, new terms appear in the model:

– α_{0i} accounts for total abundances variation across samples;

– $x_i'\alpha$ quantifies how much of the abovementioned variation in total abundance can be explained by the included predictors;

– β_{0j} accounts for relative abundances variation across samples;

– $x_i'\beta_j$ quantifies how much of the relative abundance variation can be explained by the predictors.

Thus, in our case larger α coefficients should be interpreted as a strong dam effect (via one of the mentioned mechanisms) on the abundances of all species (i.e., abundance-based alpha diversity), while larger β coefficients should be interpreted as a strong difference between the U and D sections in terms of relative abundances of taxa (i.e., abundance-based beta diversity), related to the presence of the dam. Since we wanted to fit a GEE separately for each species, we assumed no correlation between species so that the correlation matrix was $R = I$ (i.e., identity matrix composed of ones along the diagonal and all other values equal to zero).

To fit the GEE, we used the manyglm function in the R package mvabund (Wang et al. 2012). The package, designed to analyse multivariate abundances, allows the specification of the distribution of the abundance using the argument "family." We used the argument "family = negative.binomial" to fit the model, as negative binomial distribution is suggested to be a good choice for multivariate abundance data (Warton 2005). To assess the potential effect of the SHPP dam on beta diversity we also set "composition = TRUE" in the manyglm function.

The statistical significance of the terms included in our GEE model was assessed through a bootstrapped Analysis of Variance (ANOVA, significance level = 0.05, number of bootstraps = 999, test statistics = Likelihood Ratio) using the "anova.manyglm" function.

3.2.2 | Evaluating the SHPP Dam Effect on the Environmental Variables

Differences in the environmental variables between U and D sites were tested using a permutational analysis of variance (PEMANOVA, Anderson 2001). The significance level α was set at 0.05 (999 permutations, distance matrix: Euclidean). A separate test for homogeneity of dispersions using the PERMDISP routine was used before performing PERMANOVA (Šarauskienė et al. 2021). Differences between the U and D sections were also visually inspected using principal component analysis (PCA). Prior to the PEMANOVA and PCA analyses, data were standardized to *Z* scores. We retained only the parameters for which the standard deviation (SD) was different from zero. To produce the PCA biplot we used the PRIMER v.7 software (Clarke and Gorley 2015).

3.2.3 | Evaluating the Association Between Environmental Variables and the Hyporheic Copepod Assemblage

We evaluated the association between environmental variables and hyporheic copepod abundances by looking at the size of the standardized coefficients estimated for such variables within a mSDM, which is essentially a negative binomial GLM modelling the relationship between the predictors and the response variable (e.g., abundance) for multiple species simultaneously. To fit the mSDM, we used the function "traitglm" in the "mvabund" package. We also applied a "Least Absolute Shrinkage and Selection Operator penalty" (LASSO penalty) to the model in order to enhance its accuracy and interpretability.

4 | Results

4.1 | SHPP Dam Effect on the Hyporheic Copepod Assemblage

Overall, 1695 individuals belonging to 18 copepod species were sampled (15 species recorded in U and 12 in D). Out of these 18 species, 8 belonged to the order Cyclopoida and 10 to the order Harpacticoida. Regarding their groundwater specialization, 3 out of the 18 sampled species were stygobites, with *Diacyclops aprutinus* being sampled only downstream.

Analyses employing both parametric and non-parametric species richness estimators uniformly revealed a high level of sampling efficiency. Indeed, the number of potentially unrecorded species ranged from none (as suggested by Chao 1 and UGE estimators) to a maximum of six (as indicated by the Jackknife 2 estimator) (Data S1).

By examining the deviance table of the GEE model fitted to investigate the effect of the dam both on the alpha and beta diversity of the VEN hyporheic copepod assemblage (Table 1), it appears that there are differences between U and D hyporheic

TABLE 1 | Deviance table of the GEE model; response variable: Venacquaro stream hyporheic copepod abundances.

