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RESEARCH ARTICLE

Slow drawdown, fast recovery: Stream macroinvertebrate communities improve quickly after large dam decommissioning

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Abstract

1. Dam removal is increasingly considered as a river restoration tool for impoundments that harm the environment or have exceeded their lifespan. However, few studies report the ecological consequences of large dam removal.
2. We performed a multiple before-after/control-impact (mBACI) study to investigate the consequences of the decommissioning of a large dam (42 m high) on in-stream habitat and invertebrate communities in a temperate, forested catchment of northern Spain.
3. Before decommissioning, lack of fine sediments and high concentrations of manganese and iron occurred below the dam but decreased downstream. Invertebrate taxa richness and diversity were reduced, and pollution-sensitive taxa were missing just below the dam.
4. The drawdown of the reservoir, the first step towards its decommissioning, mobilized stored sediments causing frequent turbidity peaks downstream, which nevertheless, caused no detrimental effects on macroinvertebrate communities. One year after drawdown, the communities downstream from the dam, as well as those in the newly formed stream in the area formerly impounded by the reservoir, became very similar to those in control reaches, showing a successful restoration project.
5. *Synthesis and applications*. Dam decommissioning helps restore instream habitats and facilitates the recovery of invertebrate communities in a very short time frame if there are nearby sources of potential colonizers. Slow drawdown reduces the transport of the sediments accumulated in the reservoir and their potential downstream impacts, even more if prior to drawdown the reservoir is kept full for years to promote the deposition of sediments in marginal areas that will later be readily colonized by trees.

KEYWORDS
before-after/control-impact, connectivity, dam removal, ecosystem structure, mountain stream, restoration, sediment release

1 | INTRODUCTION

Concerns about environmental degradation and the loss of ecosystem services have stimulated major ecosystem restoration efforts (Bernhardt et al., 2007; Moreno-Mateos et al., 2017; Stoffers et al., 2024). However, depending on the type of the ecosystem (Jones & Schmitz, 2009) and the nature of the disturbance (Abella et al., 2018), complete ecosystem recovery may take a very long period (Moreno-Mateos et al., 2017). Aquatic systems tend to recover faster than forest ecosystems (Jones & Schmitz, 2009). Because of their highly dynamic nature, streams and rivers could recover especially fast as long as there is a nearby source of potential colonists (Sundermann et al., 2011).

Streams and rivers are among the most threatened ecosystems on Earth, and flow regulation and river fragmentation are two of their main stressors (Dudgeon, 2019). Thus, major restoration efforts include the recovery of longitudinal connectivity (Wohl, 2017). Dam decommissioning [i.e. partial or total removal of dams (Perera et al., 2021)] has gained momentum over the last 50 years, spurred in part by the safety concerns and maintenance costs of obsolete dams (Bellmore et al., 2019). So far, thousands of dams were removed in the United States and Europe (Habel et al., 2020), although the environmental consequences have seldom been assessed (Vahedifard et al., 2021). Therefore, we lack key information on how to optimize dam removal strategies. This is especially the case of large dams and reservoirs (i.e. higher than 15 m or 5–15 m in height and impounding more than 3 hm^3) (ICOLD, 2020), which have been removed in much lower numbers (Habel et al., 2020) and which could cause strongest impacts during dam removal. Besides, most of the studies published only assessed physical changes or fish communities (Bellmore et al., 2017). Monitoring the effects of dam removal on other ecosystem components and processes is necessary to assess the recovery of ecological integrity (Palmer et al., 2005; Wohl et al., 2005).

Macroinvertebrates can be severely affected by dams (Wang et al., 2020) and their decommissioning (Carlson et al., 2018), thus affecting the energy transfer to higher trophic levels (Mor et al., 2018; Morley et al., 2020). Dams affect downstream invertebrate community composition (Morley et al., 2008), reducing density (Dolédec et al., 2021; Martínez et al., 2013), diversity (Holt et al., 2015), taxa richness (Ellis & Jones, 2016; Wang et al., 2020) and biotic indices (Mellado-Díaz et al., 2019), and changing life histories and dispersal processes (Tonkin et al., 2009). Usually, these impacts decrease with downstream distance from the dam (Holt et al., 2015; Mellado-Díaz et al., 2019), and depend, among others, on dam characteristics (Ellis & Jones, 2013).

Although dam decommissioning could eliminate these impacts in the long term (Hansen & Hayes, 2012), the downstream mobilization of nutrients and sediments (Ahearn & Dahlgren, 2005) can also impair invertebrate communities in the short term (Matthaei et al., 2010), resulting in an initial decline in sensitive taxa (Carlson et al., 2018; Mahan et al., 2021). Invertebrate communities can recover rapidly from dam decommissioning (Chiu et al., 2013; Mahan et al., 2021), but sometimes the recovery may take over 3 years (Hansen & Hayes, 2012; Renöfält et al., 2013), depending on factors such as the size of the dam and the quality of the sediments stored (Foley et al., 2017). Clearly, more information is needed on this topic to optimize dam removal strategies.

