Effects of the decommissioning of the Enobieta Dam (Navarre, North Iberian Peninsula) on stream ecosystem structure and functioning

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Contents

Summary

Ageing dams and the rising efforts to restore stream ecosystems are increasing the number of dam decommissioning programs. Although dam decommissioning aims at improving in-stream habitat, biodiversity, and ecosystem functioning in the long-term, it might also cause ecological impacts in the short-term, mainly due to the mobilization of the sediment accumulated in the reservoir. Worldwide, more than 2000 dams have been already removed, but the impacts and benefits of this major intervention are still poorly understood, especially in the case of large dams. Additionally, there is less information on the effects of dam removal on stream ecosystem functioning, even though impacts are likely since hydraulics, channel morphology and biodiversity are all tightly linked to ecosystem processes. This dissertation explored the effects of the decommissioning of Enobieta, a large dam in the north of the Iberian Peninsula, on stream ecosystem structure and functioning, in what constitutes a whole-ecosystem manipulation. Following a multiple before-after/control-impact (mBACI) design, which allows controlling spatial and temporal variability, we assessed abiotic and biotic changes during the drawdown and the first stages of ecosystem recovery.

Before the start of the dam decommissioning, we observed sediment starvation in downstream reaches. We also measured high concentrations of manganese and iron downstream from the dam, caused by hypoxic hypolimnetic conditions during stratification. Nevertheless, these concentrations decreased with distance, the concentrations in the furthest impact site being similar to those measured in control sites. Ammonium concentration followed a similar pattern. As expected, the dam caused large differences in the structure of macroinvertebrate communities, including density, taxa richness and Shannon diversity index. In contrast, biofilm biomass, Chl-*a* concentration, nutrient uptake, and metabolism, but not organic matter breakdown, were similar in control and impact reaches.

The drawdown of the Enobieta Dam triggered the erosion and the downstream transport of sediments accumulated in the reservoir, especially when a small dam that emerged in the basin of the reservoir was removed. The sediment transport resulted in downstream turbidity peaks, mostly during rain events. However, these peaks were not higher than the ones observed in nearby basins. During drawdown, concentrations of manganese, iron and ammonium rose. With the exception of biomass and organic matter breakdown, the rest of the variables measured for biofilm decreased, likely because of the changes in sediment characteristics. Surprisingly, the differences in macroinvertebrate communities observed before dam decommissioning decreased during the drawdown phase. After

one year since the start of the decommissioning of the Enobieta Dam, all variables except organic matter breakdown were similar in control and impact reaches, showing the success of this restoration project. This success was also evident when looking at the communities and the functioning of the stream in the area formerly drowned by the reservoir, as well as when looking at the rapid recovery of the forest therein.

Overall, the Enobieta Dam constituted a black spot in the Artikutza valley, fragmenting the river and altering the geomorphology, water quality and the structure and functioning of biological communities. This study evidenced a positive effect of reservoir drawdown on stream structure and functioning with no noticeable impacts, although the impacts and benefits of dam decommissioning could highly depend on site-specific conditions.

Laburpena

Presen zahartzeak eta ibaiak leheneratzeko ahaleginek presak kentzeko proiektuen kopurua handitzea eragin dute. Presak eraistearen helburua epe luzera ibai eta erreketako habitata, biodibertsitatea eta funtzionamendua hobetzea bada ere, epe laburrean inpaktu ekologikoak eragin ditzake, batez ere urtegian metatutako sedimentuen garraioaren ondorioz. Mundu osoan, 2.000 presa baino gehiago eraitsi dira jada, baina hala ere, eskuhartze horren eragin eta onuren inguruko informazioa eskasa da, batez ere presa handien kasuan. Honetaz gain, ekosistemen funtzionamenduan dituen ondorioei buruzko informazio gutxi dago, nahiz eta eraginak nahiko probableak diren ibai ekosistemetan ematen diren prozesuek hidraulika, ubidearen morfologia eta biodibertsitatearekin duten lotura estua dela eta. Tesi honen helburua Iberiar Penintsularen iparraldean kokatuta dagoen Enobieta presa hustutzeak ibai ekosistemen egitura eta funtzionamenduan duen eragina aztertzea izan zen. Horretarako, *multipe before-after/control-impact* (mBACI) deritzon diseinu esperimentala erabili zen, aldakortasun espazial eta tenporala kontrolatzeko aukera ematen duena.

Enobietako presa hustu baino lehen, tamaina txikieneko sedimentu falta somatzen zen urtegitik behera. Bestalde, manganeso eta burdin kontzentrazio altuak neurtu ziren, estratifikazioaren ondorioz hipolimnionean sortutako egoera hipoxikoak eraginda. Hala ere, metalen kontzentrazioak behera egin zuen presarekiko distantzia handitzearekin batera, urrutien kokatutako puntuan kontrol tramuetako balioak neurtu zirelarik. Amonio kontzentrazioak metalen antzeko patroia jarraitu zuen. Espero bezala, presak desberdintasun handiak eragin zituen makroornogabe-komunitatearen egituran, dentsitatea, taxoi aberastasuna eta Shannon dibertsitate indizea barne. Aitzitik, materia organikoaren deskonposaketa ez ezik, biofilmaren biomasa, klorofila kontzentrazioa, mantenugaien atxikimendua eta metabolismoa antzekoak ziren kontrol eta inpaktu tramuetan.

Enobietako presa hustean, urtegian metatutako sedimentuen erosioa eta garraioa gertatu ziren, batez ere urtegiaren barruan azaleratu zen presa txikia eraitsi zenean. Hustuketa fasean zehar sedimentu finen garraioak eraginda uhertasunak handitu zen urtegitik behera, balio altuenak euriteetan behatu zirelarik. Hala ere, balio horiek ez ziren inguruko arroetan ohikoak diren balioak baino altuagoak izan. Honetaz gain, hustuketa fasean zehar manganeso, burdin eta amonio kontzentrazioak handitu egin ziren. Biofilmari dagokionez, biomasa eta mantenugaien atxikimendua izan ezik, gainontzeko aldagaiek behera egin zuten kontrolekin konparatuta, sedimentuen garraioan izandako emendioagatik segur aski. Azkenik, harrigarria suertatu bazen ere, urtegia beteta zegoenean makroornogabeen komunitatean atzemandako desberdintasunak txikitu egin ziren hustuketa fasean zehar. Enobietako

urtegia hustu eta urtebete igaro ondoren, materia organikoaren deskonposaketan ez ezik, gainontzeko aldagaietan antzeko balioak neurtu ziren kontrol eta inpaktu tramuetan, errestaurazio proiektu honen arrakastaren adierazle. Arrakasta hori nabaria izan zen, halaber, lehen urtegia zegoen ingurunean kontrol tramuetako balioak behatu zirelako, bai eta basoa berreskuratzen hasi zelako ere.

Oro har, Enobietako presa Artikutzako haranean puntu beltza zen, ibaia zatitu eta geomorfologia, uraren kalitatea eta funtzionamenduan eragiten zuena. Ikerketa honen arabera, inpaktu negatibo handirik sortu gabe presa kentzeak ondorio positiboak izan zituen errekaren egitura eta funtzionamenduan, nahiz eta erantzunak lekuan lekuko baldintza espezifikoen mende egon daitezkeen.

Resumen

Debido al envejecimiento de las presas y el mayor interés por restaurar los ecosistemas fluviales, el número de proyectos de desmantelamiento de presas ha aumentado en las últimas décadas. Aunque el objetivo del desmantelamiento de presas es mejorar el hábitat, la biodiversidad y el funcionamiento de los ecosistemas fluviales a largo plazo, también puede causar impactos ecológicos a corto plazo, principalmente debido a la movilización del sedimento acumulado en el embalse. En todo el mundo ya se han eliminado más de 2.000 presas, pero los impactos y beneficios de esta importante intervención han sido poco estudiados, especialmente en el caso de las grandes presas. Además, hay aún menos información sobre los efectos de la demolición de presas en el funcionamiento de ecosistemas que en otras variables. No obstante, los impactos son probables ya que la hidrología, la morfología del cauce y la biodiversidad están estrechamente vinculados a los procesos ecosistémicos. Esta tesis explora los efectos del desmantelamiento de Enobieta, una presa de gran tamaño localizada en el norte de la Península Ibérica, en la estructura y el funcionamiento de los ecosistemas fluviales. Para ello se aplicó un diseño experimental denominado *multipe before-after/control-impact* (mBACI), que permite controlar la variabilidad espacial y temporal.

Antes de que comenzara el desmantelamiento de la presa, observamos la falta de sedimento aguas abajo de la presa. También se midieron altas concentraciones de manganeso y hierro, causadas por la hipoxia creada en el hipolimnion durante la estratificación. Sin embargo, estas concentraciones disminuyeron conforme aumentaba la distancia desde la presa, llegando en el punto más lejano a la presa a valores similares a los medidos en los tramos control. La concentración de amonio siguió un patrón similar al observado para los metales. Como cabía esperar, la presa causó grandes efectos sobre la estructura de las comunidades de macroinvertebrados, incluyendo su densidad, su riqueza taxonómica y su índice de diversidad de Shannon. Por el contrario, la concentración de clorofila y biomasa del biofilm, así como la captación de nutrientes y el metabolismo, pero no la descomposición de materia orgánica, fueron similares en los tramos control e impacto.

El vaciado de la presa de Enobieta provocó la erosión y el transporte aguas abajo de los sedimentos acumulados en el embalse, especialmente cuando se retiró el azud que emergió en el vaso del embalse. El transporte de sedimentos resultó en picos de turbidez aguas abajo, principalmente durante los eventos de lluvia. Sin embargo, esos picos no fueron superiores a los observados en las cuencas cercanas. Durante la fase de vaciado, las concentraciones de manganeso, hierro y amonio aumentaron. Con excepción de la biomasa y la captación de nutrientes, el resto de las variables

relacionadas con el biofilm disminuyeron, probablemente debido al aumento en el transporte de sedimento. Sorprendentemente, las diferencias observadas en las comunidades de macroinvertebrados disminuyeron durante la fase de vaciado. Un año después, todas las variables excepto la descomposición de la materia orgánica, fueron similares en los tramos control e impacto, lo que demuestra el éxito de este proyecto de restauración. Este éxito también se evidenció con la rápida recuperación de las comunidades acuáticas y el bosque en la zona anteriormente anegada por el embalse.

En general, la presa de Enobieta constituía un punto negro en el valle de Artikutza, fragmentando el río y alterando su geomorfología, la calidad del agua y la estructura y el funcionamiento de las comunidades biológicas. Este estudio demuestra un efecto positivo del vaciado de la presa en la estructura y el funcionamiento del río sin apenas efectos negativos apreciables. No obstante, los impactos y beneficios del desmantelamiento de presas podrían depender en gran medida de las condiciones específicas de la zona afectada.

1. General Introduction

Stepping into the dam removal era

Streams and rivers provide goods and services essential for the sustainability of human societies (Palmer et al. 2005), but at the same time, human activities often lead to the degradation and over-exploitation of freshwater ecosystems (Dudgeon 2005). For instance, 60% of surface waters in the EU fail good ecological status (European Environment Agency 2018). During the last decades, increased awareness on the consequences of a degraded environment has led to new legislation, such as the EU Water Framework Directive, as well as an exponential increase of the number of river restoration projects (Bernhardt et al. 2005; Wohl et al. 2015). Given the global prevalence of flow regulation and river fragmentation by dams and their strong impact on freshwater ecosystem health (Vörösmarty et al. 2010; Dudgeon 2019), the removal of these infrastructures has become a key restoration action in many river networks (Bednarek 2001; Bellmore et al. 2017). Nonetheless, knowledge on the ecological effects of dam removal is still scarce, thus impeding a proper design and implementation of dam removal projects.

A dam(n)ed world

Globally, half of all river reaches show truncated connectivity (Grill et al. 2015, 2019). By 2020, over 58,000 large dams were built worldwide, which cumulatively stored approximately 16% of global surface water resources (Perera & North 2021; Scanlon et al. 2023). As the best placements for dam construction run out (Grill et al. 2015) and the society gets aware of their impacts, their removal outpaces their construction in some countries (Perera et al. 2021). However, this pattern is not evenly distributed worldwide, since in some regions, such as South America, South and East Asia or Africa, over 3,700 hydroelectric dams are already under construction or planned (Zarfl et al. 2015, 2019). The main functions of reservoirs created by dams are irrigation, hydropower, water supply, and flood control (Perera & North 2021), which are essential for developed societies.

Although necessary, dams alter flow regime (Poff et al. 1997; Graf 2006), disrupt the natural flux of sediments (Syvitski et al. 2005; Dethier et al. 2022) and the cycles of carbon, nutrients and metals (Friedl & Wüest 2002; Maavara et al. 2020), thus impacting downstream channel form (Graf 2006) and water quality (Ellis & Jones 2013) and quantity (Lehner et al. 2011). Downstream geomorphologic adjustments can vary depending on the size and storage capacity of reservoirs (Mellado-Díaz et al.

2019), their purpose (*e.g.,* energy supply, water supply) and management (Friedl & Wüest 2002; Richter & Thomas 2007; Ellis & Jones 2013). Usually, reduced sediment fluxes cause sediment starvation, streambed coarsening and armoring, narrowing and channel incision (Kondolf 1997), often disconnecting streams from their floodplains (Cluer & Thorne 2014; Lane et al. 2022). Water physicochemical responses to damming also depend on the features of each system (Ahearn et al. 2005), including hydrological (*i.e.,* water residence time) (Maavara et al. 2020), physical (*e.g.,* stratification), chemical (*e.g.,* hypolimnetic oxygen depletion) (Winton et al. 2019) and biological characteristics (Puig et al. 1987). In general, dams and reservoirs alter downstream thermal regimes (Hester & Doyle 2011) and act as sinks for phosphorus (Maavara et al. 2015; Winton et al. 2019) and nitrogen (Akbarzadeh et al. 2019; Ellis & Jones 2013). In addition, oxygen depletion in the reservoir may trigger the solubilization of reduced compounds [Mn (II) and Fe (II) among others] (Friedl & Wüest 2002).

The ecological consequences of large dams are multiple and affect biological communities (*e.g.,* Ruiz-González et al. 2013; Cooper et al. 2016; Mellado-Díaz et al. 2019) and ecosystem functioning (Colas et al. 2013; Ponsatí et al. 2015; von Schiller et al. 2016; Mor et al. 2018). These effects extend to the areas drowned by the reservoir, but also upstream and downstream, as dams alter the flux of water and sediments, as well as the movement of many groups of organisms (Arantes et al. 2019; Dare et al. 2020). In the drowned areas of reservoirs, there is a shift from lotic (*i.e.,* running water) to lentic (*i.e.,* stagnant water) conditions concomitant to the inundation of areas formerly covered by terrestrial vegetation. This causes drastic changes in water physicochemistry, geomorphology, biological communities and ecosystem functioning in the areas covered by reservoirs (Sabater 2008).