GEE coefficients	Res DF	DF Diff	Deviance	p
β_{0j}	198	17	77.14	**0.001**
α	197	1	17.30	**0.001**
α_{0i}	186	11	13.38	0.279
β_j	170	17	58.87	**0.001**

Note: (distribution = negative binomial). Statistically significant model parameters have their p-value shown in bold.
Abbreviations: DF Diff, degrees of freedom difference; Res DF, Residuals degrees of freedom.

sections in terms of alpha and beta diversity linked to the presence of the dam (α and β_j; $p = 0.001$). It's noteworthy that the highest explained deviance was associated with coefficients representing the effect of the dam on beta diversity (β_{0j} deviance = 77.14; β_j deviance = 58.87).

Many species showed a decline in relative abundances in the downstream section (post-SHPP). The most drastic reductions were observed for the stygoxene harpacticoid species *Bryocamptus pygmaeus* and *B. echinatus*. Interestingly, an increase in relative abundances in the downstream section was recorded for the stygobitic cyclopoid species *Diacyclops italianus* and *D. aprutinus* (Figure 3).

4.2 | SHPP Dam Effect on the Environmental Variables

Out of the initial set of 116 environmental variables, only 10 satisfied the inclusion criteria adopted for the multivariate analysis (TOC, DOC, POM, chloride, potassium, sodium ions, pH, temperature, and percentage of dissolved oxygen).

The results of the PERMANOVA indicated a statistically significant distinction between the U and D sites ($p = 0.003$), a disparity not attributable to variance heterogeneity among the variables as indicated by PERMDISP routine ($p = 0.599$). Nevertheless, the PCA biplot (Figure 4) displayed a discernible but not pronounced separation between U and D sites, with the first two principal components (PC1 and PC2) explaining 52.2% of the total variance. On average, the D sites showed higher levels of pH, temperature, and sodium ion concentration compared to U sites, which, in turn, showed higher E.C. and oxygen and POM concentrations (see table in Data S1).

4.3 | Association Between Environmental Variables and the Hyporheic Copepod Assemblage

While environmental factors generally had a limited influence on hyporheic copepod abundances, the negative binomial LASSO GEE model highlighted a few notable exceptions. Specifically, temperature and pH play significant roles in shaping copepod populations. Additionally, DOC and chloride ion concentrations also emerge as important factors (Figure 5).

In detail, the abundances of *Eucyclops serrulatus* and *Diacyclops italianus* showed a positive correlation with temperature, reflected in LASSO coefficients of 0.42 and 0.35, respectively. Furthermore, a slight positive association was observed between pH values and the abundances of *Diacyclops aprutinus* and *D. italianus*, with LASSO coefficients of 0.36 and 0.33, respectively. The model also revealed a positive relationship between *D. aprutinus* abundance and chloride ion concentrations, indicated by a LASSO coefficient of 0.34. Conversely, *E. serrulatus* exhibited a moderate negative correlation with DOC concentration, as denoted by a LASSO coefficient of −0.32.

5 | Discussion

In this study, we conducted a three-phased investigation to explore the impacts of a SHPP dam on the hyporheic copepod assemblage of the VEN, a low-order, groundwater-fed Apennine stream in Central Italy. Initially, we assessed the dam effect on VEN copepod diversity by comparing the alpha and beta diversity between the U and D dam sections using a GEE model. Subsequently, we analysed the environmental changes in the hyporheic sites of VEN, possibly associated with the dam presence, both visually and statistically employing PERMANOVA and PCA, respectively. Finally, we explored the relationship between hyporheic environmental variables and copepod abundances using a mSDM. Our findings indicate that the SHPP dam significantly altered both the copepod assemblage structure, primarily in terms of relative abundances of the collected species (beta diversity), and environmental variables. However, the outcome of the mSDM showed negligible correlations between the biotic and abiotic compartments of the VEN hyporheic zone, except for the species *Diacyclops italianus*, *D. aprutinus* and *Eucyclops serrulatus*. The abundances of these species appear to be weakly influenced by a small set of environmental variables, namely temperature, pH, DOC, and chloride ion concentrations. Given these outcomes, the significant changes in copepod beta diversity observed within the hyporheic zone of VEN between the U and D sections may be primarily attributed to the dam disrupting hyporheic connectivity, rather than to environmental changes arising from its presence.