The present study analysed the response of stream invertebrates to reservoir drawdown in one of the largest dams decommissioned in Europe to date (Habel et al., 2020). We predicted that (1) before drawdown, reduced water quality and streambed coarsening would reduce invertebrate density and diversity below the dam, these effects decreasing downstream; (2) during drawdown, the mobilization of the sediment stored in the reservoir would further reduce invertebrate density and diversity; and (3) after drawdown, invertebrate communities in the reservoir and downstream sites would resemble the communities found in nearby undammed tributaries.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in Artikutza, a headwater basin on schist, sandstone and granite located in the north of the Iberian Peninsula with an extraordinary conservation status (Figure 1). In 1947, water managers built the 42-m tall Enobieta Dam to supply drinking water to San Sebastian. Nevertheless, geotechnical issues and recurrent problems with high metal concentrations led local authorities to build, in 1976, the Añarbe Dam (79-m tall and 43.8 hm^3 capacity) further downstream in the catchment. Thereafter, the Enobieta Dam fell progressively into disuse and became a safety issue. For decades, the dam was not actively managed, the reservoir being permanently full of water, until in 2016 the municipality decided to decommission it.

The first stage in the Enobieta Dam decommissioning was the drawdown of the reservoir. To allow the stabilization of the emerging sediment by the colonizing vegetation and minimize the sediment export, the reservoir was slowly emptied during 2018 using some old siphons and water-serving pipes that mainly released surface water. We called it the before period. When the water level in the reservoir was approximately 4-m deep (December 2018), the bottom gate was repaired and opened, marking the start of the drawdown period. In October 2019, an older 3.5 m-tall weir, located 200 m upstream from the large dam, was demolished. In the rainy November 2019, the Enobieta Stream carved a new channel through the sediment retained by the weir, resulting in a last period of high turbidity. This marked the completion of the drawdown process and the initiation of the recovery period, referred to as the after period. Currently, the reservoir is empty, the bottom gate is open and authorities are deliberating whether to completely remove the dam or create a 7 m-wide notch to eliminate the barrier effect (Atristain et al., 2023). This field study had the permission granted by the municipality of San Sebastian and by the Government of Navarre. The study did not require ethical approval.

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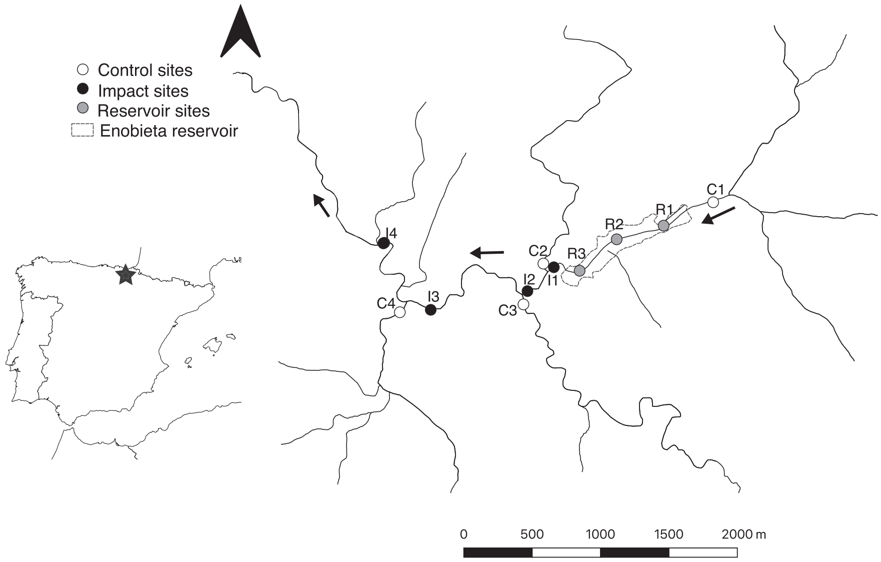

FIGURE 1 Study area showing the location of the 11 study sites [four control sites (C1, C2, C3 and C4), four impact sites (I1, I2, I3 and I4) and three sites in the former reservoir (R1, R2 and R3)] in the Artikutza Valley (northern Iberian Peninsula). The dashed line indicates the area drowned by the Enobieta Reservoir. Dark arrows indicate flow direction.

2.2 | Experimental design

Our study followed a multiple before-after/control-impact (mBACI) design (Underwood, 1994). We defined four control sites, one (C1) upstream from the dam and three (C2–C4) in free-flowing tributaries, as well as four impact sites (I1–I4) at increasing distances downstream from the dam. All eight reaches were sampled before (before period), during (drawdown period) and after (after period) the drawdown. Additionally, three sites located within the reservoir (R1–R3) were also sampled in the after period (Figure 1). These sites could not be sampled either in the before period, when the reservoir was full, or during drawdown, when safe wading in the newly carved stream channel was still impossible.

2.3 | Habitat characteristics

We characterized benthic substrate composition following Wolman (1954), with 100 substrate particles collected per site and period while zigzagging along 100 m-long reaches. For each site and period, we estimated median grain size (D_{50}), and the relative abundance of very fine gravel (2–4 mm) or sand-silt (<2 mm).

We also measured water temperature (T, °C), dissolved oxygen (DO) saturation (%), electrical conductivity (EC, $\mu S\,cm^{-1}$) and pH with a handheld multiparametric probe (Multi 3630 IDS, WTW, Germany) and took water samples to determine the concentration of iron (Fe, $mg\,L^{-1}$), manganese (Mn, $mg\,L^{-1}$) and nutrients [soluble reactive phosphorus (SRP, $\mu g\,P\,L^{-1}$) and ammonium (NH_4^+, $\mu g\,N\,L^{-1}$)] (Atristain et al., 2023).