Regarding downstream effects, a key agent in biogeochemical cycles and aquatic food webs (Besemer 2015; Battin et al. 2016) can be severely affected (Ponsatí et al. 2015). Autotrophic biofilms tend to be favored by the hydrological stability and reduced scouring caused by flow regulation, which promotes biomass and metabolism below large dams (Morley et al. 2008; Aristi et al. 2014; Smolar-Žvanut & Mikoš 2014). On the contrary, the activity of heterotrophic biofilms has been reported to decrease below dams (Muehlbauer et al. 2009; Colas et al. 2016), suggesting that for these organisms the detrimental effects of altered thermal regimes and water chemistry override the effects of hydrological stability. Dams also impact downstream invertebrate communities, affecting their composition (*e.g.,* Morley et al. 2008), reducing density (*e.g.,* Martínez et al. 2013; Dolédec et al. 2021; but see Wu et al. 2019), diversity (*e.g.,* Holt et al. 2015), taxa richness (Ellis & Jones 2016; Wang et al. 2020; but see Krajenbrink et al. 2022) and biotic indices (*e.g.,* the ones related to pollution intolerant taxa) (Mellado-Díaz et al. 2019; Wu et al. 2019), and altering life histories and dispersal processes

(Tonkin et al. 2009). River fragmentation by dams also has major implications on fish migration and dispersal (Barbarossa et al. 2020), having a negative impact on spawning and reducing abundance and diversity (Wu et al. 2019).

Box 1. Glossary of the main terms used in this dissertation. Terms are shown in alphabetical order.

Dam ageing: the gradual deterioration of a dam infrastructure beyond the initial five years of operation (Zamarrón-Mieza et al. 2017).

Dam decommissioning: the activities undertaken when a dam ceases to be functional, which ends with its total or partial removal (Perera et al. 2021).

Ecosystem functioning: ecosystem-level processes that regulate energy and matter fluxes in ecosystems due to the joint activity of organisms, including organic matter decomposition, nutrient cycling, biomass accrual, secondary production or ecosystem metabolism (von Schiller et al. 2017).

Ecosystem services: value or good provided to humans by ecosystems. Examples are food production, water provision, self-purification capacity and recreation (Isbell et al. 2017).

Ecosystem structure: abiotic and biotic attributes that shape ecosystems, such as channel form, water quality and biological communities (*i.e.,* microbes, plants, and animals) (Sabater & Elosegi 2013).

Large dam: a dam higher than 15 m (Poff & Schmidt 2016).

Nonstaged dam removal: a dam removal project that proceeds following a relatively rapid drawdown (hours to days) of the impoundment (Duda & Bellmore 2022).

Reservoir drawdown: lowering the water level of an impoundment controlled by a dam.

Small barrier or Low barrier: a dam lower than 15 m.

Staged dam removal: a dam removal project that proceeds in stages, either by drawing out the reservoir as the dam is incrementally dismantled (Duda & Bellmore 2022), or first emptying the reservoir and then partially or totally dismantling the dam.

Boom and bust

Since the first dams were built before 2000 BCE in the Egyptian empire, thousands more have been built to benefit human society (Maavara et al. 2020). Dam building upsurged in the mid-20th century and peaked in the 1960´s and 1970´s coinciding with the growth in population and economy in the global north (Fig. 1.1) (Doyle et al. 2008; Maavara et al. 2020; Perera & North 2021). Afterwards, dam construction declined progressively (Fig. 1.1) (Perera et al. 2021) to the point that in some regions, especially in the US, dam decommissioning outpaced dam building (Beatty et al. 2017). However, as stated earlier, in many regions many large dams are still under construction or planned (Zarfl et al. 2015, 2019).

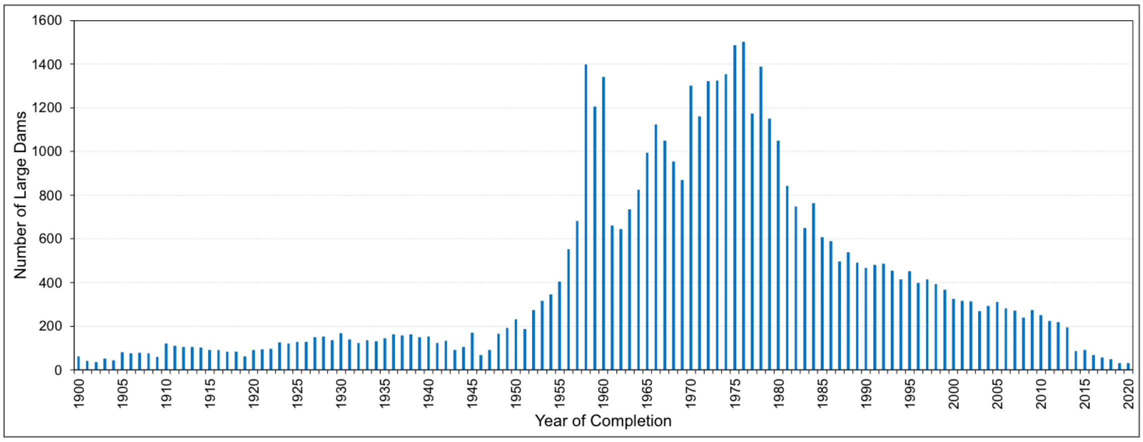

Figure 1.1. Annual construction of large dams worldwide since 1900. From Perera et al. (2021).

Dams, as any other infrastructure, have a design life. Some authors (*e.g.,* Perera et al. 2021) set an arbitrary age of 50 years as the point when “a human-built, large concrete structure such as a dam that controls water would most probably begin to express signs of ageing”. Thus, most dams built during the dam boom (*i.e.*, 1960´s and 1970´s) are approaching or have already surpassed the end of their life expectancy. Dam ageing usually is associated to reservoir sedimentation, loss of functionality and effectiveness, and even dam failures, which all increase the costs of repair and maintenance (Perera et al. 2021). Additionally, during the last 40 years, scientists have become aware of the deleterious environmental impacts of dams on river ecosystems (Baxter 1977; Brittain & L´Abeé-Lund 1995; Graf 2006). Consequently, given safety concerns, maintenance costs and the rising environmental concern of the ageing and obsolete dams, dam decommissioning has gained momentum over the last 50 years (Schiermeier 2018; Bellmore et al. 2019). It has been estimated that between years 1968 and 2019, 1654 dams were removed in the US, whereas in Europe 342 dams were removed between years 1996 and 2019 (Habel et al. 2020). In both cases, most removed infrastructures were low barriers (Fig. 1.2), and the percentage of large dams removed was 1% in the US and 2% in Europe (Habel et al. 2020).

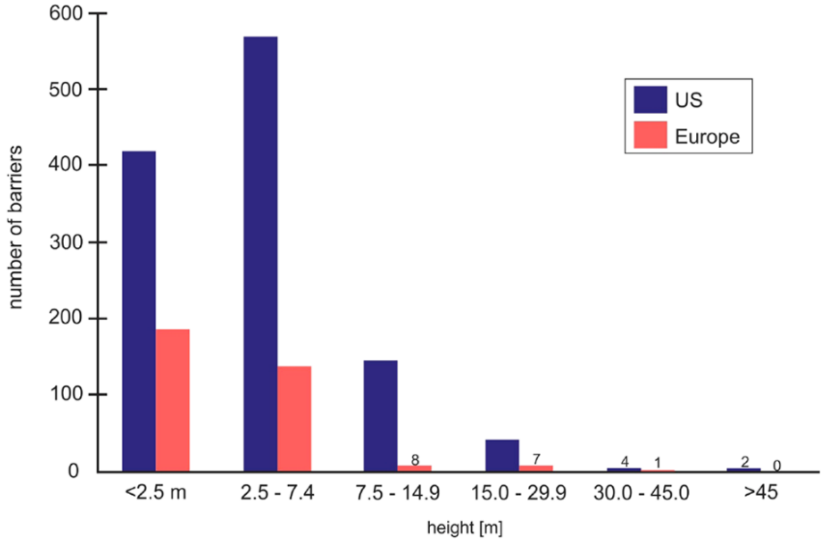

Figure 1.2. The height of dams removed from rivers in the US and in Europe from 1968 to 2019. From Habel et al. (2020).

Dam decommissioning and river ecosystems

Although dam decommissioning is becoming a widespread management strategy, its consequences and benefits are still poorly understood because less than 10% of the interventions have been monitored in detail (Vahedifard et al. 2021). A search in the *Web of Science* for articles with terms "dam remov*" in either the title, key words or abstract, published between 1997 and January 2023 yielded a total of 368 peer-reviewed articles. However, only *c.a.* 36% corresponded to studies analyzing biophysical responses, the rest of the studies focusing on socioeconomical, barrier removal prioritization or modeling aspects. Additionally, the vast majority (*c.a.* 71%) of these studies were performed in small dams (Table 1.1). The remaining 29% corresponded to large dams, but most studies described the case study of the Elwha and Glines Canyon dam removals in Washington State, US. Regarding the variables analyzed in these studies, hydrogeomorphology was the most assessed one both in small (54%) and large (56%) dam decommissioning projects. It was followed by fish community monitoring, which corresponded to 35% and 29% of the total small and large dam studies, respectively. Other variables, such as biofilm or stream functional attributes, which are also key components of stream ecosystems, were significantly understudied (Table 1.1).

All these studies showed that dam removal interventions restore fluvial communities and processes in the medium to long term, although, in the short term, they can result in significant impacts. These interventions ranged from staged actions [*e.g.,* Elwha and Glines Canyon Dams (East et al. 2015) or Stronach Dam (Burroughs et al. 2009)] that try to minimize the impacts, to non-staged works [*e.g.,* dynamiting the dam as in Sunbeam Dam (Salmon River, Idaho) (Pohl 2002) or blasting a hole into the base as in Condit Dam (White Salmon River, Washington) (Wilcox et al. 2014)] that cause acute impacts on the ecosystems. However, even if the magnitude of the consequences differs between intervention types, they all involve the use of heavy machinery right inside the stream channel that results in significant impacts. The main and most concerning impact is the movement of the sediments stored in the reservoir for several years after dam removal (Tullos et al. 2016). These sediments can bury and suffocate benthic organisms in downstream reaches (Bellmore et al. 2019). Additionally, in some catchments, these impacts can be exacerbated by contaminants (*e.g.,* metals and PCBs) accumulated in the reservoir (Bushaw-Newton et al. 2002). Although the duration of the impact mostly depends on the amount and size of the sediments stored in the reservoir, hydrology, dam size, removal method (Foley et al. 2017) and nearby potential colonizers, most of the papers analyzed showed that, after one to two years, ecosystems start to recover. The recovery of specific taxa is linked to their mobility, life history traits, source of colonists, and the existence of other barriers in the catchment. For instance, fish or flying insects are more likely to colonize these reaches than crustaceans or mussels (Sethi et al. 2004). Similarly, microorganisms are expected to show a faster response (Steinman & McIntire 1990; Battin et al. 2016), but empirical evidence is scarce (Bellmore et al. 2019).

Overall, dam decommissioning results in short-term impacts after which fluvial communities and processes are restored. However, the whole process is site-specific, and it is still a young research field in which out of *c.a*. 2000 interventions, only the effects of less than 10% have been monitored (Vahedifard et al. 2021). Furthermore, the vast majority of these studies were carried out in small dams and focused on hydrogeomorphology and fish. Therefore, this PhD thesis aims at bringing some light on the effects of large dam decommissioning on different components of stream ecosystems during the intervention and the recovery phase. This is an important topic since dam decommissioning is expected to gain momentum in the oncoming decades, and the experience gained in past projects is essential to optimize future removal projects.

Table 1.1. State of the art: number of papers studying main response variables in dam decommissioning projects following a search in the *Web of Science* for articles with terms “dam remov*”. Dams are classified as “small” or “large” according to the way it is defined by the authors of each paper.

Dam size	Variable	Number of articles	Source
Small	Hydrogeomorphology	51	Jones et al. (2023), Lu et al. (2022), Kim et al. (2022), Chiu et al. (2021), Bubb et al. (2021), Fields et al. (2021), Magilligan et al. (2021), Sun et al. (2021), Wyżga et al. (2021), Mikuś et al. (2021), Gilet et al. (2021), Cashman et al. (2021), Nagayama et al. (2020), Collins et al. (2020), Scorpio et al. (2020), Marteau et al. (2020), Korpak & Lenar-Matyas (2019), Magilligan et al. (2019), Itsukushima et al. (2019), Łapuszek (2019), Cook & Sullivan (2018), Collins et al. (2017), Land et al. (2017), Katz et al. (2017), Pace et al. (2017), Ibisate et al. (2016), Gillette et al. (2016), Claeson & Coffin (2016), Van Dyke (2016), Magilligan et al. (2016), Costigan et al. (2016), Gartner et al. (2015), Zunka et al. (2015), Wang et al. (2014), Tullos et al. (2014), Cantwell et al. (2014), Pearson et al. (2011); Im et al. (2011), Kibler et al. (2011), Walter & Tullos (2010), Orr et al. (2008), Maloney et al. (2008), Granata et al. (2008), Thomson et al. (2005), Wildman & MacBroom (2005), Sethi et al. (2004), Doyle et al. (2003), Stanley et al. (2002), Bushaw-Newton et al. (2002), Kanehl et al. (1997)
	Water physicochemistry	14	Lei et al. (2023), Jones et al. (2023), Abbott et al. (2022), Kim et al. (2022), Lewis et al. (2021), Cook & Sullivan (2018), Bohrerova et al. (2017), Muehlbauer et al. (2009), Orr et al. (2008), Granata et al. (2008), Riggsbee et al. (2007), Sethi et al. (2004), Ahearn & Dahlgren (2005), Bushaw-Newton et al. (2002)
	Biofilm	5	Kim et al. (2022), Muehlbauer et al. (2009), Orr et al. (2008), Thomson et al. (2005), Bushaw-Newton et al. (2002)
	Invertebrates	22	Mahan et al. (2021), Sun et al. (2021), Mikuś et al. (2021), Poulos et al. (2019), Itsukushima et al. (2019), Cook & Sullivan (2018), Sullivan & Manning (2017), Gillette et al. (2016), Adams & Marks (2016); Claeson & Coffin (2016), Tullos et al. (2014), Renöfält et al. (2013), Hansen & Hayes (2012), Kil & Bae (2012), Muehlbauer et al. (2009), Orr et al. (2008), Maloney et al. (2008), Thomson et al. (2005), Pollard & Reed (2004), Stanley et al. (2002), Bushaw-Newton et al. (2002)

	Fish	33	Jones et al. (2023), Cancel Villamil & Locke (2022)4/25/2023 5:14:00 PMBubb et al. (2021), Magilligan et al. (2021), Sun et al. (2021), Mikuś et al. (2021), Muha et al. (2021), Nagayama et al. (2020), Im et al. (2019), Sullivan et al. (2019), Hill et al. (2019), Itsukushima et al. (2019), Ding et al. (2019), Cook & Sullivan (2018), (Watson et al. 2018), Birnie-Gauvin et al. (2017), Davis et al. (2017), Livermore et al. (2017), Poulos & Chernoff (2017), Gillette et al. (2016), Magilligan et al. (2016), Lasne et al. (2015), Kornis et al. (2015), Hogg et al. (2015), Poulos et al. (2014), Hogg et al. (2013), Gardner et al. (2013), Fjeldstad et al. (2012), Hitt et al. (2012), Marks et al. (2010), Burroughs et al. (2010), Stanley et al. (2007), Kanehl et al. (1997)
	Ecosystem functioning	5	Sullivan et al. (2018), Gibson et al. (2018), Muehlbauer et al. (2009), Orr et al. (2008), Doyle et al. (2003)
	Others	5	Kim et al. (2022), Lisius et al. (2018), Stephens (2017), Riggsbee et al. (2012), Wells et al. (2008)
Large	Hydrogeomorphology	19	Brown et al. (2022), Estigoni et al. (2020), East et al. (2018), Harrison et al. (2018), Ritchie et al. (2018), Chang et al. (2017), Peters et al. (2017), Hatten et al. (2016), Wang & Kuo (2016), Magirl et al. (2015), Randle et al. (2015), Warrick et al. (2015), East et al. (2015), Zunka et al. (2015), Draut & Ritchie (2015), Young & Ishiga (2014), Wilcox et al. (2014), Chiu et al. (2013)
	Water physicochemistry	3	Ba et al. (2023), Atristain et al. (2022), Chang et al. (2017)
	Biofilm	2	Atristain et al. (2022), Chang et al. (2017)
	Invertebrates	2	Chang et al. (2017), Chiu et al. (2013)
	Fish	10	Fraik et al. (2021), Smith et al. (2021), Duda et al. (2021), Quinn et al. (2021), Hess et al. (2021), Birnie-Gauvin et al. (2020), Brenkman et al. (2019), Chang et al. (2017), Hatten et al. (2016), McMillan et al. (2015)
	Ecosystem functioning	4	Amani et al. (2022), Atristain et al. (2022), Morley et al. (2020), Tonra et al. (2015)
	Others	7	Brown et al. (2022); Ravot et al. (2020); Kane et al. (2020); Prach et al. (2019); Chang et al. (2017); Cubley & Brown (2016); (Chiu et al. 2013)

2. Objectives

The overarching objective of this dissertation is to assess the effects of the drawdown of a large reservoir, the first step towards its final decommissioning, on stream ecosystem structure and functioning. To do so, we combined different methodologies to investigate the changes on stream geomorphology, water quality, biofilm structure and functioning, and invertebrate communities.