Research on the impact of hydropower dams on aquatic ecosystems has predominantly focused on surface waters, encompassing both large- and small-scale hydroelectric facilities. The impact on hyporheic ecosystems has been largely overlooked. According to a recent global meta-analysis by Trottier et al. (2022), the presence of hydroelectric dams exerts a negative effect on the riverine macroinvertebrate communities specifically by reducing the species richness in the

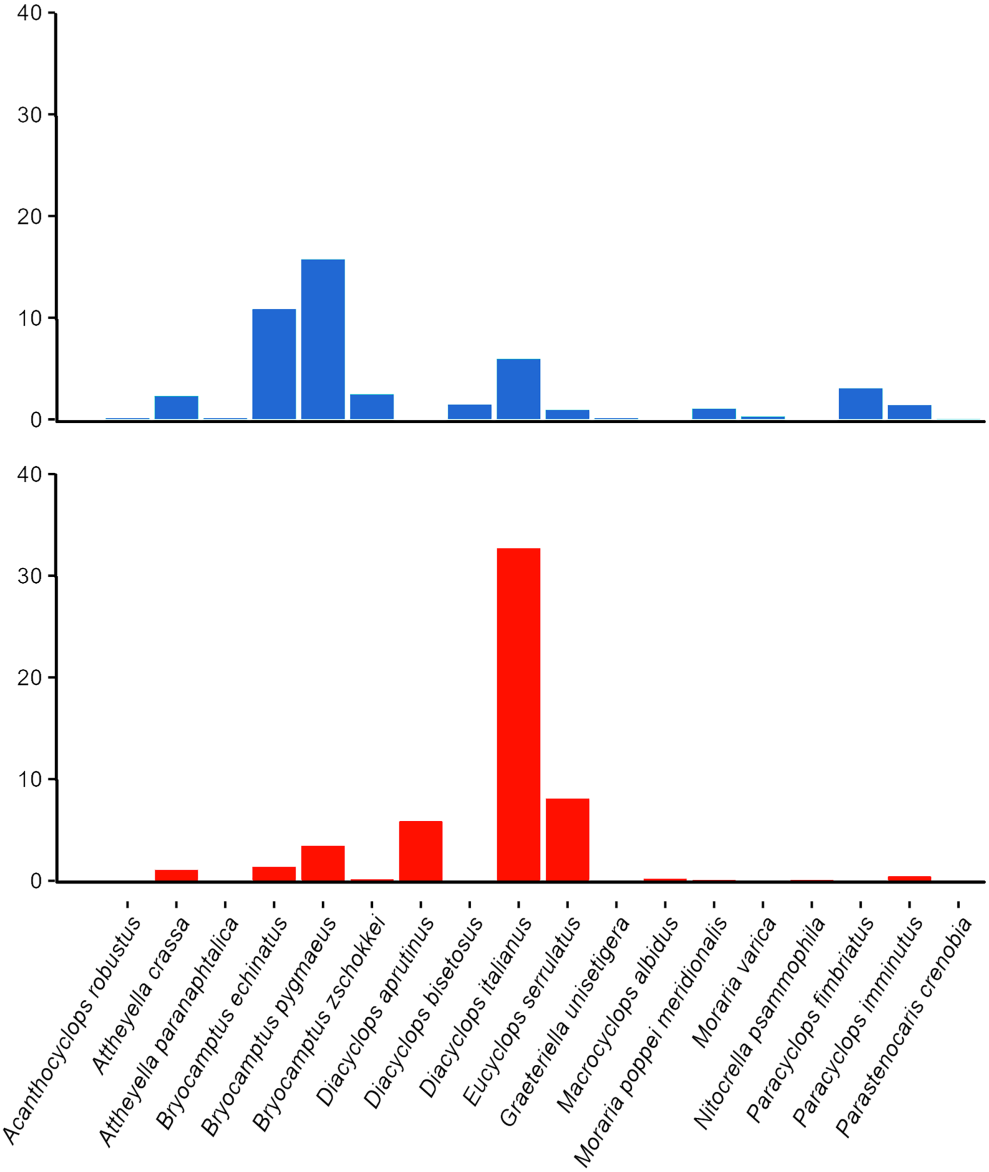

FIGURE 3 | Changes in hyporheic copepod assemblage compositions between upstream (blue) and downstream (red) sites of the venacquaro stream. [Color figure can be viewed at wileyonlinelibrary.com]