2.4 | Benthic invertebrates

Invertebrates were sampled in November 2017 (before), October 2019 (drawdown) and November 2020 (after), 1 year after the end of the drawdown. On each occasion and site, we took five random samples with a Surber net (0.09 m^2, 500 μm-mesh) and preserved them in 70% ethanol. Invertebrates were sorted in the laboratory, counted and identified under a binocular microscope (Tachet et al., 2010). Most invertebrates were identified to genus level (74.6% of the taxa), but some Amphipoda, Coleoptera, Ephemeroptera, Trichoptera, Mollusca and Diptera were only identified to family level (13.6%). Acari and Oligochaeta were left at these taxonomic levels (see Table S4).

We estimated taxa richness (S), Shannon–Wiener diversity index (H´) and total density (TD, individuals m^{-2}) for each sample. We also estimated the Iberian Average Score Per Taxon (IASPT) index, which is widely used in Spanish biomonitoring programs to represent average sensitivity to pollution of the taxa found (Guareschi et al., 2017). IASPT is calculated as the IBMWP value (Alba-Tercedor, 2002) divided by the number of scoring families present.

2.5 | Statistical analyses

To assess the impact of the dam and its decommissioning, we conducted linear mixed-effects (LME) models using restricted maximum likelihood (Pinheiro & Bates, 2006). We included period (before/drawdown/after) and reach (control/impact) as fixed factors, with sampling site as a random factor. We used the 'lmer' function from the 'lme4' package in R (Bates et al., 2015). The overall effect of the drawdown was shown by the interaction between period and reach (BDA:CI). To further analyse the impact of reservoir drawdown and subsequent restoration efforts, we examined the output from each LME model with the 'summary' function in R. We focused on three key aspects: (1) the comparison between control and impact sites before drawdown (BCI), to assess any pre-existing effects on the impact sites; (2) the before-drawdown/control-impact (BD:CI) interaction to evaluate the impact of the drawdown on the affected areas; and (3) the before-after/control-impact (BA:CI) interaction to determine whether the impacted areas had recovered from the effects of the drawdown. The baseline for the fixed factors was set at the control sites during the before period. Additionally, we carried out LME models with REML to compare control sites with newly emerged reservoir sites during the after period. In these models, reach (control/reservoir) was used as a fixed factor and site as random factor. In all cases, we assessed residuals to confirm that the models did not depart from normality and homoscedasticity. When required, variables were log transformed. To test whether the effects of the dam decreased downstream, we calculated effect sizes for all variables and periods by determining the natural logarithm (Ln-ratio) between the value at each impact site and the mean among all control values. Negative values of the ratio indicated a decrease below the dam, while positive values indicated increases.

To examine similarities and changes in community composition, we performed non-metric multidimensional scaling (NMDS; Clarke, 1993) and permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). These analyses were based on a Bray–Curtis dissimilarity matrix of Hellinger-transformed data, using the 'vegan' package (Oksanen et al., 2020). The quality of the NMDS projections was evaluated using a stress value, which represents the deviation from the relationship between the distances among samples in the original Bray–Curtis dissimilarity matrix and their distances in the ordination plot. The PERMANOVA considered the interaction between period (before/drawdown/after) and reach (control/impact) as fixed factors. All statistical analyses were conducted using R software (version 4.0.3, R Core Team, 2020; Austria).

3 | RESULTS

3.1 | Habitat characteristics

Before drawdown, riverbed was coarser below the dam (I1) than in the rest of the sites but coarsening decreased downstream and was not noticeable at sites I3 and I4 (Table 1). Grain size decreased substantially following the drawdown of the reservoir with a 50% reduction of D_{50} in I1 and a 30% reduction in I2, I3 and I4 (Table 1). The percentage of particles smaller than 4 mm remained relatively constant across all downstream sites during drawdown and did not change with respect to the before period (Table 1). During the after period, grain size reduction was still noticeable in I1 (D_{50} = 45 mm), and fine gravel percentage increased by 12%. The median bed particle size in the newly emerged reservoir sites approached those found in nearby undisturbed sites, except R3, where D_{50} was 50% lower than in control sites. All three reservoir sites showed no sand or fine gravel in the after period.

Data revealed weak evidence of reservoir drawdown affecting SRP and NH_4^+ concentrations, EC, DO saturation or T (see Table S2). In contrast, there was a strong evidence of effects on total Fe and Mn (BDA:CI_{Fe}, $p < 0.001$; BDA:CI_{Mn}, $p < 0.001$; see Table S2). Fe and Mn were initially higher in impact reaches, particularly at sites I1 and I2 (see Tables S1 and S3). These differences were maintained during the drawdown period (BD:CI_{Fe}, $p = 0.96$; BD:CI_{Mn}, $p = 0.31$; see Table S3), but Fe and Mn decreased in the impact sites during the after period to levels comparable to undammed reaches (BA:CI_{Fe}, $p < 0.01$; BA:CI_{Mn}, $p < 0.0001$; see Tables S1 and S3).

In the after period, water physicochemical characteristics were similar in control, impact and reservoir sites (see Table S1), with some exceptions. Water temperature and DO saturation peaked in R2 and R3 (see Table S1), likely due to the open canopy since riparian vegetation was still scarce. Nevertheless, the effect size for these variables was small (see Table S1). Similarly, EC and metal concentrations increased from R1 to R3, although values did not depart much from those in control sites.

3.2 | Benthic invertebrates

In the 135 benthic samples, we found 21,188 invertebrates comprising 78 taxa (see Table S4). Most abundant were the amphipod *Echinogammarus* (21.3%); the caddisfly *Hydropsyche* (12.1%); and the mayflies *Baetis* (9.9%), *Habroleptoides* (9.1%) and Heptageniidae (4.8%).