Specifically, this dissertation addresses the following questions:

1. What are the environmental effects of the reservoir? Do the impacts decrease as the distance from the dam increases?
2. How does the drawdown of the reservoir affect ecosystem structure and functioning? Do the impacts decrease as the distance from the dam increases?
3. Does the stream ecosystem recover after drawdown?

Helburuak

Tesi honen helburu orokorra presa haundi bat hustutzeak, ondoren eraisteko lehen urratsa, ibai ekosistemako egitura eta funtzionamenduan duen eragina aztertzea da. Horretarako, hainbat metodologia konbinatu ditugu ibaiaren geomorfologian, uraren kalitatean, biofilmaren egitura eta funtzionamenduan, eta ornogabeen komunitateetan gertatu diren aldaketak aztertzeko.

Zehazki, hurrengo hauek dira tesi honen galderak:

1. Zein da urtegiaren eragina? Gutxitu egiten al dira inpaktuak presarekiko distantzia handitu ahala?
2. Nola eragiten dio presa hustutzeak ekosistemaren egitura eta funtzionamenduari? Gutxitu egiten al dira inpaktuak presarekiko distantzia handitu ahala?
3. Ekosistema berreskuratzen al da hustuketaren ondoren?

Objetivos

El objetivo general de esta tesis es evaluar los efectos del vaciado de una gran presa, el primer paso para su puesta fuera de servicio, en la estructura y el funcionamiento del ecosistema fluvial. Para ello, se combinaron diferentes metodologías para investigar los cambios en la geomorfología del río, la calidad del agua, la estructura y el funcionamiento del biofilm, y las comunidades de invertebrados.

Específicamente, esta tesis aborda las siguientes preguntas:

1. ¿Cuáles son los efectos del embalse? ¿Disminuyen los impactos aguas abajo?
2. ¿Cómo afecta el vaciado del embalse a la estructura y el funcionamiento del ecosistema? ¿Disminuyen los impactos aguas abajo?
3. ¿Se recupera el ecosistema después del vaciado?

3. Methodology

Study site

The Artikutza Valley is a mountain headwater catchment located in the north of the Iberian Peninsula (Fig. 3.1). The hydrological network of Artikutza drains a 3,683-ha basin over schist, granite, and sandstone (Government of Navarre, IDENA). Average annual rainfall is 2604 mm per year and the mean annual air temperature is 12.3 °C (http://meteo.navarra.es/). The entire catchment has been strictly conserved since the municipality of San Sebastian acquired it in 1919 to ensure the supply of good quality drinking water. Therefore, Artikutza catchment is mostly covered by mature forests dominated by beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) stands, dense autochthonous riparian vegetation with alder (*Alnus glutinosa* (L.) Gaertner) and ash (*Fraxinus excelsior* L.), some old exotic plantations of conifers and red oaks (*Quercus rubra* L.), and pasturelands on the highest terrain (Lozano & Latasa 2019).

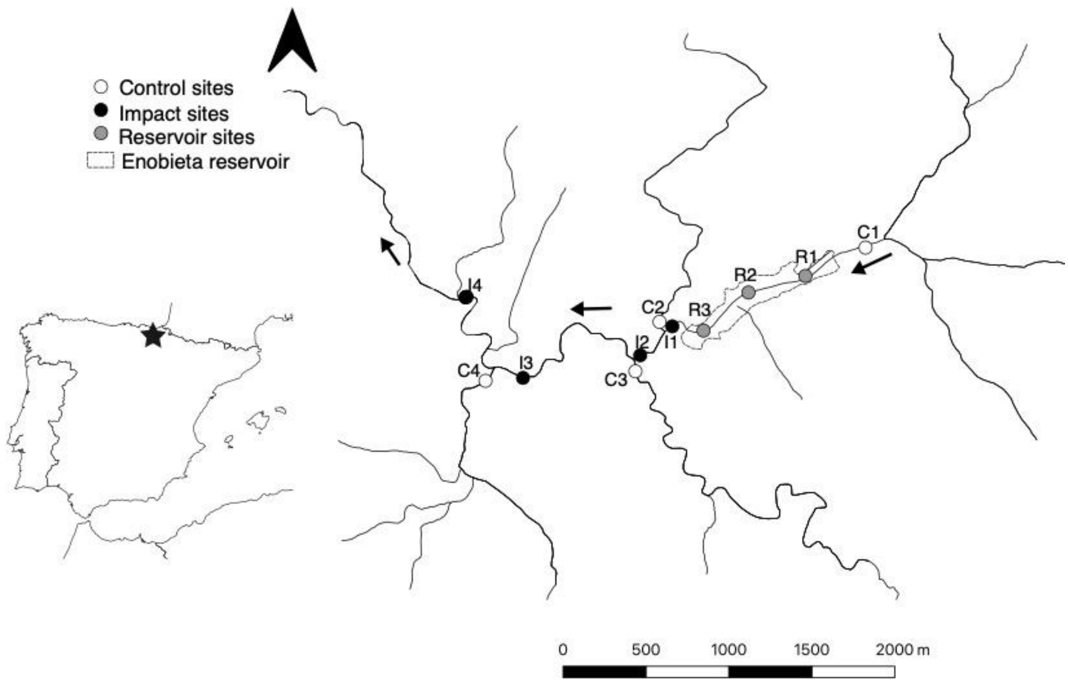

Figure 3.1. Study area showing the location of the 11 study sites [4 control sites (C1, C2, C3 and C4), 4 impact sites (I1, I2, I3 and I4) and 3 sites in the former reservoir (R1, R2 and R3)] in the Artikutza Valley (northern Iberian Peninsula). The dashed line indicates the area drowned by the Enobieta Reservoir. Dark arrows indicate flow direction.

Background of the Enobieta Dam decommissioning project

The Enobieta Dam was designed with a water storage capacity of 2.5 hm^3, but geotechnic issues forced the municipality to reduce its capacity to 1.6 hm^3 when finished in 1947. The reservoir supplied water to San Sebastian for some decades, but metal concentrations (especially Fe and Mn) were often over legal thresholds for drinking water, and the town faced water shortages because of the small capacity of the modified dam. Therefore, in 1976, the Añarbe Dam (79-m tall and 43.8 hm^3 reservoir capacity) was built further downstream in the catchment. Afterwards, the Enobieta Dam lost its strategic value, fell progressively in disuse, and had little or no maintenance, to the point of becoming a safety issue. Indeed, for decades the dam gate and pipes remained closed, and the reservoir was not actively managed, thus being permanently full of water (Fig. 3.2). In 2014, to restore the hydrological connectivity in the basin, the municipality removed seven weirs that remained as legacies from past activities (*e.g.,* ironworks) (Elosegi et al. 2019). Then, in 2016, managers decided to decommission the last artificial obstacle in the entire headwaters: the Enobieta Dam.

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 volume of sediment exported, the reservoir was slowly emptied during 2018 using some old siphons and water-serving pipes that mainly released surface water. We call this the before period. When the water level in the reservoir was circa 4-m high (December 2018), the bottom gate was repaired and opened, thus starting a period of sediment release (what we called drawdown period) with high turbidity episodes. This turbidity was mainly caused by the Enobieta Stream carving a new channel across the sediment stored in former channel and riparian areas, whereas the sediment in the rest of the reservoir was mostly retained on site by the fast-growing vegetation (Elosegi et al. 2022). When the reservoir was empty, an older 3.5 m-tall weir emerged 200 m upstream from the large dam. The local managers demolished this weir in October 2019, and during the very rainy month of November 2019 the Enobieta Stream carved a new channel across the sediment retained by the weir, thus producing a last period of high turbidity. From this moment on, we considered the drawdown process to be finished, thus giving start to what we call the after period. Currently, the reservoir is empty, the bottom gate open, and the authorities are discussing whether to totally remove the dam or to open a 7-m wide notch to remove the barrier effect. The final decision will depend exclusively on the expected damage and benefits each alternative can cause on the local biodiversity. Whatever the case, it has been estimated that any of these alternatives will mobilize considerably less sediment than that mobilized so far (Elosegi et al., 2022), and thus, will have smaller impacts than the drawdown here reported.

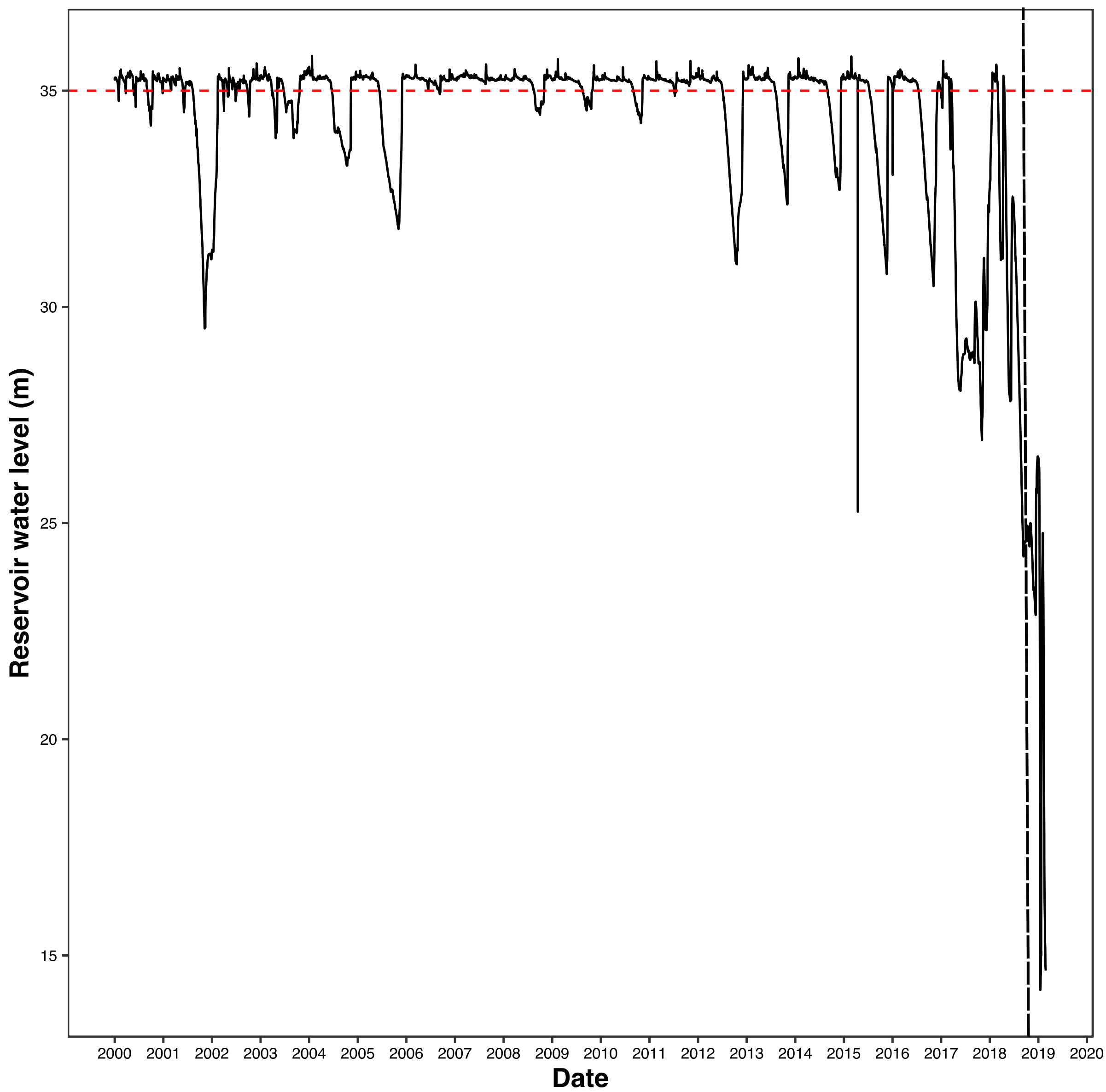

Figure 3.2. Reservoir water level (m) from year 2000 to year 2019. The horizontal dashed red line indicates the level of the spillway. The vertical dashed line indicates the opening of the Enobieta Dam bottom gate.

Experimental design

Overall, our study followed a multiple before – after / control – impact (mBACI) design (Underwood 1994). We defined four control monitoring sites, one (C1) upstream from the dam and three (C2 to C4) in free-flowing tributaries, as well as four impact sites (I1 to I4) at increasing distances downstream from the dam. Additionally, three sites located within the former reservoir (R1 to R3) were also defined in the after period (Fig. 3.1). These latter sites could not be sampled either in the before period, when the reservoir was full or during the drawdown period, as the newly carved stream channel was still too unstable for safe wading. In the control and impact sites, water quality, sediment size, biofilm and macroinvertebrates were analyzed during the three periods, whereas the R sites were mostly studied during the after period (Table 3.1). We tried to measure biofilm in the R sites in the after period, but the instability of the channel resulted in the loss of all artificial substrates we deployed, thus preventing us from getting any result.

Table 3.1. Variables measured (grey shaded) during the before, drawdown and the after periods in each river site.