downstream sections. An in-depth review of existing literature revealed only one relevant study that examines the effects of SHPP on the invertebrate hyporheic-dwelling fauna (Bruno et al. 2009). The study by Bruno et al. (2009) explored the longitudinal shift in diversity, abundances, and specialization to groundwater of hyporheic invertebrates caused by the SHPP activity: in the hyporheic section 6 km downstream from the SHPP dam, authors reported a reduction in species richness and a shift in species composition, with stygoxene species replacing stygobitic ones. The authors hypothesized that these changes were due to alterations in the hyporheic zone's physical–chemical environment caused by SHPP hydropeaking. Key downstream changes in the physical–chemical characteristics of the hyporheic habitat included sediment clogging, which in turn influenced the thermal regime due to higher water residence times linked to altered flow paths. Our findings only partially align with those of Bruno et al. (2009). We also observed a decrease in species richness in the D section relative to the U one. Nonetheless, our GEE model did not highlight any statistically significant association between the SHPP presence and the observed alpha diversity pattern. Conversely, a statistically significant dam impact was highlighted by the GEE model for the relative abundances, indicating a beta diversity shift. Interestingly, the observed beta diversity pattern is the exact opposite of the one reported by Bruno et al. (2009). Downstream the SHPP, we observed a pronounced drop in the relative abundances of the stygoxene species in favour of stygobitic ones. In the downstream section, we observed a notable decline in the relative abundances of two dominant stygoxene species, namely *Bryocamptus pygmaeus* and *B. echinatus*. These species typically thrive in environments characterized by fine sediments, low water flow, and high hydrometric levels, as reported by Fiasca et al. (2014) and Petitta et al. (2015). Although our study did not directly assess these specific environmental variables, there is substantial evidence suggesting that SHPP reservoir zones—upstream SHPP sites—significantly modify the habitat, creating the conditions that favours the presence of these species

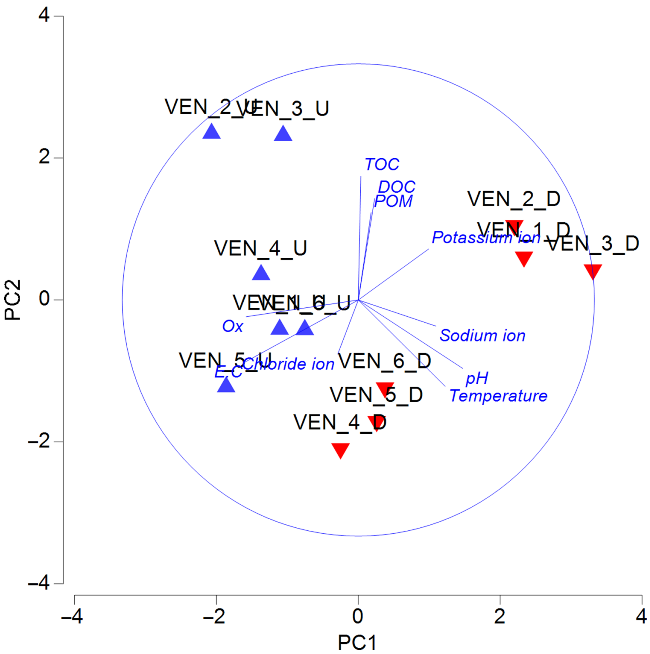

FIGURE 4 | Principal component analysis (PCA) biplot for the physicochemical parameters measured in venacquaro Stream (VEN) hyporheic sites located upstream (U) and downstream (D) of the SHPP dam. Abbreviations: DOC, Dissolved Organic Carbon; E.C., Electrical Conductivity; Ox, Oxygen Saturation (%); POM, Particulate Organic Matter; TOC, Total Organic Carbon. [Color figure can be viewed at wileyonlinelibrary.com]