Before drawdown, invertebrate density was 48% lower in the impact than in control reaches ($TD_C = 1973.9 \pm 236.3$ and

TABLE 1 Median bed particle size (D_{50}, mm) and percentage of particles smaller than 4 mm in control (C1, C2, C3 and C4), impact (I1, I2, I3 and I4) and reservoir sites (R1, R2 and R3) during periods before, drawdown and after.

		Reach										
Variable	Period	C1	C2	C3	C4	I1	I2	I3	I4	R1	R2	R3
D_{50} (mm)	Before	90	90	90	90	180	128	90	90	–	–	–
	Drawdown	64	128	64	90	90	90	64	64	–	–	–
	After	45	90	64	64	45	90	64	64	64	45	22.6
<4 mm particles (%)	Before	3	4	2	3	0	1	1	2	–	–	–
	Drawdown	3	5	2	3	0	1	2	1	–	–	–
	After	4	3	0	0	12	3	0	1	0	0	0

Note: R sites were sampled only during the after period.

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$TD_I = 1030.6 \pm 184.6$). The effect was highest just below the dam (effect $size_{I1} = -1.94$) and decreased downstream (Figure 2). There was very weak evidence that drawdown affected invertebrate density of impact reaches (BDA:CI_{TD}, $p = 0.08$; see Table S5) that increased especially in sites I1 and I2 (Figure 2). During drawdown, differences in density between control and impact reaches disappeared, mainly due to the increase of the density in the impact reaches ($TD_C = 1985.6 \pm 250.6$ and $TD_I = 1978.9 \pm 266.6$) (BD:CI_{TD}, $p < 0.05$; see Table S6). In the after period, invertebrate densities were similar in control and impact reaches as densities in the impact reaches were higher compared to the before period ($TD_C = 1644.4 \pm 258.4$ and $TD_I = 1617.2 \pm 234.0$) (BA:CI_{TD}, $p = 0.05$; see Table S6) (Figure 2).

Evidence associated the drawdown of the reservoir with changes in taxonomic richness (BDA:CI_S, $p < 0.01$; see Table S5) and diversity (BDA:$CI_{H'}$, $p < 0.05$; see Table S5). Before drawdown, taxonomic richness and diversity were lower in the impact reaches ($S_C = 21.9 \pm 1.3$ and $S_I = 13.2 \pm 1.7$; $H'_C = 2.3 \pm 0.1$ and $H'_I = 1.7 \pm 0.1$) (BCI_S, $p < 0.01$; $BCI_{H'}$, $p < 0.05$; see Table S6), the effect being highest in site I1 (Figures 3 and 4). Although richness and diversity increased in impact reaches during drawdown (BD:CI_S, $p < 0.01$;

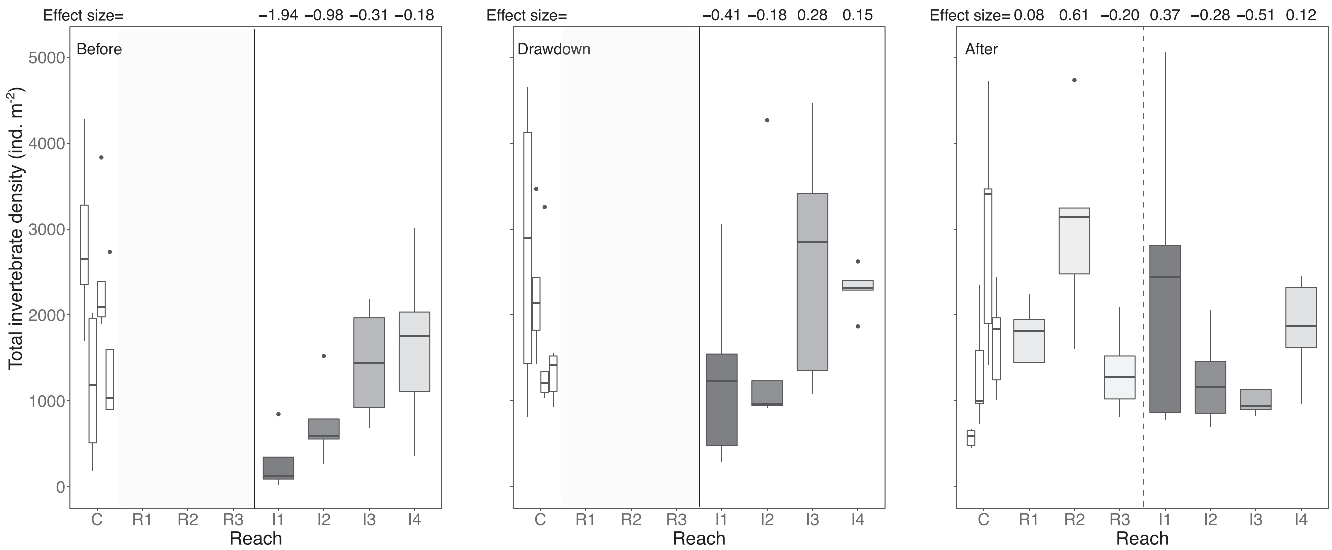

FIGURE 2 Total invertebrate density (ind. m^{-2}) in control (C), impact (I) and newly created sites (R) before, during and after the drawdown of the reservoir. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The grey scale of I sites reflects distance downstream from the dam (darker = closer). Effect sizes on top represent the Ln-transformed ratio of the average for each impact site divided by the overall average of the control sites for each period. Continuous line and the light grey area represent the dam and the full reservoir, respectively, and intermittent lines represent the emptied reservoir. Note that R reaches were sampled only during the after period.