<table>
<tr><th></th><th colspan="11">Before</th></tr>
<tr><th></th><th>C1</th><th>C2</th><th>C3</th><th>C4</th><th>R1</th><th>R2</th><th>R3</th><th>I1</th><th>I2</th><th>I3</th><th>I4</th></tr>
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<tr><th></th><th colspan="11">Drawdown</th></tr>
<tr><th></th><th>C1</th><th>C2</th><th>C3</th><th>C4</th><th>R1</th><th>R2</th><th>R3</th><th>I1</th><th>I2</th><th>I3</th><th>I4</th></tr>
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<tr><th></th><th colspan="11">After</th></tr>
<tr><th></th><th>C1</th><th>C2</th><th>C3</th><th>C4</th><th>R1</th><th>R2</th><th>R3</th><th>I1</th><th>I2</th><th>I3</th><th>I4</th></tr>
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Methods

Geomorphological adjustment in the reservoir area

To examine the geomorphological adjustment in the reservoir, including sediment export and stream channel evolution, we combined data collected from two aerial drone flights. The first flight was performed during early drawdown when the reservoir was empty but the small weir inside was still intact (April 2019). The second flight was conducted one year after (June 2020). The photographs so obtained were processed photogrammetrically with Agisoft Photoscan (Agisoft LLC, Sant Petersburg, Russia), to generate a 3D reconstruction of the site formerly covered by the reservoir from Digital Elevation Models. The differences in elevation between 2020 and 2019 were used to compute the changes in sediment volumes and therefore to estimate the total volume of sediments exported. Additionally, we regularly repeated photographs in the Enobieta Reservoir at fixed sites during the before, drawdown and the after periods.

During the after period, we also characterized benthic substrate composition in the reservoir area using the Wolman pebble count method (Wolman 1954), with 100 substrate particles collected per site and period while zig-zagging along 100 m-long reaches. For each site, we estimated median grain size (D_{50}) and the percentage of particles smaller than 4 mm on the streambed.

Quantification of exported suspended solids

We measured turbidity in Nephelometric Turbidity Units (NTU) every 10 minutes from July 2018 to September 2020 by means of two turbidimeters (Solitax sc Sensor, Hach Company, USA). One was installed at site I2 and the other at site C2, which have a similar drainage area (11.35 km^2 and 7.32 km^2, respectively). The turbidity data were converted into concentration of suspended solids (mg L^{-1}) applying an empirical formula obtained at the Añarbe gauging station (Zabaleta et al. 2007), located *c.a.* 8 km further downstream in the same catchment. The concentration of suspended solids was then converted into load of exported fine sediments (mg s^{-1}) by multiplying by discharge (L s^{-1}), estimated as 12.8% of the discharge measured continuously at the Añarbe gauging station (the percentage contribution of Enobieta sub-basin to the Añarbe drainage basin). The data so obtained were summed to calculate the mass of fine sediment exported per period (Mg). Because the extent of each period was different (before: 158, drawdown: 348 and after: 285 days, respectively), we reported the exported suspended solid in units of mass per day (Mg day^{-1}).

Characterization of total sediment exported

To characterize the sediments exported from the reservoir, we combined the estimates of the volume of sediments exported (differences in photogrammetry between the two drone flights) and the estimates of the load of suspended solids exported [continuous monitoring of turbidity and empirical formula linking turbidity to suspended solids in Añarbe Zabaleta et al. (2007)] with two additional values: i) the density of fine sediments stored in the reservoir, measured from sediment cores collected in July 2018 and ii) the composition of sediments stored into main categories (fine sediments, coarse inorganic sediments and organic litter), estimated from visual inspection of the newly-carved stream banks.

To convert the load of suspended sediments into volume of fine sediments lost, we collected 7 fine sediment core samples throughout the entire impoundment in July 2018. Once in the laboratory, we measured the dry mass (g) of 10 mL sediment subsamples by gravimetry. The result, 231 kg m^{-3}, was used to convert the mass of suspended solid exported (Mg) into volume of fine sediments lost (m^3).

To estimate the volume of the two other main components of sediments lost, leaf litter and coarse (beadload) inorganic materials, we estimated the proportion of fine sediments (clay and silt), sand to cobbles, and organic litter among the sediments stored in the reservoir. For that purpose, we surveyed and photographed the banks carved by the newly formed Enobieta Stream channel, including a ruler bar in all 28 photographs (Fig. S1). Then we analyzed the photographs to measure the thickness of the different accumulated sediment layers (*i.e.,* clay and silt, sand to cobbles, and organic litter). We then estimated the proportion of each major component of the sediment and applied this proportion to extrapolate the volume of sand-to-cobble and organic litter lost.

Characterization of downstream fluvial geomorphology

To measure changes in channel dimensions, as well as aggradation or degradation of stream channels, before the reservoir drawdown we established six fixed transversal transects every *c.a.* 10 m in all eight control and impact sites. Every transect consisted of two nails hammered into trees in opposing banks of the stream and identified with numbered metallic plates. On each occasion, we tied a marked rope between both nails and measured every 0.5 m the height between the rope and the streambed using a ruler bar. We then drew the shape of the channel in each transect. Changes in elevation were estimated subtracting the height measured in the after period sampling to the height measured in the before period sampling.

We also characterized benthic substrate composition (see above) during the before, drawdown and the after periods in the same eight sites and estimated both D_{50} and the percentage of particles smaller than 4 mm per site and period.

Water physicochemical characteristics

On each sampling date and site, we measured water temperature (°C), dissolved oxygen (DO) saturation (%), electrical conductivity (EC, µS cm^{-1}) and pH with a hand-held probe (Multi 3630 IDS, WTW, Germany). Additionally, we collected water samples. Samples for the determination of metal concentrations [iron (Fe, mg L^{-1}) and manganese (Mn, mg L^{-1})] were fixed with 65% nitric acid (HNO_3) and stored in the fridge at 4 °C until they were analyzed by inductively coupled plasma mass spectrometry (ICP-MS) (Fernández-Turiel et al. 2000). The rest of the samples were filtered through 0.7 µm-pore size pre-combusted fiberglass filters (Whatman GF/F, Whatman International, UK) and stored in the laboratory at -20 °C until analysis. We determined soluble reactive phosphorus [SRP µg P L^{-1}; molybdate method (Murphy & Riley 1962)] and ammonium [NH_4^+ µg N L^{-1}; salicylate method (Reardon et al. 1966)] by spectrophotometry (Shimadzu UV-1800 UV-Vis, Shimadzu Corporation, Japan).

Additionally, to detect potential pulses of hypoxia during drawdown we installed recording oxygen probes (miniDOT Logger, PME, USA) at sites I1 to I4 two days before the opening of the bottom gate and kept them in place for 2 weeks.

Biofilm structure and functioning

We measured biofilm structure (*i.e.,* biomass and Chl-*a*) and three benthic biofilm functions (*i.e.,* metabolism, nutrient uptake, and organic matter decomposition) using standard substrata. For functions dominated by autotrophic biofilms (metabolism and nutrient uptake), we used biofilm carriers (51.45 cm^2, SERA GmbH D52518, Heinsberg, Germany) similar to those used in previous research (Elosegi et al. 2018; Pereda et al. 2020). For decomposition, dominated by heterotrophic biofilms, we used tongue depressors made of untreated poplar wood (*Populus nigra x canadiensis* Moench; 15x1.8x0.2 cm (Arroita et al. 2012). Approximately 2 months before the beginning of the experiment, we randomly deployed six biofilm carriers and five wooden sticks per reach tied with nylon line to metal bars or roots.

The biofilm carriers were used to determine biomass, Chl-*a*, metabolism, and nutrient uptake. We recovered them after at least two months and on each occasion deployed six more carriers to be colonized for the next sampling campaign. After collection, we stored the biofilm carriers in stream water inside plastic containers to carry them to the laboratory. These biofilm carriers were used in a bioassay to determine biofilm metabolism and nutrient uptake. Once in the laboratory, biofilm carriers were acclimatized to local conditions (10 °C and 180 mmol m^{-2} s^{-1} light) for 30 minutes in 500 mL of modified Chu culture medium (Andersen 2005). This medium is widely used for freshwater algal growth since it ensures the supply of essential macro- (*e.g.,* nitrogen) and micronutrients (*e.g.,* calcium, silica, or sodium) during the incubation. After acclimation, biofilm carriers were individually placed in light (n = 3 per site) and dark (n = 3 per site) 60-mL septa bottles completely filled with the same solution spiked with 10 mM solutions of phosphate (K_2HPO_4) and ammonium (NH_4Cl) to reach a final concentration of 5 µM (155 µg P L^{-1} and 70 µg N L^{-1}, respectively). These concentrations ensured saturating conditions for the biofilm and allowed estimating nutrient uptake from the concentration decline during the incubation. Then, we incubated the biofilm carriers for 2 h under the same conditions of temperature and light as during acclimation. Non-colonized biofilm carriers were also incubated as blanks. Afterwards, we measured DO concentrations (mg L^{-1}) with a portable fiber optic oxygen meter coupled to a syringe-like probe (Microsensor NTH-PSt7 on Microx4, Pre4Sens, Germany) and filtered (Whatman GF/F) 20 mL of solution for SRP and NH_4^+ analyses for each bottle (colonized and non-colonized). Biofilm metabolism was calculated from the difference in DO concentration between colonized and non-colonized bottles and expressed based on the incubation time interval and accounting for the water volume in the bottle and the surface of the biofilm carrier (mg O_2 h^{-1} m^{-2}). Changes in DO concentration in light bottles were used to compute net community production (NCP) and those in dark bottles to compute community respiration (CR). Gross primary production (GPP) was calculated as the sum of NCP and CR (Hall & Hotchkiss 2017). The uptake of SRP and NH_4^+ was calculated as the difference between the mean SRP and NH_4^+ concentration of the control (*i.e.,* non-colonized) and the colonized substrates and accounting for the incubation volume and time and then expressed per surface unit (µg P h^{-1} m^{-2} and µg N h^{-1} m^{-2}) (Elosegi et al. 2018). Since we did not detect any differences between light and dark bottles, SRP and NH_4^+ uptake rates calculated from both light and dark bottles were used as replicates to determine average biofilm uptake per reach and date.

Once incubations were finalized, all biofilm carriers were frozen at -20 °C until analysis of biomass and Chl-*a*. We scraped the biofilm carriers in 100 mL of deionized water and divided the obtained slurry into two subsamples for biomass and Chl-*a* determination (50 mL each, approximately), which were filtered through pre-weighed and pre-combusted filters (0.7-µm pore size). Filters for biomass determination were oven-dried (70 °C, 72 h), weighed, ashed (500 °C, 5 h) and weighed again to estimate ash-free dry mass (AFDM). This value was corrected by the fraction of the filtered subsample to total sample and divided by the area of the biofilm carriers to express the result per surface unit (g AFDM m^{-2}). For Chl-*a* extraction and quantification, filters were placed in 90% v/v acetone overnight at 4 °C and the extracted samples were measured spectrophotometrically (Shimadzu UV-1800 UV-Vis) (Steinman et al. 2017) after sonicating (3 min; Selecta sonication bath, operating at 360 W power, 50/60 Hz frequency, JP Selecta S.A., Spain) and centrifuging (2000 rpm, 10 min; P-Selecta Mixtasel, JP Selecta S.A., Spain). We corrected Chl-*a* values by the fraction of the filtered subsample to total sample and divided by the area of the biofilm carriers to express the result per surface unit (mg Chl-*a* m^{-2}).

The wooden tongue depressors were used to determine organic matter decomposition. Before deployment, they were first punched to make a hole for later tying them with nylon line to metal bars and then oven-dried (70 °C, 72 h) and individually weighed. Every four months after deployment, they were recovered and replaced by new ones for the next sampling occasion. Upon recovery, depressors were rinsed with tap water to remove attached invertebrates and mineral particles before the AFDM was measured by gravimetry as done for biofilm AFDM (72 h at 70 °C, 5 h at 500 °C). To convert initial dry mass to AFDM, unexposed depressors were placed in tap water for 24 h after which they were analyzed following the methods of deployed depressors. Organic matter decomposition rate (k, day^{-1}) was calculated assuming the negative exponential model (Petersen & Cummins 1974) using the calculated initial AFDM from the regression and the measured end AFDM and the length of deployment.

Benthic invertebrates

We always sampled benthic invertebrates in autumn to minimize the effects of seasonal changes on the comparison among the different sampling campaigns. Specifically, we collected samples within a single day in November 2017 (before), in October 2019 (drawdown), and in November 2020 (after), one year after the end of drawdown. On each sampling occasion, we randomly took 5 invertebrate samples per reach with a Surber net (quadrat area: 0.09 m^2; mesh-size: 500 µm) and preserved them in 70% ethanol until analysis. In the laboratory, invertebrates were sorted, counted, and identified to the lowest possible taxonomic level under a binocular microscope (Tachet et al. 2010). Most of the invertebrates captured (74.6%) were identified to genus level, but some Niphargidae (Amphipoda), Coleoptera, Ephemeroptera, Trichoptera, Mollusca and Diptera were only identified to family level (13.6%). Acari and Oligochaeta were left at these taxonomic levels (Table S3).

We estimated taxa richness (S), Shannon-Wiener diversity index (H´) and total density (T, individuals m^{-2}) for each sample to describe invertebrate communities. We also estimated the IASPT (Iberian Average Score Per Taxon) index, which is widely used in Spanish biomonitoring programs to represent average sensitivity of the taxa found (Guareschi et al. 2017; Mellado-Díaz et al. 2019). IASPT is calculated as the division of the IBMWP value (Alba-Tercedor 2002) by the number of scoring families detected.

Data analysis

To determine the effect of the dam removal on downstream reaches, we compared control and impact reaches for the three periods. Specifically, we used linear mixed-effects (lme) models with restricted maximum likelihood (Pinheiro & Bates 2000) for all the variables except turbidity and geomorphology (*i.e.,* exported sediment volume, benthic substrate composition, photogrammetry, aggradation and degradation processes), using period (before/drawdown/after) and reach (control/impact) as fixed factors. Sampling date within each period and sampling site were used as random factors in the models. All the models were fit using the “lmer” function of 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 explore the effect of the reservoir drawdown and the afterwards restoration success, we observed the full output of each lme model using the “summary” function in R. Considering that the intercept for the fixed factors was control reaches during the before period, from the full output we extracted i) the control-impact comparison during the before period (BCI) to determine whether there was any effect on the impact reaches previous to the reservoir drawdown, ii) the before-drawdown/control-impact (BD:CI) interaction to determine whether the drawdown of the reservoir had any effect on the impact reaches and iii) the before-after/control-impact (BA:CI) interaction to determine whether impact reaches recovered from the effects of the reservoir drawdown. For invertebrates, we also performed linear mixed-effects models with REML in which we compared control and newly emerged reservoir reaches during the after period to explore whether the previously impounded sites became similar to nearby undisturbed reaches. Accordingly, we used reach (control/reservoir) as fixed factor and site as random factor in the models. In all cases, we assessed the behavior of residuals to avoid departures from normality and homoscedasticity in the models. If data did not meet these specifications, variables were log transformed to fulfil the requirements. Additionally, to test whether the effects of the dam and the drawdown phase was mitigated downstream, we calculated effect sizes for all variables and periods as Ln-ratios between the value at each impact site and the average among all control values. Negative values of the ratio indicate reduced values below the dam, whereas positive values show increases.