(Tomczyk et al. 2021; Tomczyk and Wiatkowski 2021). This suggests that the habitat modifications associated with SHPPs may be responsible for the observed downstream decline of *B. pygmaeus* and *B. echinatus*. While previous research indicates that VEN is predominantly fed upstream the SHPP by groundwater (Petitta et al. 2015), the observed statistically significant shift in relative abundances favouring stygobitic species downstream of the SHPP leads us to hypothesize the probable existence of small and diffuse upwelling groundwater flows in the downstream section since, as extensively documented, stygobites are good tracers of groundwater upwelling particularly at the habitat and microhabitat scale in which they tend to be more abundant (Bertrand et al. 2012; Di Lorenzo, Stoch, and Galassi 2013; Bruno et al. 2009; Dole-Olivier et al. 2022). Furthermore, the fact that the stygobitic species *D. aprutinus* was exclusively found at D sites strengthens our hypothesis of a local upwelling downstream of the SHPP dam. Regarding the upstream-downstream differences in physicochemical parameters, our findings align with previous research that examined the impact of SHPPs on riverbed alterations across several countries, including France (Frémion et al. 2016), Greece (Kamidis and Sylaios 2017), Germany (Hahn et al. 2018), and Poland (Tomczyk et al. 2021). Specifically, we observed reduced E.C. and pH values downstream of SHPP intakes; this is indicative of finer sediment grains being trapped by the SHPP reservoirs, which favours the deposition of larger sediments immediately after the SHPP (downstream section). Interestingly, our observations regarding dissolved oxygen (DO) levels deviate from those reported in other studies in which DO levels are generally higher downstream of SHPPs due to hydropeaking effects (Tomczyk and Wiatkowski 2021). In contrast, we recorded lower DO values in downstream sampling sites, which further supports our hypothesis pointing towards diffuse upwelling of groundwater that is typically more anoxic than its surface and subsurface counterpart. Nevertheless, the mSDM did not highlight relationships between oxygen values and downstream stygobitic species abundances. Therefore, the influence of groundwater inflows in the downstream segment of the VEN warrants further detailed investigation.

In summary, our research revealed that the presence of SHPPs in river ecosystems leads to significant changes in the alpha and beta diversity of copepod assemblage within the hyporheic zone. This shift is primarily due to SHPP disruption of the longitudinal connectivity of hyporheic channels linked to fine sediment accumulation in the SHPP reservoir. Managing sediment transport and accumulation is critical for SHPPs, not only because of the economic and energy-related implications, such as increased maintenance costs and reduced efficiency in energy production (Sangal, Singhal, and Saini 2018; Azrulhisham and Azri 2019), but also due to its significant role in habitat degradation, which is one of the main cause of aquatic biodiversity loss worldwide (Obolewski et al. 2021; Mohanavelu, Shrivastava, and Naganna 2022). While technologies to mitigate excessive sedimentation in SHPP reservoirs exist, some of the methods currently implemented, like sediment flushing, only offer a partial solution. Although they may reduce sediment accumulation, they can still adversely affect aquatic invertebrate communities (Espa et al. 2013). A more cost-effective and eco-friendly approach is provided by sediment bypass tunnels (SBTs). SBTs are designed to transport fine sediment particles downstream, thereby preventing habitat alteration, excessive sedimentation in upstream areas and abrupt sediment flushing downstream. It has been demonstrated that this technology can effectively preserve habitat quality and, consequently, the diversity of benthic invertebrates downstream of SHPPs (Kobayashi et al. 2023). We hypothesize that a similar protective effect could be achieved for hyporheic communities.