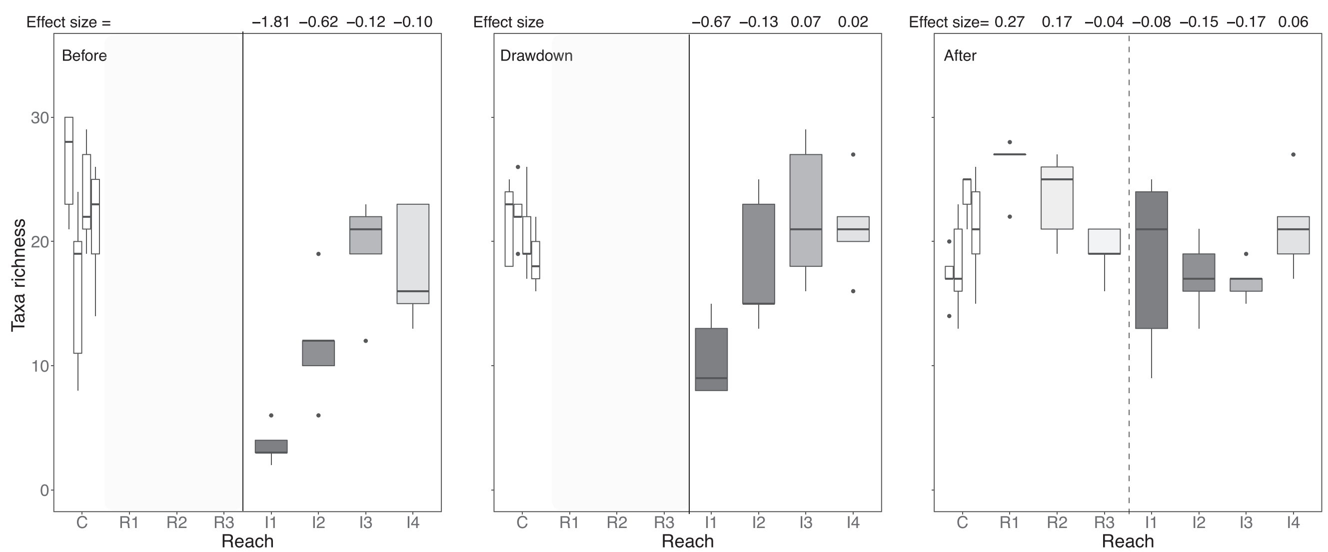

FIGURE 3 Taxa richness in control (C), impact (I) and newly created sites (R) before, during and after the drawdown of the reservoir. The design of the figure follows that of Figure 2.

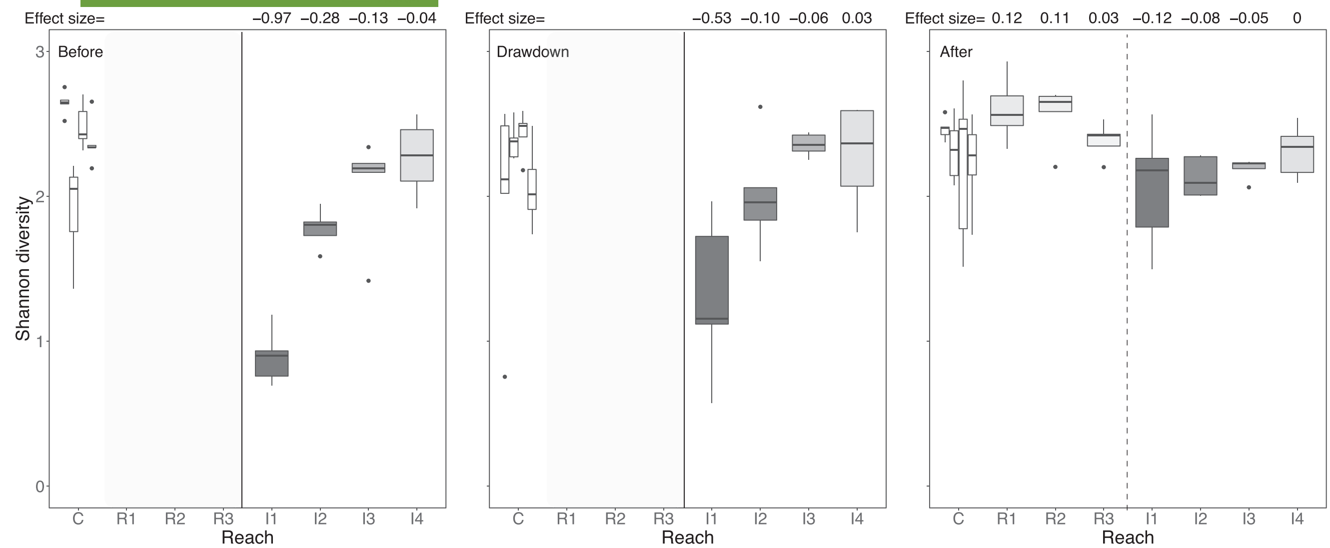

FIGURE 4 Shannon diversity index in control (C), impact (I) and newly created sites (R) before, during and after the drawdown of the reservoir. The design of the figure follows that of Figure 2.