For invertebrates, to examine similarities and changes in community composition, we performed nonmetric multidimensional scaling (NMDS; Clarke 1993) and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Both NMDS and PERMANOVA were constructed from a Bray-Curtis dissimilarity matrix of Hellinger transformed data ("vegan" package; Oksanen et al. 2020). The PERMANOVA included the interaction between period (before/drawdown/after) and reach (control/impact) as fixed factors. To minimize the use of binary significance language, instead of using the arbitrary $p = 0.05$ threshold, we describe statistical results using a gradual language of evidence (Muff et al. 2022). All statistical analyses and figures were done with R software (version 4.0.3, R Core Team 2020; Austria).

4. Results and Discussion

4.1. Geomorphology and water physicochemistry

As a restoration measure, dam decommissioning attempts at eliminating the impacts of dams. However, dam removal can also cause negative downstream effects in the short–term (Bellmore et al. 2019). Previous studies have documented the erosion of stored sediment (Randle et al. 2015), and the resulting increased export of sediment (Ritchie et al. 2018), organic matter (Riggsbee et al. 2007) and inorganic nutrients (Ahearn & Dahlgren 2005) after dam removal. Thus, dam decommissioning disturbs both the upstream (*i.e.,* impoundment) and the downstream reaches, as the impoundment undergoes lentic-to-lotic ecosystem transition. These disturbances tend to be strongest during the initial stages, since most of the reservoir sediment erosion occurs in the first post-restoration years (Sawaske & Freyberg 2012; Ferrer-Boix et al. 2014). The downstream disturbances and the afterwards recovery are site-specific, and conditioned by a wide variety of environmental factors, as well as by details of the decommissioning process (Riggsbee et al. 2007; Sawaske & Freyberg 2012; Ibisate et al. 2016).

Here, we examined the changes in geomorphology and water physicochemistry that occurred in the reservoir area and in downstream fluvial sites following the drawdown of the Enobieta Reservoir. First, we predicted that the slow drawdown would favor the stabilization and revegetation of emerged sediments and, consequently, minimize the downstream export of sediments. Second, we predicted channel incision and increased particle size in the reservoir area, and channel aggradation and decreased particle size in the downstream sites. Third, we predicted downstream metal and inorganic nutrient loads to decrease with the reservoir drawdown, rapidly reaching values close to those of nearby undisturbed reaches.

Results

Geomorphological adjustment in the reservoir area

During the 1.5 years that took the drawdown of the Enobieta Reservoir, the Enobieta Stream carved a new channel along the recently exposed sediment. In most places, the new channel coincided with the one present before the construction of Enobieta dam, as shown by the stumps of trees that formed the ancient riparian forest, which emerged along the new channel (Fig. 4.1.1). The riverbanks were mostly vertical and 1-1.5 m in height, very cohesive, and predominantly made up of silt and clay, gravel, and leaf litter (Figs. 4.1.2 & S1).

Figure 4.1.1. Upper panel: narrow Enobieta Stream channel without noticeable erosion before the removal of the small weir (February 2019). Lower panel: channel incision and widening, and sediment coarsening after the removal of the small weir (June 2020). Pictures: Miren Atristain.

Figure 4.1.2. Detailed photo of the riverbank excavated by the Enobieta Stream in the reservoir tail area. The terrace is made up by discrete layers of leaf litter, silt and clay, and gravel. Note iron precipitates in the bottom part. Picture: Arturo Elosegi.

This newly formed stream channel followed a downstream progression as the water level of the reservoir receded. First, the stream carved a very narrow (*c.a.* 50 cm-wide) channel that went as deep as 1.5 m. During flood periods, the channel widened, always keeping vertical banks, and frequent processes of channel avulsion occurred, whereas the lowermost emerged areas registered streambed aggradation and braidening (Figs. 4.1.3, 4.1.4 & 4.1.5). By summer 2019, when the reservoir was already empty, two braided sections were formed, one upstream from the Enobieta Dam, the other upstream from the small unnamed weir that emerged in the former reservoir (Fig. 4.1.5). After the removal of this weir in October 2019, upstream knickpoint migration and channel degradation occurred through the retained sediments (Figs 4.1.1 & 4.1.6). Conversely, aggradation occurred downstream from the removed weir, and the stream channel braided even more (Fig. 4.1.7). The photogrammetric comparison between 2019 and 2020 showed that the level of the accumulated sediments hardly changed, except for the newly carved Enobieta Stream channel (Fig. 4.1.8) that coincides with the small weir removal. From the photogrammetric surveys, the volume of sediments lost was estimated at 6896 m^3 (*ca*. 8% of the total accumulated sediment), which corresponds almost entirely to the newly carved Enobieta Stream channel.

Figure 4.1.3. Upper panel: gravel accumulation in the reservoir tail area on the Enobieta streambed prior to the drawdown of the reservoir in 2015. Bottom panel: incision in the reservoir tail area derived from the reservoir drawdown in 2019. Pictures: Arturo Elosegi.

Figure 4.1.4. Upper panel: degraded narrow channel in the newly emerged sediment in 2018. Lower panel: widening of the Enobieta Stream in the reservoir tail area. Pictures: Arturo Elosegi.

Figure 4.1.5. Braided Enobieta Stream channel upstream from the small weir (July 2019). Picture: Arturo Elosegi.

Sediment export

During the before period, both control and impact sites showed similar turbidity values (median: control before = 0.93 NTU, impact before = 1.01 NTU) resulting in I/C ratios near 1 (Fig. 4.1.9). When the bottom gate was first opened in December 2018, turbidity in the impact site increased remarkably (initially, up to 292 NTU) (Fig. S2) due to sediment released from the reservoir. Frequent turbidity peaks indicated sediment transport events, linked either to rain events (even small ones) or to sudden adjustments of the stream channel (Fig. 4.1.9). The last noticeable turbidity peak (up to 760 NTU) caused by the drawdown happened when the small weir within the reservoir was removed in October 2019 (Fig. S2). After this episode, turbidity values were similar in the control and impact sites (median: control after = 1.39 NTU, impact after = 1.15 NTU) (Figs. 4.1.9 and S2), suggesting a small effect of sediments mobilized from the reservoir.

Figure 4.1.6. Upper panel: knickpoint creation after the small weir removal in October 2019. Lower panel: channel widening of the same site after a rainy November in 2019. Notice that water percolating through organic sediments produces red iron precipitates. Pictures: Arturo Elosegi.

Figure 4.1.7. Braided Enobieta Stream channel between the small weir (located near the background of the picture) and the large dam, from which the picture was taken (July 2020). Picture: Arturo Elosegi.

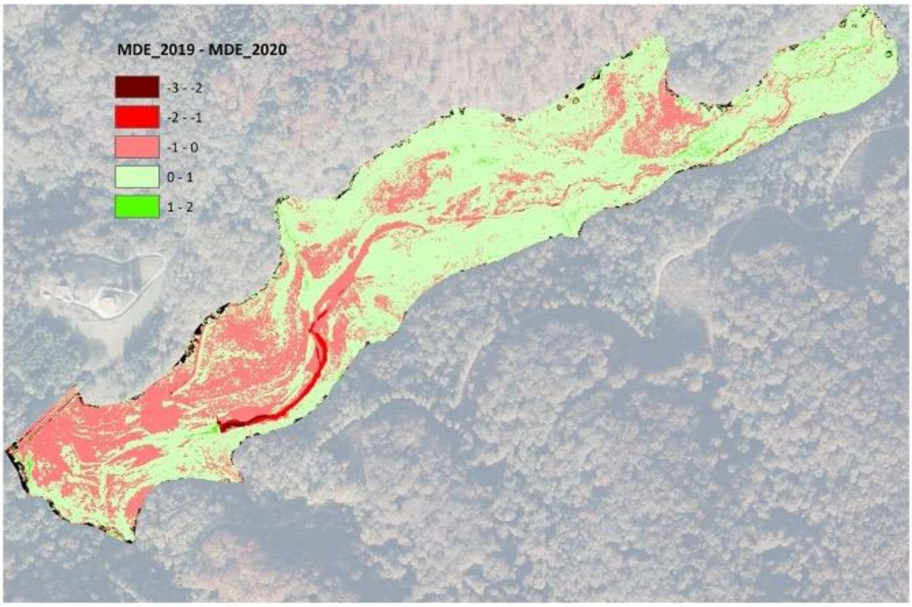

Figure 4.1.8. Comparison of Enobieta Reservoir sediment elevation prior to and after the removal of the small weir. Units are m.

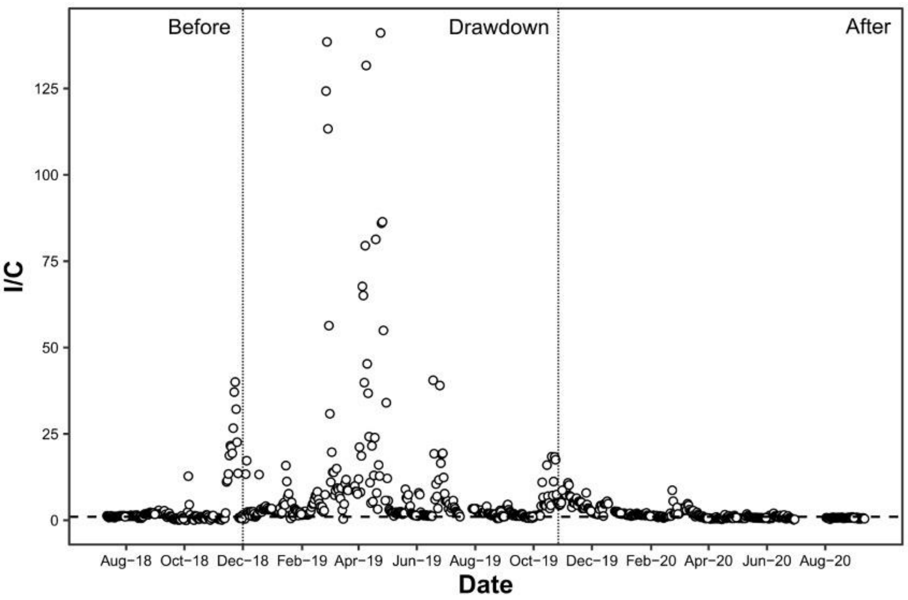

Figure 4.1.9. Turbidity time series data represented as impact/control (I2/C2) ratio during the before, drawdown and after periods (separated by vertical dashed lines). Values near the dashed line denote similar turbidity in impact and control sites, with points above the line having higher turbidity in the impact site.

We estimated that 11.7 Mg of suspended solids were transported during the before period, 419.7 Mg during the drawdown period, and 55.7 Mg during the after period. These amounts were equivalent to 74.5 kg day^{-1}, 1206 kg day^{-1} and 195.3 kg day^{-1} of daily suspended solid transport during the before, drawdown and the after periods, respectively. In total, 1816.7 m^3 suspended solids were exported from the reservoir to the downstream sites. On average, the excavated riverbanks were made up of 23.4% silt or clay, 4.1% sand or gravel, 22.8% cobbles and pebbles, and 49.6% leaf litter (Fig. 4.1.2). Therefore, extrapolating from the 1816.7 m^3 of fine sediments exported, the total volume of sediments exported amounted to 7763.7 m^3.

Downstream fluvial geomorphological changes

Before reservoir drawdown, riverbed coarsening was noticeable just below the dam (site I1) compared to the rest of the sites, as indicated by the higher median bed particle size (D_{50} = 180 mm) and the absence of sand or fine gravel (Table 4.1.1). This effect decreased during drawdown at I1, but the change was not noticeable at sites I3 and I4 (Table 4.1.1). In the after period, grain size decreased substantially, with a reduction of 50% in site I1 and of 30% in sites, I2, I3 and I4 (Table 4.1.1). The percentage of particles smaller than 4 mm did not vary significantly in any of the downstream sites during reservoir drawdown (Table 4.1.1). During the after period, grain size reduction was still noticeable in site I1 (D_{50} = 45 mm), where also the percentage of fine gravel increased by 12%.

Table 4.1.1. Median bed particle size (D_{50}, mm) and percentage of particles smaller than 4 mm in control (C1, C2, C3, C4), impact (I1, I2, I3, I4) and reservoir sites (R1, R2, R3) during periods before, drawdown, and after. Note that R sites were sampled only during the after period.

Variable	Period	Reach										
		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

Minor channel bed aggradation occurred in all control sites within the study period, whereas we did not observe any consistent pattern in the impact sites. We detected almost no changes in bed level in the sites closest to the dam (I1 and I2), whereas sites I3 and I4 underwent aggradation and degradation processes, respectively (Table 4.1.2).

Table 4.1.2. Changes in average stream bed elevation (λh, cm) in both control (C1, C2, C3 eta C4) and impact (I1, I2, I3 and I4) site during the study period. Mean and SE were calculated from the 6 cross-sections measured during the before (n = 1) and the after (n = 1) periods.

Reach	λh (cm)
C1	7.4 $\pm$ 7.8
C2	4.3 $\pm$ 7.6
C3	8.1 $\pm$ 19.2
C4	7.4 $\pm$ 5.2
I1	-1.7 $\pm$ 10.1
I2	-0.7 $\pm$ 2.2
I3	5.90 $\pm$ 9.14
I4	-5 $\pm$ 5.6

Water physicochemistry

Artikutza stands out for the excellent water quality in the valley. The streams in there have low conductivity, and pH is always around circumneutral values (*i.e.,* pH values are around 7). Additionally, streams are oligotrophic (*i.e.,* inorganic nutrient concentrations are low), and oxygen saturation is constantly around 100%.

The drawdown of the reservoir did not affect pH or DO saturation, but altered the rest of the physicochemical attributes (Table 4.1.4). There was weak evidence that the drawdown of the reservoir altered nutrient concentrations (SRP and NH_4^+), EC or T (Table 4.1.4). The concentration of NH_4^+ followed the clearest pattern related to the drawdown of the reservoir (Table 4.1.3). During the before period, comparison between control and impact reaches showed evidence that concentrations were, on average, higher in the impact reaches (BCI_{NH4+} $p < 0.01$; Table S1). Such effect was highest in site I1 and lowest in site I4 (Table 4.1.3). This pattern was maintained during the drawdown period ($BD{:}CI_{NH4+}$ $p = 0.40$; Table S1), but data revealed evidence that during the after period NH_4^+ concentrations were reduced to the point that they were similar in control and impact reaches ($BA{:}CI_{NH4+}$ $p < 0.05$) (Table 4.1.3 and Table S1). On the contrary, there was a lack of evidence that during the before period SRP concentrations were different in control and impact reaches (BCI_{SRP} $p = 0.24$; Table S1). Overall, during the drawdown and the after periods SRP concentrations decreased more in the control than in the impact reaches ($BD:CI_{SRP}$ $p = 0.06$; $BA:CI_{SRP}$ $p = 0.10$; Table S1), differences between reach types becoming very small (Table 4.1.3).