6 | Conclusion

This study demonstrates the significant ecological impacts of SHPPs on the hyporheic zone of the venacquaro stream, a low-order groundwater-fed stream in Central Italy. The findings reveal that SHPPs alter both the biological and environmental dynamics of the hyporheic zone, primarily through disruptions in connectivity and sediment accumulation. These changes have led to a notable shift in copepod assemblage structure, with increased abundances of stygobitic species downstream of the SHPP, which suggests groundwater upwelling therein. The alterations in environmental variables such as pH, temperature, and DOC in the downstream section further underscore the ecological disturbances caused by SHPP facilities. This research highlights the urgent need for sustainable management practices, such as Sediment Bypass Tunnels, to mitigate the adverse effects of SHPPs on hyporheic ecosystems. By enhancing our understanding of SHPP impacts, this study contributes valuable insights for the conservation of riverine ecosystems and the development of more ecologically sustainable hydropower infrastructures. Future research should focus on long-term monitoring and comprehensive assessment of

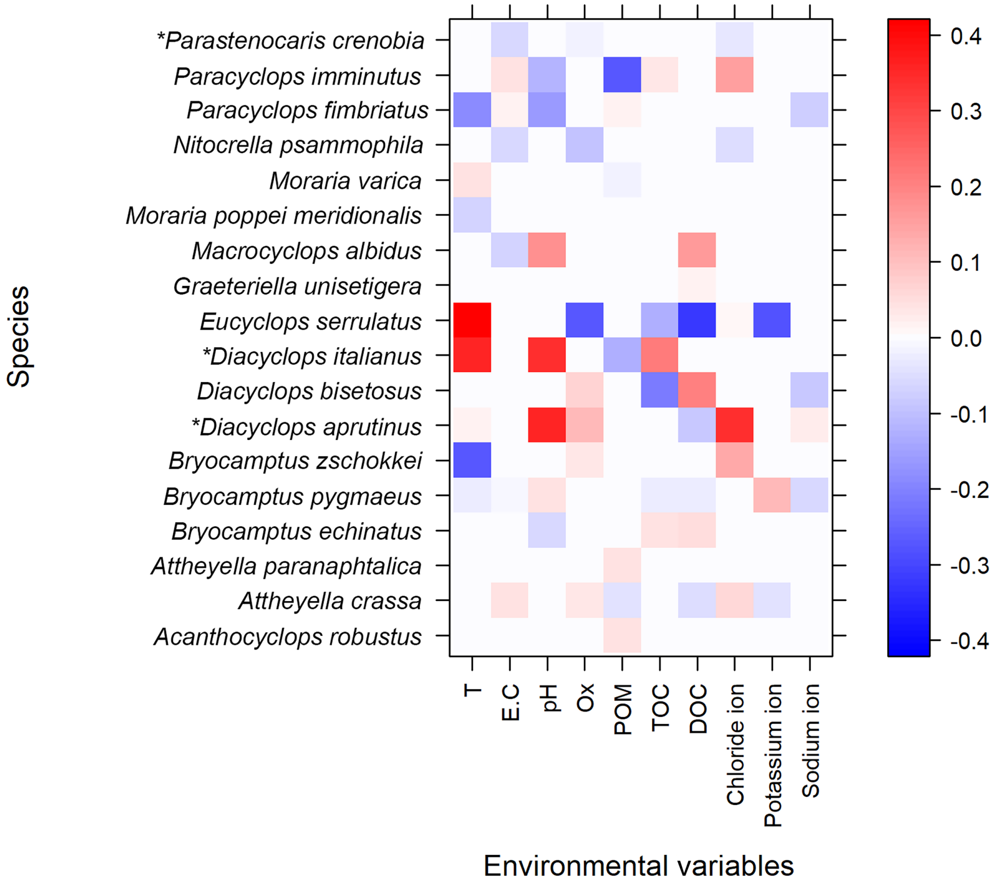

FIGURE 5 | Heatmap of the standardized coefficients from negative binomial LASSO GEE fit (response variables: Hyporheic copepod species abundances in the venacquaro stream, explanatory variables: Environmental variables. Red: Positive values; Blue: Negative values; darker colours correspond to stronger effects. Asterisks: Stygobitic species. Abbreviations: DOC, Dissolved Organic Carbon; E.C., Electrical Conductivity; Ox, Oxygen Saturation (%); POM, Particulate Organic Matter; TOC, Total Organic Carbon. [Color figure can be viewed at wileyonlinelibrary.com]

mitigation strategies to ensure the preservation of the critical ecotones hyporheic environments represent.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw data can be obtained from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.