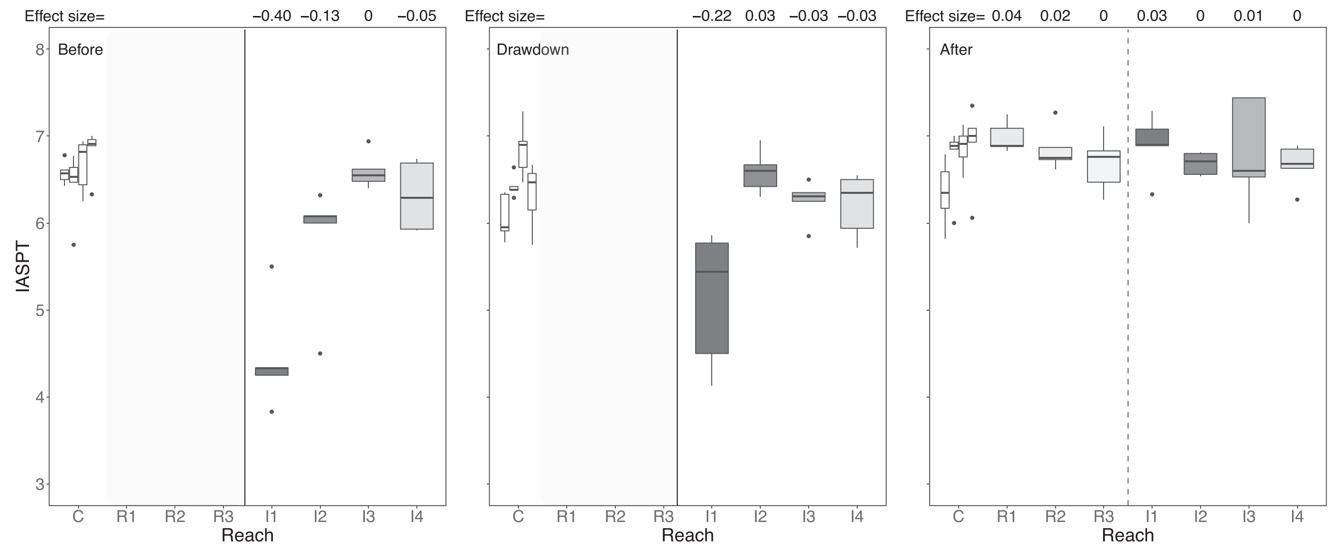

FIGURE 5 Iberian Average Score Per Taxon (IASPT) index in control (C), impact (I) and newly created sites (R) before, during and after the drawdown of the reservoir. The design of the figure follows that of Figure 2.

BD:$CI_{H'}$, $p<0.05$; see Table S6), values in I1 were still below those in control sites (Figures 3 and 4). During the after period, all impact sites increased their values (BA:CI_S, $p<0.001$; BA:$CI_{H'}$, $p<0.01$; see Table S6) and reached values similar to those of control sites. The IASPT biomonitoring index followed a similar pattern. During the before period, it was 13% lower in impact reaches ($IASPT_C = 6.6 \pm 0.1$ and $IASPT_I = 5.8 \pm 0.2$) (BCI_{IASPT}, $p<0.05$; see Table S6), especially in I1 (effect $size_{I1} = -0.40$) (Figure 5). There was strong evidence that the drawdown promoted pollution-sensitive taxa in the impact sites (BDA:CI_{IASPT}, $p<0.001$; see Table S5), as shown by the near-zero effect sizes and the significant BD:CI and BA:CI interactions (BD:CI_{IASPT}, $p<0.05$ and BA:CI_{IASPT}, $p<0.0001$; see Table S6) (Figure 5).

Before drawdown, communities in sites I1 and I2 occupied a region of the NMDS biplot well separated from those in control sites, but differences decreased during the drawdown and after periods (Figure 6). Thus, the drawdown of the reservoir made the composition of the invertebrate communities downstream from the dam similar to those of control sites (PERMANOVA BDA:CI, $p<0.01$).

3.3 | Reservoir colonization

The stream channel newly formed as the reservoir level receded during drawdown was initially devoid of invertebrates, but after drawdown invertebrate community measures were similar in the