There was strong evidence that the drawdown of the reservoir altered total Fe and Mn ($BDA:CI_{Fe}$ $p < 0.001$; $BDA:CI_{Mn}$ $p < 0.001$; Table 4.1.4). During the before period, Fe and Mn concentrations were higher in the impact reaches (BCI_{Fe} $p < 0.01$; BCI_{Mn} $p < 0.01$; Table S1), especially in sites I1 and I2 (Table 4.1.3). Mn precipitation was easily visible in the sites just below the dam during this period (Fig. 4.1.10). Differences between control and impact reaches were maintained during the drawdown period, as shown by the non-significant before-drawdown/control-impact interaction ($BD:CI_{Fe}$ $p = 0.96$; $BD:CI_{Mn}$ $p = 0.31$; Table S1). During the after period, data revealed strong evidence that Fe and Mn concentrations were reduced to nearby undammed reach values ($BA:CI_{Fe}$ $p < 0.01$; $BA:CI_{Mn}$ $p < 0.0001$; Table S1) (Table 4.1.3).

Figure 4.1.10. Manganese precipitation in the site just below the dam before the drawdown of the reservoir in 2018.

Regarding to the reservoir area, overall, during the after period all water physicochemical characteristics were similar in control, impact, and reservoir sites (Table 4.1.3). However, water temperature and DO saturation peaked in R2 and R3, likely due to the open canopy since they were emerged later, and riparian vegetation was not as developed. Nevertheless, variability in these attributes was high and the effect size small. Similarly, EC as well as the concentration of metals showed an increase from R1 to R3 and decreased with distance to the reservoir in impact sites, although we measured similar values in some control sites. Besides, the probes deployed during the opening of the bottom gate detected almost no effect of the bottom water release on oxygen levels, which were always above 90% saturation, even at site I1.

Table 4.1.3. 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). Values shown are mean ± standard error. Values in brackets represent the Ln-transformed ratio of the average for each Impact site divided by the overall average of the Control sites for each period. Note that R reaches were sampled only during the after period.

Variable	Period	Reach										
		C1	C2	C3	C4	R1	R2	R3	I1	I2	I3	I4
T (°C)	Before	11.3 ± 1	11.2 ± 1.2	11.4 ± 1.1	11.5 ± 0.8	-	-	-	13.3 ± 1.6 (0.16)	12.5 ± 1.4 (0.10)	12.4 ± 1.3 (0.09)	12.2 ± 1.1 (0.07)
	Drawdown	12.2 ± 1.3	12.5 ± 1.4	11.8 ± 1.5	11.9 ± 1	-	-	-	13.8 ± 1.8 (0.13)	12.6 ± 1.1 (0.04)	12.5 ± 1.4 (0.03)	12.2 ± 1.3 (0.01)
	After	11.7 ± 2.1	10.9 ± 2.5	10.2 ± 2.1	10.2 ± 1.3	11.9 ± 2.45 (0.1)	12.8 ± 2.8 (0.1)	13.9 ± 3 (0.1)	12.9 ± 2.6 (0.18)	11.7 ± 2.2 (0.08)	10.5 ± 2 (-0.02)	9.7 ± 1.3 (-0.10)
EC (μS cm^{-1})	Before	58.7 ± 1.9	60.9 ± 2.9	48.4 ± 1.9	105.2 ± 6.3	-	-	-	95.9 ± 9 (0.34)	83.3 ± 6.5 (0.20)	73.2 ± 5.5 (0.07)	85.8 ± 5.4 (0.24)
	Drawdown	61.3 ± 3.1	62.3 ± 1.9	50.2 ± 2	109.9 ± 8.1	-	-	-	103.4 ± 6.6 (0.39)	91.9 ± 6.5 (0.27)	76.7 ± 6 (0.09)	91.7 ± 7.2 (0.27)
	After	61.4 ± 2.5	66.8 ± 2.1	50.7 ± 1.1	110.4 ± 8.7	74.4 ± 6.7 (0.1)	101.8 ± 6.5 (0.4)	114.7 ± 8.2 (0.5)	117.8 ± 8 (0.49)	98.5 ± 6.7 (0.31)	80.4 ± 5.5 (0.11)	94.1 ± 7.3 (0.26)
pH	Before	7.2 ± 0.2	7.4 ± 0.1	7.1 ± 0.2	7.5 ± 0.4	-	-	-	7.5 ± 0.1 (0.02)	7.5 ± 0.2 (0.02)	7.5 ± 0.1 (0.02)	7.7 ± 0.1 (0.05)
	Drawdown	7.2 ± 0.1	7.2 ± 0.1	7.2 ± 0.1	7.6 ± 0.1	-	-	-	7.4 ± 0.1 (0.01)	7.3 ± 0.1 (0)	7.4 ± 0.1 (0)	7.4 ± 0.2 (0.01)
	After	7.5 ± 0.3	7.6 ± 0.2	7.4 ± 0.3	7.6 ± 0.1	7.2 ± 0.4 (0)	7.6 ± 0.2 (0)	8 ± 0.3 (0.1)	7.7 ± 0 (0.03)	7.6 ± 0.1 (0)	7.5 ± 0.1 (0)	7.3 ± 0.1 (-0.03)

DO sat. (%)	Before	99.7 ± 0.5	101.6 ± 0.5	101.1 ± 0.6	102.5 ± 0.5	-	-	-	100.1 ± 0.4 (-0.01)	101.6 ± 0.7 (0)	101.8 ± 0.5 (0)	102.5 ± 0.6 (0.01)
	Drawdown	100.1 ± 1.2	101.6 ± 0.6	100.4 ± 0.7	101.8 ± 0.6	-	-	-	100.1±1.3 (0)	100.8 ± 0.7 (0)	101.2 ± 0.7 (0)	101.5 ± 1.1 (0)
	After	102 ± 1.2	101.1 ± 0.4	100.7 ± 0.2	101.7 ± 0.1	101.7 ± 10.2 (0)	103.4 ± 6 (0)	104.75 ± 11.5 (0)	101.6 ± 0.1 (0)	101.9 ± 0.2 (0)	100.9 ± 0.5 (0)	101.1 ± 0.1 (0)
SRP ($\mu g\ L^{-1}$)	Before	17.3 ± 5.1	8.8 ± 35.8	16.4 ± 8.6	12.9 ± 8.3	-	-	-	14.8 ± 12.4 (-0.06)	11.3 ± 7.3 (-0.21)	11.6 ± 7.2 (-0.18)	12.9 ± 8.3 (-0.07)
	Drawdown	9.2 ± 2	12.5 ± 1.1	12.6 ± 1.9	9.2 ± 2.7	-	-	-	6.4 ± 1.3 (-0.30)	6.1 ± 1.8 (-0.36)	9.9 ± 2.4 (0.13)	10.3 ± 3 (0.17)
	After	8.3 ± 2.3	10.9 ± 3	8.35 ± 3.9	5.2 ± 0.7	8.7 ± 2.1 (-0.5)	7.6 ± 1.6 (-0.6)	8.7 ± 1.4 (-0.5)	6 ± 1.5 (0.18)	4.4 ± 1.5 (0.08)	5.2 ± 0.7 (-0.02)	6 ± 1.5 (-0.10)
NH_4^+ ($\mu g\ L^{-1}$)	Before	3.3 ± 0.8	4.9 ± 1.6	7.8 ± 3.1	5.4 ± 2.1	-	-	-	21.1 ± 7.5 (1.37)	16.3 ± 5.5 (1.12)	8.4 ± 2.8 (0.45)	7.5 ± 1.8 (0.33)
	Drawdown	15.6 ± 5.7	21 ± 7.3	7.9 ± 2.3	11.7 ± 3.3	-	-	-	61.4 ± 37.3 (1.45)	20 ± 6.1 (1.06)	9 ± 2 (0.26)	13.7 ± 6.6 (0.19)
	After	2.5 ± 0	2.5 ± 0	2.5 ± 0	2.5 ± 0	4.1 ± 1.6 (0.3)	4.1 ± 1.6 (0.3)	5 ± 2.5 (0.1)	2.5 ± 0 (0)	2.5 ± 0 (0)	2.5 ± 0 (0)	2.5 ± 0 (0)
Fe ($\mu g\ L^{-1}$)	Before	18.1 ± 6	10 ± 0	15.5 ± 3.7	10 ± 0	-	-	-	131.4 ± 43.6 (2.28)	126.8 ± 63.3 (2.25)	54.9 ± 18.8 (1.41)	29.9 ± 7 (0.80)
	Drawdown	46.3 ± 14.4	10 ± 0	34 ± 16.7	62.3 ± 33.6	-	-	-	298.3 ± 127.7 (2.06)	233.2 ± 107.1 (1.81)	272.5 ± 137.3 (1.97)	36 ± 13.1 (-0.06)
	After	10 ± 0	42.3 ± 18.2	19.1 ± 4.7	17.4 ± 3.7	11.5 ± 5.9 (-0.7)	34.8 ± 12.6 (0.4)	63 ± 11.7 (1)	63.3 ± 15.9 (1.05)	32 ± 7.1 (0.37)	24 ± 6.4 (0.08)	15.5 ± 5.5 (-0.36)

Mn ($\mu g\ L^{-1}$)	Before	5 ± 0	5 ± 0	5 ± 0	5 ± 0	-	-	-	106.3 ± 30.5 (3.06)	85.8 ± 31 (2.84)	42.1 ± 19.3 (2.13)	15.9 ± 3.9 (1.16)
	Drawdown	8.3 ± 3.3	5 ± 0	21.7 ± 16.7	16.3 ± 7.2	-	-	-	131 ± 44 (2.32)	78.5 ± 27.9 (1.81)	105.1 ± 73.1 (2.10)	8.1 ± 3.1 (-0.46)
	After	5 ± 0	7.5 ± 2.5	5 ± 0	5 ± 0	3 ± 0.5 (-0.5)	18.8 ± 7.4 (1.3)	26.4 ± 3.8 (1.7)	31.6 ± 3.9 (1.73)	15.6 ± 0.9 (1.02)	5 ± 0 (-0.12)	5 ± 0 (-0.12)

Table 4.1.3. 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. Sampling date within each period and sampling site were used as random factors. Bold values indicate statistically significant results with $p < 0.05$. Degrees of freedom were estimated with Satterthwaite´s method.

Variable	Source of variation	d.f.	F value	p value
T (°C)	BDA	2, 12.01	0.23	0.8
	CI	1, 6.66	5.28	0.06
	BDA:CI	2, 91.02	2.86	0.06
EC ($\mu S\ cm^{-1}$)	BDA	2, 11.94	0.7	0.52
	CI	1, 6.03	2.16	0.19
	BDA:CI	2, 89.2	2.83	0.06
pH	BDA	2, 11.94	0.35	0.71
	CI	1, 7.35	1.09	0.33
	BDA:CI	2, 90.03	1.77	0.18
DO sat (%)	BDA	2, 11.95	0.17	0.85
	CI	1, 6.56	0.02	0.9
	BDA:CI	2, 91.03	0.25	0.78
T (°C)	BDA	2, 12.01	0.23	0.8
	CI	1, 6.66	5.28	0.06
	BDA:CI	2, 91.02	2.86	0.06
SRP ($\mu g\ L^{-1}$)	BDA	2, 9	0.1	0.91
	CI	1, 6.21	0.23	0.65
	BDA:CI	2, 74.03	2.5	0.09
NH_4^+ ($\mu g\ L^{-1}$)	BDA	2, 10.02	7.23	**< 0.05**
	CI	1, 7.1	4.29	0.08
	BDA:CI	2, 81.13	2.44	0.09
Fe ($\mu g\ L^{-1}$)	BDA	2, 10	2.3	0.15
	CI	1, 6.22	12.2	**< 0.05**
	BDA:CI	2, 82	8.77	**< 0.001**
Mn ($\mu g\ L^{-1}$)	BDA	2, 10	2.75	0.11
	CI	1, 6.16	10.68	**< 0.05**
	BDA:CI	2, 82	9.01	**< 0.001**

Discussion

It has been estimated that *c.a.* 2000 dams have been removed worldwide (Habel et al. 2020), but so far, the consequences of only 10% of these projects have been empirically documented (Bellmore et al. 2019; Habel et al. 2020; Vahedifard et al. 2021). Geomorphology, together with fish migration and fish population improvement, are the most studied variables in available publications (Foley et al. 2017; Liuyong Ding et al. 2019; Duda et al. 2021). However, several authors remark that it is still necessary to study more cases to understand the fate of reservoir sediments (Sawaske & Freyberg 2012), especially in the case of large dams (Randle et al. 2015; Foley et al. 2017). This is also the case for downstream water quality, since there is still insufficient understanding on the effects of dam removal on the release of nutrients and contaminants (Bohrerova et al. 2017; Maavara et al. 2020). Our results revealed that prior to decommissioning, the Enobieta Dam had subtle but negative effects on downstream water quality and physical habitat complexity and heterogeneity, although these effects were greatly attenuated along our study section, as reported by other authors (Ellis & Jones 2013). Drawdown caused some additional downstream impacts, such as increased suspended solids and higher heavy metal and ammonium releases. However, habitat heterogeneity and water quality in the impact sites rapidly resembled nearby undammed sites, as reported by others (Magilligan et al. 2016; Abbott et al. 2022). Besides, as others did (Ibisate et al. 2016), we also observed degradation in the reservoir area sediment deposits, although erosion was mainly reduced to the newly carved stream channel, probably due to the slow drawdown, to the physical properties of deposited sediments and to the rapid plant colonization, which resemble other cases described by Sawaske & Freyberg (2012) and Orr & Stanley (2006), respectively.

To identify the main drivers of the erosion of sediments stored in reservoirs, Sawaske & Freyberg (2012) went beyond conceptual (Pizzuto 2002) and numerical studies that predict potential sediment erosion and channel evolution (Cui et al. 2006a; Cui et al. 2006b) and compiled empirical data from 12 primarily small dam removal case studies within the US. Results indicated lower erosion in fine, cohesive, and consolidated sediments and in stratified deposits. They also included deposit geometry (*i.e.,* deposit depth), annual watershed sediment yield, and dam decommissioning timeline (*i.e.,* staged vs nonstaged) as the most important parameters that influence reservoir erosion rates. The Enobieta Reservoir sediment deposits were both cohesive and stratified and deposited in a far wider area than the former stream channel, as a consequence of many years maintaining the reservoir full of water. These sediment characteristics should explain their stability. Furthermore, emerged sediments were quickly colonized by vegetation, probably due to the favorable climatic conditions and the arrival of new propagules from the dense surrounding vegetation. This colonization was initially dominated by *Persicaria maculosa* (S.F. Gray), later substituted by *Juncus* sp. (L.), and *Urtica dioica* (L.), then by shrubs [*Rubus ulmifolius* (Schott) and *Cytisus scoparius* (L.)], and eventually by trees, especially black alder [*Alnus glutinosa* (L.) Gaertn.] but including also many other native species such as willow [*Salix* sp. (L.)] or ash [*Fraxinus excelsior* (L.)]. We also observed a few individuals of invasive species, such as *Cortaderia selloana* [(Schult. & Schult.f.) Asch. & Graebn. 1900], *Robinia pseudoacacia* (L.) or *Buddleja davidii* (Franch.), but these individuals were quickly removed by the local rangers.