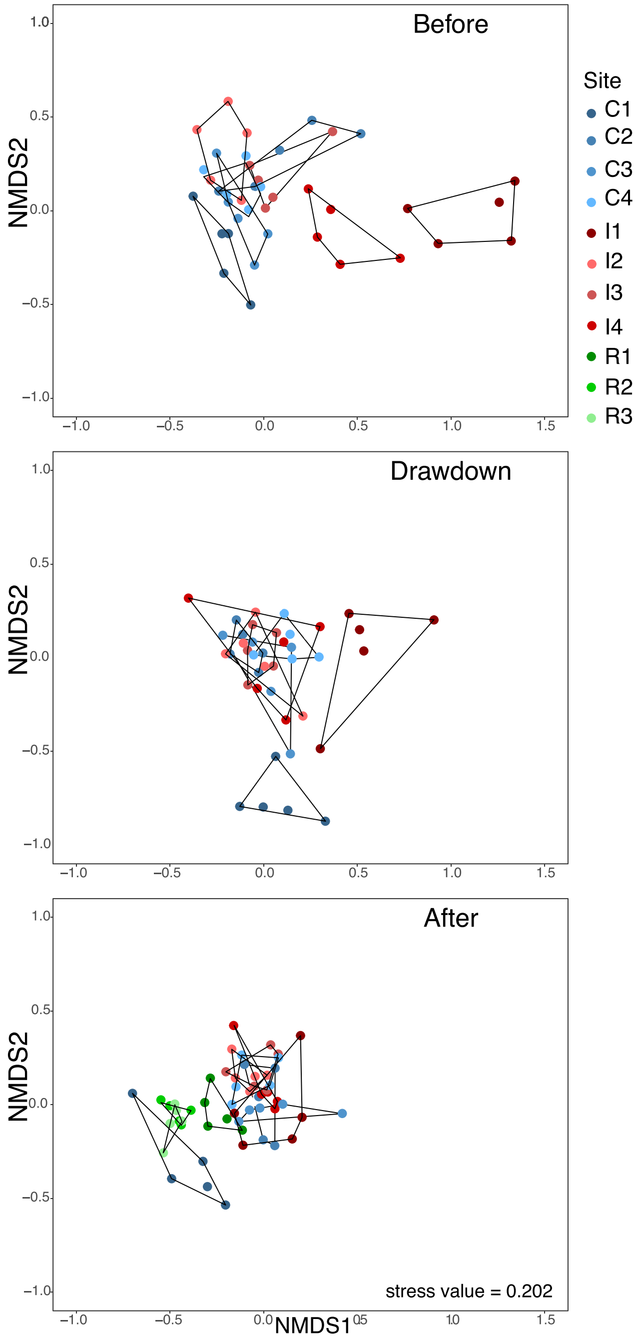

FIGURE 6 Non-metric multidimensional scaling (NMDS) analysis of invertebrate community composition in control (C), impact (I) and newly created sites (R) before, during and after the drawdown. Blue dots represent control sites. Red dots represent impact sites: the darkest dots represent I1 site and the lightest ones I4 site. Green dots represent sites in the newly created channel within the former reservoir area: the darkest dots represent the area that first emerged during the drawdown and the lightest ones represent the site closest to the dam. Note that R reaches were sampled only during the after period.

reservoir and control reaches (CR_{TD}, $p=0.47$; CR_S, $p=0.28$; CR_{IASPT}, $p=0.45$; see Table S7). Diversity was an exception, being slightly higher in the reservoir ($H'_C=2.3\pm0.1$ and $H'_R=2.5\pm0.1$) ($CR_{H'}$, $p<0.05$; see Table S7) (Figure 4). By the end of the study, samples in the reservoir sites occupied a region of the NMDS biplot close to the control sites, although community composition did not totally resemble that in control sites (PERMANOVA CR, $p<0.0001$) (Figure 6).

4 | DISCUSSION

Benthic invertebrate communities are useful indicators of the ecological responses to stream and river restoration projects (Jähnig et al., 2011; Miller et al., 2010). Nevertheless, many restoration projects lack proper monitoring of ecological outcomes (Bernhardt et al., 2005) and often fail to improve invertebrate communities (Griffith & McManus, 2020; Palmer et al., 2010). This lack of response has been attributed to other limiting factors (Palmer et al., 2010) or to the absence of potential colonizers in nearby sites (Sundermann et al., 2011). Additionally, the response of invertebrates can differ among seasons, habitats or reaches (Flores et al., 2017; Sullivan & Manning, 2017), making it complex to assess (Griffith & McMcManus, 2020). In our case, the drawdown of Enobieta Reservoir, the first step towards its decommissioning, caused no detrimental effects to the downstream invertebrate communities, and 1 year afterwards, the communities below the dam, even those in the newly formed river channels in the reservoir area, were very similar to those in undammed streams in the valley. These results may be conditioned by the excellent ecological status and high diversity of nearby stream reaches (Elosegi et al., 2019), as well as by the torrential characteristics of the local streams that reduced legacy effects and promoted the colonization of impact reaches. Dam removal can cause impacts, for instance, caused by the remobilization of toxic sediments (Ashley et al., 2006) or by promoting the spread of invasive species (Foley et al., 2017). Besides, in streams and rivers subjected to multiple pressures, the response to dam removal can be limited (Palmer et al., 2010).

Contrary to other sites (Dolédec et al., 2021; Martínez et al., 2013), the main downstream impact of the Enobieta Reservoir seemed to be caused by effects on water quality, not on hydrology. This reservoir had been out of use for decades, the bottom gate closed and the reservoir full of water, and thus, the discharge released from the spillway roughly resembled the discharge it received from the basin. In Enobieta, low IASPT values downstream suggest impaired water quality, very probably linked to high iron and manganese concentrations (Atristain et al., 2023), which can be detrimental for the biota directly when dissolved (Cadmus et al., 2018) or indirectly when precipitated (Kotalik et al., 2019). Atristain et al. (2023) observed black manganese precipitations as far as reach I4. Metal oxide deposits in streams can affect invertebrates by a variety of mechanisms (Wilson et al., 2019): they can clog the interstitial space among rocks or smother benthic organisms thus reducing the abundance and richness of biofilm and invertebrates (Cadmus et al., 2016; Kotalik et al., 2019). Sediment starvation could also affect invertebrate communities downstream from the dam, limiting the abundance of sand- or gravel-dwelling invertebrates, as has been reported elsewhere (Mellado-Díaz et al., 2019).