According to field- (Wildman & MacBroom 2005) and flume-scale experiments (Coveleski & Curran 2012; Ferrer-Boix et al. 2014; Curran & Coveleski 2021), as well as to conceptual models (Doyle et al. 2002; Pizzuto 2002), reservoir sediment erosion and channel evolution in response to dam removal follows six steps: a) reservoir drawdown and base-level lowering, b) degradation and knickpoint migration, c) continued degradation and narrowing, d) continued degradation and widening, e) aggradation and widening and f) quasi-equilibrium after vegetation colonization and floodplain development (Randle et al. 2015). In Enobieta Dam, decommissioning is being performed in two main stages, which first include a slow drawdown, followed by the opening of the bottom gate and the removal of the small weir. During the slow reservoir drawdown, as the reservoir delta prograded towards the dam, steps a), c), d), e) and f) (see above) occurred simultaneously at different reaches. As water level receded, multiple channel creation, degradation and narrowing were observed in the newly emerged sediment, until the dominant channel (*i.e.*, the one with the highest discharge) captured the flow from the other channels, as also happened in the Elwha restoration process (Randle et al. 2015). Then, stream channel widening occurred, probably because pre-dam channel bottom was reached after continuous degradation, mostly during high flows (Wildman & MacBroom 2005; Coveleski & Curran 2012), or because as the delta prograded, sediments were deposited across the receded reservoir. During this widening process stream braidening and aggradation also occurred, as shown by others (Randle et al. 2015). After the removal of the small weir that emerged within the reservoir, all six steps that lead to rapid changes in channel morphology were observed. Indeed, as reported for other nonstaged dam removals (Wildman & MacBroom 2005), a small chute was created in the channel immediately upstream from the weir, which rapidly migrated upstream to the point that the stream reached bedrock during the very rainy month of November 2019. Henceforth, degradation slowed, and widening, braidening, and aggradation also occurred in the channel located between the large and the small dam. Thus, the major channel adjustments occurred after flood discharge. Aggradation processes were linked to both, coarser sediment transport within the reservoir channel and vegetation colonization. The total estimated sediment erosion was *c.a.* 8%, which coincides with the low erosion percentage measured in staged dam decommissioning case studies (Burroughs et al. 2009) or in case studies with highly cohesive deposits (Doyle et al. 2003a).

Few dam removal projects have included the monitoring of deposited sediment erosion and the afterwards downstream sediment release from the reservoir (Bellmore et al. 2017). The main concerns regarding the drawdown of the Enobieta Reservoir were the potential downstream impacts of the sediment released. First, the potential impact on biodiversity, as suspended solids can have detrimental effects on riverine communities (Wood & Arrmitage 1997; Izagirre et al. 2009; Davis et al. 2018), to the point that they are included among the most prevalent contaminants in streams (USEPA

2000). Second, the adverse effects that the sediment released might cause in the Añarbe Reservoir, located *c.a.* 10 km further downstream. Nevertheless, the latter was of minor concern, since the sediments stored were not polluted (Ekos 2016) and their total volume did not exceed 88000 m^3 (Girder 2016), which amounts to only 71.5% of the annual inputs to Añarbe, estimated at 123000 m^3 per year (CEDEX 2005). In agreement with previous studies (Tullos et al. 2014; Magilligan et al. 2016; Peters et al. 2017), we observed that the drawdown of the reservoir substantially reduced median bed grain size in the impact sites, especially in the ones located closest to the dam (I1 and I2). These changes were probably also associated to the natural dynamism of the stream since variation in control sites was also observed both during and after the drawdown of the reservoir. Another possible explanation is that reach I1 was continuously receiving fine sediment from site R3, which would reduce mean bed sediment grain size during the first-year post restoration in the reach just below the dam. Eventually, D_{50} may increase as coarser material reaches both R3 and I1 sites, unless natural conditions prevent it. Although frequent peaks of turbidity occurred during drawdown, these were short-lived and in general below 300 NTU, which is not an unusual turbidity in streams in the region (Zabaleta & Antigüedad 2012). Even if during most of the drawdown period the riverbed appeared covered by a mm-thin layer of fine sediments (personal observation), changes in channel dimensions were almost unnoticeable and there was no channel aggradation, showing the erosive power of Artikutza Stream.

Higher inorganic nutrient, manganese and iron concentrations were also released along with the sediment transport. As remarked in other reservoirs (Friedl & Wüest 2002; Betancourt et al. 2010; Munger et al. 2017) during the summer stratification Enobieta Reservoir released high Fe and Mn concentrations due to the low redox potential in the hypolimnion, which dissolved soluble Fe (II) and Mn (III) forms. But, downstream from the dam, at circumneutral pH and oxygenated water, metals precipitated, and black manganese deposits were observed (Fig. 4.1.10). This effect was especially noticeable in site I1, where Fe and Mn levels were, on average, 10 and 21 times higher than in control reaches (mean $\pm$ SE = 131.4 ± 43.6 μg Fe L^{-1} and 106.3 ± 30.5 μg Mn L^{-1}) and then decreased with the increasing distance to the dam. Ammonium followed the same pattern as metals: it was also accumulated (Friedl & Wüest 2002), and due to hypolimnetic water release, highest ammonium concentrations were observed below the dam. Contrary to expected, we did not detect an increase in phosphorus release during the drawdown, as others did (Orr et al. 2008). Water quality improved swiftly after drawdown, reaching by the end of the experiment the values of nearby undammed reaches for most variables.

This case study may be a precedent for other large dam decommissioning projects, as it shows slow drawdown to minimize the potential downstream ecological impacts. Additionally, we should remark the importance of the conservation status of the surrounding catchment, as this will also condition both the prolongation of the useful life of the reservoir (small inputs of sediments) and the downstream impacts during the eventual drawdown.

4.2. Biofilm structure and functioning

Dam removal usually triggers the downstream movement of large amounts of sediment stored in the reservoir (Wilcox et al. 2014; Randle et al. 2015) which typically scours and reduces autotrophic biofilm biomass and activity (Francoeur & Biggs 2006; Izagirre et al. 2009; Bellmore et al. 2019). However, autotrophic biofilm could recover shortly after these sediment disperse, as it shows high resilience to physical disturbances (Steinman & McIntire 1990). Nevertheless, empirical information is limited to small dams or, in the case of large dams, to modeling exercises (Bellmore et al. 2019). Regarding organic matter breakdown, in which heterotrophic biofilms play a key role, information is limited to one publication on total leaf litter breakdown (Muehlbauer et al. 2009) that showed little response to dam removal. In any case, to our knowledge the effects of large dam decommissioning on stream biofilm functioning still needs to be assessed.

We investigated changes in biofilm biomass and chlorophyll-a (Chl-*a*) as well as in three benthic biofilm functions (*i.e.,* metabolism, nutrient uptake, and microbial organic matter decomposition) before, during and after the drawdown. Our general hypothesis was that reservoir drawdown would affect water physicochemical characteristics, which, in turn, would cause shifts in the studied functions. Therefore, we predicted that i) before drawdown, autotrophic biofilm metabolism and nutrient uptake would be higher downstream from the dam than in control reaches, because of hydrological stability, whereas microbial organic matter decomposition would be reduced due to degraded water quality; these effects would fade out downstream as the distance from the dam increases, ii) during reservoir drawdown, transport of suspended sediment would reduce the rates of the three studied functions, the highest effects occurring immediately downstream from the dam, and iii) after the drawdown, because of its high resilience, biofilm downstream from the dam would quick approach those from control reaches.

Results

Comparison between control and impact reaches showed no evidence that the drawdown of the reservoir affected biofilm biomass ($BDA{:}CI_{Biomass}$ $p = 0.52$; Table 4.2.1). Indeed, values were similar in control and impact reaches during the before (mean $\pm$ SE = 3.24 $\pm$ 0.68 g AFDM m^{-2} and 2.58 $\pm$ 0.43 g AFDM m^{-2}, respectively), drawdown (1.77 $\pm$ 0.14 g AFDM m^{-2} and 1.46 $\pm$ 0.11 g AFDM m^{-2}) and after periods (1.08 $\pm$ 0.07 g AFDM m^{-2} and 1.21 $\pm$ 0.10 g AFDM m^{-2}; Fig. 4.2.1). Nevertheless, effect sizes indicated that in site I1 biofilm biomass was lower than in the control sites during the before period, whereas it was higher during and after the drawdown of the reservoir (Fig. 4.2.1).

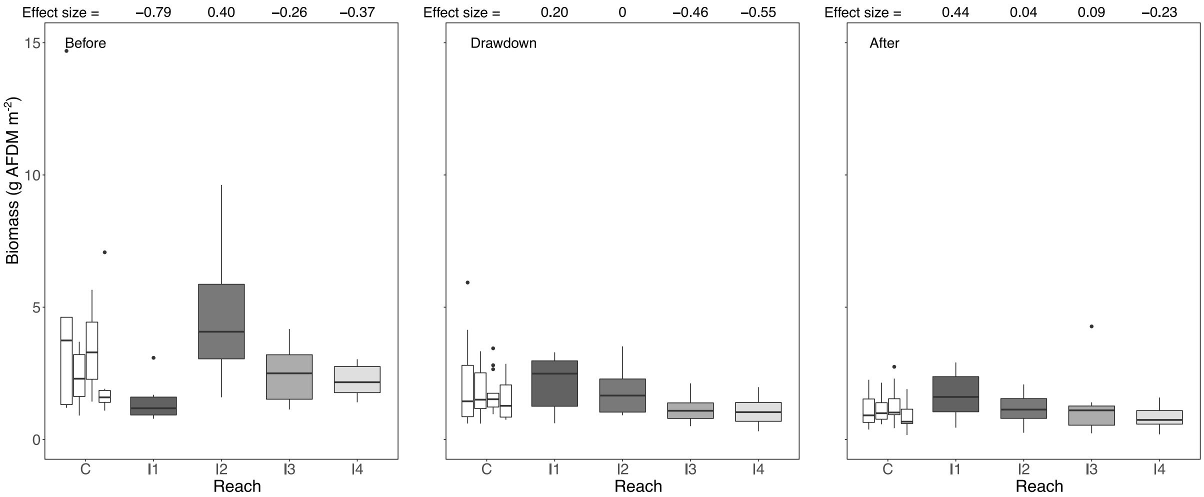

Figure 4.2.1. Biofilm biomass in control and impact sites before, during, and after the drawdown. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale reflects distance from the dam. Effect sizes on top represent the Ln-transformed ratio of the average of each impact site divided by the overall average of the control sites for each period.

Contrasting with biomass, we found evidence that the drawdown of the reservoir altered biofilm Chl-*a* concentration ($BDA{:}CI_{Chl\text{-}a}$ $p < 0.01$; Table 4.2.1). During the before period, Chl-*a* showed similar values in the control and impact reaches (mean $\pm$ SE = 2.49 $\pm$ 0.34 mg m^{-2} and 2.58 $\pm$ 0.43 mg m^{-2}, respectively) ($BCI_{Chl\text{-}a}$ $p = 0.86$; Table S2), but the drawdown of the reservoir reduced Chl-*a* by 44% in impact relative to control reaches (9.86 $\pm$ 0.99 mg m^{-2} and 5.56 $\pm$ 0.74 mg m^{-2}) ($BD{:}CI_{Chl\text{-}a}$ $p < 0.01$; Table S2 & Fig. 4.2.2). This negative effect decreased during the after period, when Chl-*a* concentration showed again similar values in control and impact reaches (7.48 $\pm$ 0.84 mg m^{-2} and 5.81 $\pm$ 0.63 mg m^{-2}) ($BA{:}CI_{Chl\text{-}a}$ $p = 0.27$; Table S2). Effect sizes also showed this trend in biofilm Chl-*a* concentration, and I1 and I3 were the sites most negatively affected during all three periods.

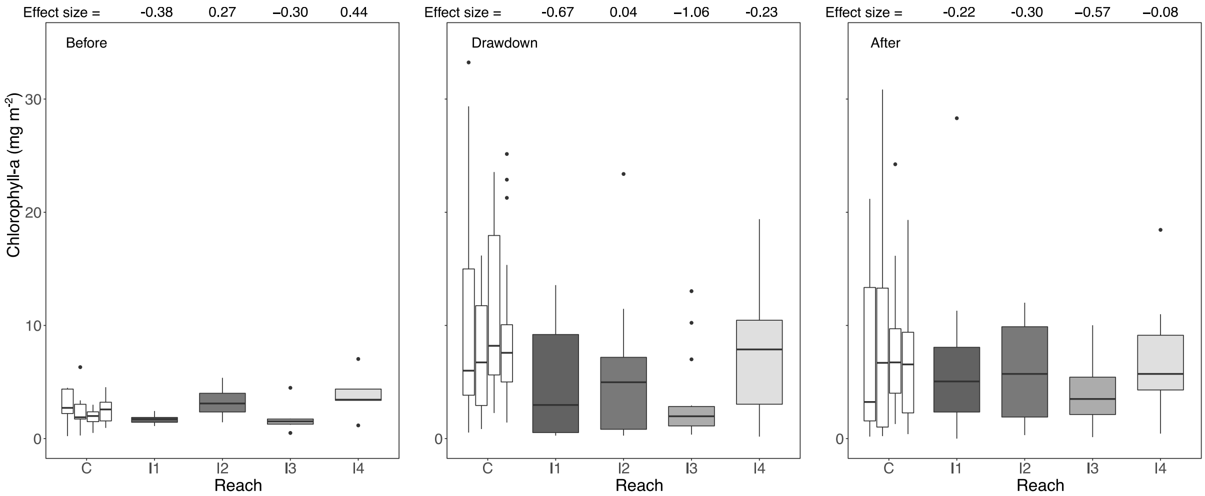

Figure 4.2.2. Chl-*a* concentration in control and impact sites before, during, and after the drawdown. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale reflects distance from the dam. Effect sizes on top represent the Ln-transformed ratio of the average of each Impact site divided by the overall average of the control sites for each period.

There was very strong evidence for a negative effect of the reservoir drawdown on biofilm metabolism (BDA:CI_{GPP} $p < 0.0001$; BDA:CI_{CR} $p < 0.0001$; Table 4.2.1 & Fig. 4.2.3). GPP and CR were, respectively, 48% and 32% lower in the impact reaches during the drawdown period (BD:CI_{GPP} $p < 0.001$; BD:CI_{CR} $p < 0.001$; Table S2), and showed a recovery trend during the after period (BA:CI_{GPP} $p = 0.06$; BA:CI_{CR} $p = 0.07$; Table S2 & Fig. 4.2.3). Effect sizes indicated that the negative effect of the drawdown of the reservoir was highest just below the dam and decreased downstream (Fig. 4.2.3).