One main goal of dam decommissioning projects is to reconnect sediment fluxes (Wohl et al., 2015), which shape channel complexity (Bellmore et al., 2019) and control water quality (Atristain et al., 2023), indirectly affecting invertebrate communities (García et al., 2017). In agreement with previous studies (Magilligan et al., 2016; Tullos et al., 2014), the drawdown of Enobieta Reservoir reduced the median bed grain size and improved water quality (Atristain et al., 2023). Streams in the Artikutza valley have very low concentrations of suspended sediments because the extensive forest cover prevents soil erosion (Elosegi et al., 2019). Despite drawdown caused high turbidity peaks, these rarely surpassed 300 NTU (Atristain et al., 2023), a common value during floods in other rivers in the area (Zabaleta & Antigüedad, 2012), and seemed not to affect invertebrate communities. Furthermore, although suspended sediment can cause anoxia in rivers, continuous records during the opening of the bottom gate showed that DO saturation was constantly over 90% (M. Atristain, unpublished data). Higher metal concentrations were also transported along with suspended sediment (Atristain et al., 2023), but they did not affect any of the invertebrate community metrics. Hence, contrary to expected, neither suspended solid nor higher metal concentrations impaired invertebrate communities during drawdown. This might be a consequence of metals being transported in dissolved form, as we did not notice metal deposition during drawdown, as well as enhanced streambed complexity counteracting the effect of high metal concentrations. Invertebrate communities can recover from the negative effects of dam decommissioning in less than 2 years (Carlson et al., 2018), although recovery time may vary among taxa (Renöfält et al., 2013), site-specific conditions or habitat type (Hansen & Hayes, 2012). In our case, at the end of the study period, that is, barely a year after the main mobilization of sediments, the impact sites reached the same density, richness, diversity and community composition as in the sites free from the effect of the reservoir.

Remarkably, as reported by others (Dézerald et al., 2023; Mahan et al., 2021), the invertebrate communities in the area formerly drowned by the Enobieta Reservoir were by the end of the experiment very similar to the communities found in the rest of the sites. This result indicates not only a very high re-colonization capacity but also that the physical habitat had recovered enough for these organisms to live there. Surprisingly, taxa richness and Shannon diversity were even higher in the reservoir than in the rest of the sites, as a consequence of a few taxa (e.g. the hemiptera *Aphelocheirus*) typically found in stagnant water, which was quite abundant in the flattest areas of the emerged sediments. Whatever the case, a fully mature invertebrate community can only be expected after the stream has recovered its natural physical habitat, including deposits of large wood, which will obviously require a longer time to develop.

Finally, we must remark that so far, we have only shown the effects of drawdown, not of the final demolition of the dam. Indeed, the dam is still in place, while the Spanish Ministry of the Environment decides whether it is better for biodiversity to remove it totally or to open a 7 m-wide trench across it. Although total removal of the dam would obviously result in a more natural setting, the demolition works, and especially the transport of all concrete remains out of the valley would take much longer (over 1 year of work, compared to 6 months for the trench, Elosegi et al., 2022), thus making the impacts longer for biodiversity. In addition, the inner galleries of the dam host several colonies of endangered bat species, which would obviously disappear if the dam was taken out. Consequently, the partial removal of the dam seems to be the best option to complete the decommissioning of the Enobieta Reservoir. The maximum volume of sediment mobilized during dam removal has been estimated at 3795 m^3, less than half of the amount eroded during the drawdown and, thus, their impact is expected to be minor at most. More importantly, the dam would not be an obstacle for invertebrates, thus allowing mixing of previously isolated populations. Nevertheless, it is advisable to make a close follow-up of the biodiversity in the zone during the demolition works to minimize unwanted effects.

In summary, our results show that the drawdown of a large reservoir, a first step towards its decommissioning, can cause little impact if it is conducted slowly, thus minimizing the volume of sediments exported and their impact downstream. Furthermore, our results show that the invertebrate communities can recover to values similar to control reaches in a short period of time provided that there is a nearby source of potential colonists.

AUTHOR CONTRIBUTIONS

The experiment and funding acquisition were co-ordinated by Arturo Elosegi, Aitor Larrañaga and Daniel von Schiller. The experiment and sampling campaigns were carried out by Arturo Elosegi, Aitor Larrañaga, Daniel von Schiller and Miren Atristain. Laboratory analyses and calculations were performed by Miren Atristain and Libe Solagaistua, while statistical analyses were conducted by Miren Atristain, Libe Solagaistua and Aitor Larrañaga. The manuscript was written by Miren Atristain and reviewed by all the authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.w3r2280ws (Atristain et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Water characteristics in control (C1, C2, C3 and C4), impact (I1, I2, I3 and I4) and reservoir sites (R1, R2 and R3) during periods before ($n=7$), drawdown ($n=6$) and after ($n=3$).

Table S2: Results of the linear mixed-effects models using period (before/drawdown/after) and reach (control/impact) as fixed factors and water physicochemical attributes as response variables.

Table S3: Full output of the results of the linear mixed-effects models of water physicochemical attributes.

Table S4: List of the taxa found on the 135 samples obtained in control (C), impact (I) and reservoir (R) reaches during the before ($n_C=20$ and $n_I=20$), drawdown ($n_C=20$ and $n_I=20$) and after ($n_C=20$, $n_I=20$ and $n_R=15$) periods.

Table S5: Results of the linear mixed-effects models using period (before/drawdown/after) and reach (control/impact) as fixed factors and invertebrate community measurements as response variables.

Table S6: Full output of the results of the linear mixed-effects models of invertebrate assemblages' measures.

Table S7: Results of the linear mixed-effects models using reach (control/reservoir) as a fixed factor and invertebrate community measurements as response variables.

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