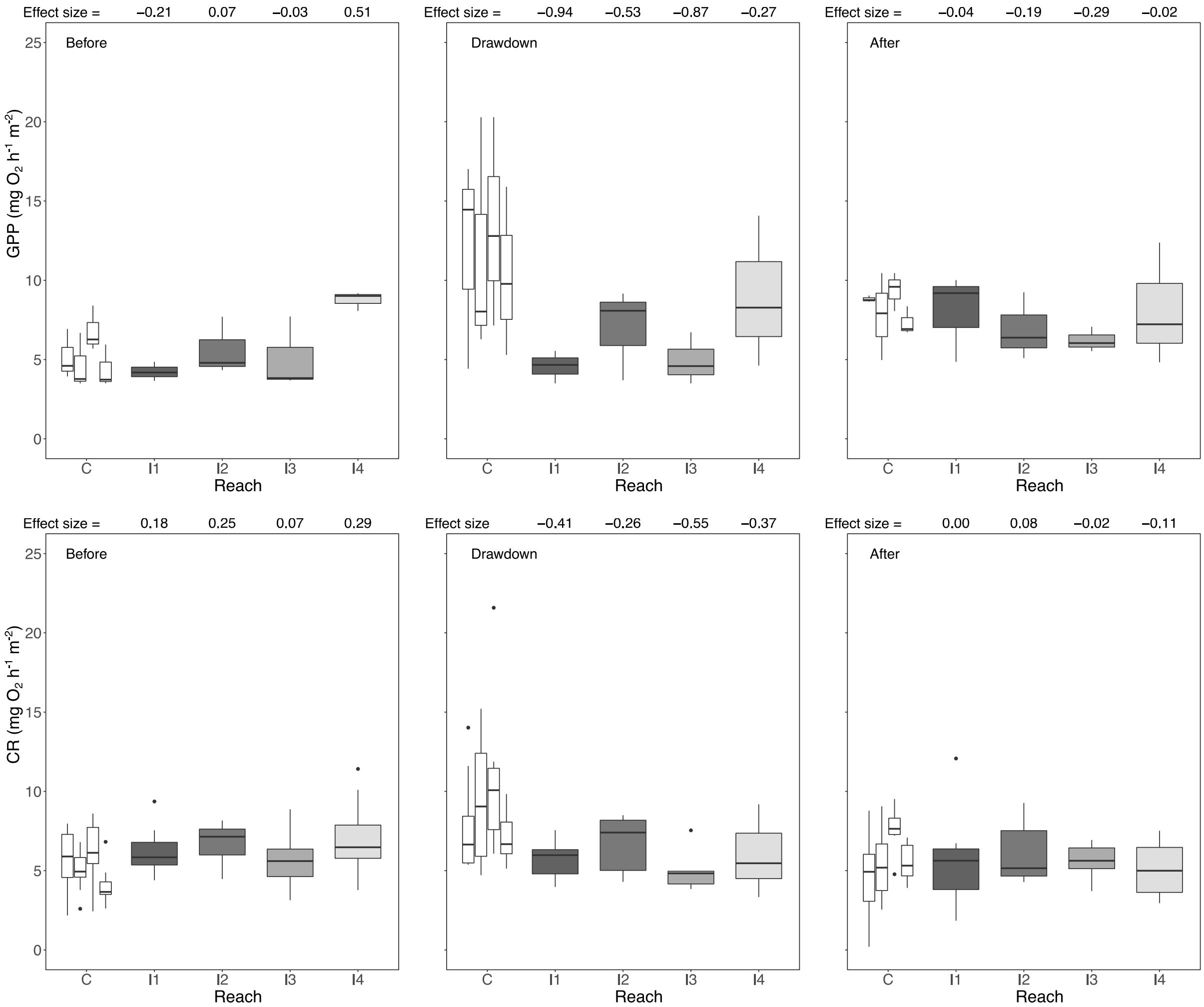

Figure 4.2.3. Biofilm gross primary production (GPP; top panels) and community respiration (CR; lower panels) in Control and Impact reaches before, during, and after the drawdown. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale reflects distance from the dam. 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.

Reservoir drawdown had minor effects on biofilm nutrient uptake ($BDA:CI_{SRPUptake}$ $p = 0.67$; $BDA:CI_{NH4+}$ $p = 0.99$; Table 4.2.1 & Fig. 4.2.4). During the before period data revealed weak evidence that SRP uptake was higher in the impact reaches (mean $\pm$ SE = 133.76 $\pm$ 12.49 µg P h^{-1} m^{-2}) than in the control reaches (92.79 $\pm$ 11.37 µg P h^{-1} m^{-2}) ($BCI_{SRPUptake}$ $p = 0.07$; Table S2), but not NH_4^+ uptake (80.89 $\pm$ 18.68 µg P h^{-1} m^{-2} and 83.68 $\pm$ 15.50 µg P h^{-1} m^{-2}) ($BCI_{NH4+Uptake}$ $p = 0.82$; Table S2). Although data did not reveal any evidence that NH_4^+ uptake changed due to the drawdown (Table 4.2.1), effect sizes indicated that differences between control and impact sites decreased from the before to the drawdown and the after periods (Fig. 4.2.4). By contrast, this ratio was quite constant within the whole study in the case of biofilm SRP uptake (Fig. 4.2.4).

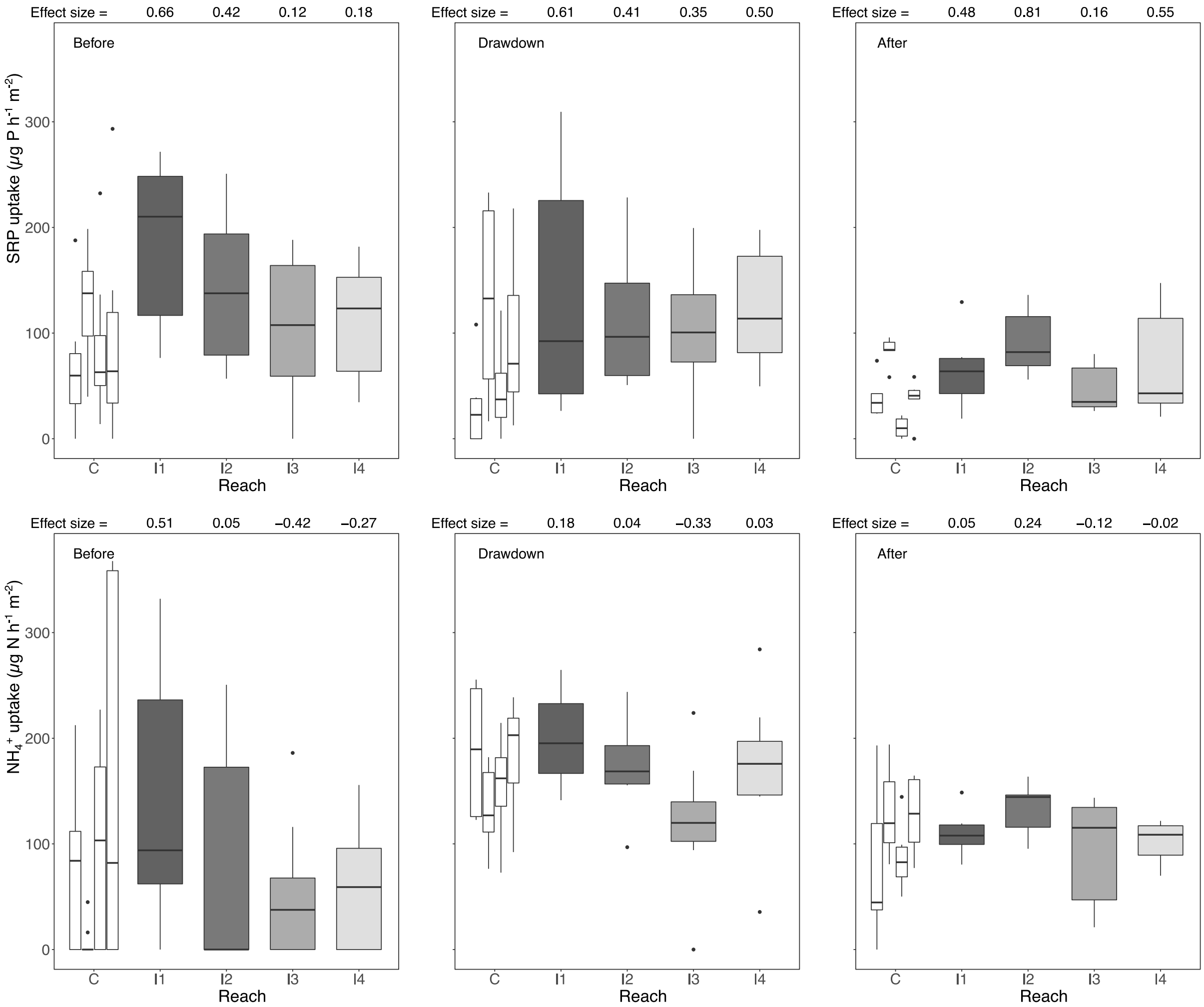

Figure 4.2.4. Biofilm uptake of soluble reactive phosphorus (SRP; top panels) and ammonium (NH_4^+; lower panels) in control and impact sites before, during, and after the drawdown. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale reflects distance from the dam. 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.

Overall, there was no clear evidence that reservoir drawdown affected organic matter decomposition (BDA:CI_k $p = 0.15$; Table 4.2.1). However, the specific interactions differed depending on the period (BD:CI_k $p = 0.05$; BA:CI_k $p = 0.22$; Table S2). During the Before period, comparison between control and impact reaches showed evidence that decomposition rates were lower below the dam (BCI $p < 0.01$; Table S2), and I1 was the most impaired site (effect size = -0.46; Fig. 6).

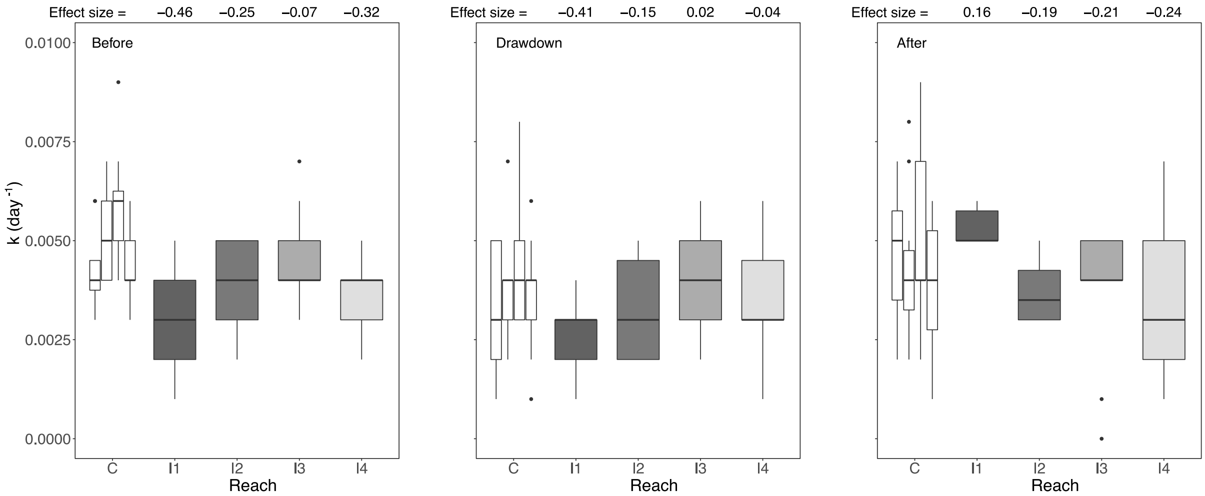

Figure 4.2.5. Organic matter decomposition rate (k) in control and impact sites before, during, and after the drawdown. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale reflects distance from the dam. 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.

Table 4.2.1. Results of the linear mixed-effects models using period (before/drawdown/after) and reach (control/impact) as fixed factors and biofilm structural and functional attributes as response variables. Sampling date within each period and sampling site were used as random factors. Bold values indicate statistically significant results with $p < 0.05$. Degrees of freedom were estimated with Satterthwaite´s method.

Variable	Source of variation	d.f.	F value	p value
Biomass (g AFDM m^{-2})	BDA	2, 4.01	3.24	0.15
	CI	1, 6.72	0.6	0.47
	BDA:CI	2, 259.78	0.65	0.52
Chlorophyll-*a* (mg m^{-2})	BDA	2, 4	0.34	0.73
	CI	1, 6.83	3.41	0.11
	BDA:CI	2, 271.6	6.14	**< 0.01**
GPP (mg O_2 h^{-1} m^{-2})	BDA	2, 6	1.4	0.32
	CI	1, 6	2.89	0.14
	BDA:CI	2, 54	14.15	**< 0.0001**
CR (mg O_2 h^{-1} m^{-2})	BDA	2, 6.02	0.87	0.47
	CI	1, 5.93	1.16	0.32
	BDA:CI	2, 54	16.12	**< 0.0001**
SRP uptake (μg h^{-1} m^{-2})	BDA	2, 5	1.23	0.37
	CI	1, 6	4.35	0.08
	BDA:CI	2, 162.2	0.4	0.67
NH_4^+ uptake (μg h^{-1} m^{-2})	BDA	2, 5.02	1.74	0.27
	CI	1, 6.04	0.04	0.86
	BDA:CI	2, 161.14	0.01	0.99
k (day^{-1})	BDA	2, 4.05	0.99	0.45
	CI	1, 6.37	5.39	0.06
	BDA:CI	2, 221.6	1.97	0.14

Discussion

Biofilms are highly sensitive to environmental changes (Battin et al. 2016), so high metal concentrations below the dam may have negatively affected biofilm structure and functioning, both during its operation and decommissioning. Indeed, against the pattern most often found below dams (Munn & Brusven 2004; Ponsatí et al. 2015), neither biofiom biomass or Chl-*a* nor metabolism were higher below Enobieta Dam. It is likely that Fe and Mn precipitating at circumneutral pH could have caused indirect physical impacts on benthic communities (Cadmus et al. 2018), such as sunlight blocking (Chon & Hwang 2000), in addition to direct toxic effects (Morin et al. 2012; Harford et al. 2015; Kosarev et al. 2022). Additionally, as it was maintained unused and full for decades, Enobieta

Reservoir had little or no regulating effect, and it may not have offered enough hydrological stability to reduce scouring and consequently enhance biofilm growth below the dam. During drawdown, Chl-*a* and metabolism were reduced downstream from the Enobieta Dam, most probably as a response to the presence of suspended solids, as reported elsewhere for small decommissioned dams (Orr et al. 2008; Chang et al. 2017). Turbidity and deposition of fine sediment can affect biofilm communities in contrasting ways. On the one hand, they reduce light penetration into the benthos (Davies-Colley et al. 1992) as well as the availability of stable attachment surfaces (Wood & Arrmitage 1997), thus limiting periphyton accrual and metabolism (Davies-Colley et al. 1992; Aspray et al. 2017; Louhi et al. 2017). On the other hand, sediments can also act as fertilizers and promote biofilm biomass and metabolism (Baattrup-Pedersen et al. 2020). In fact, Pérez-Calpe et al. (2021), in an experiment in which they exposed indoor channels to fine sediments from the Enobieta Reservoir, showed these sediments do promote biofilm biomass and metabolic activity, suggesting a fertilizing effect of the nutrient leachates. The exact balance between the potential subsidy and stress effects of fine sediments thus seems to be dependent of site-specific conditions, such as water velocity and light availability, as well as on sediment characteristics. In our case, both high turbidity and scouring episodes, as well as flow disturbances derived from the drawdown of the reservoir reduced autotrophic biofilm biomass in the Impact reaches. Anyway, such impacts disappeared during the recovery period because biofilms in sheltered microhabitats may have acted as sources for recolonization, thus confirming the high resilience of biofilm (Dzubakova et al. 2018). Contrary to Chl-*a*, biofilm biomass tended to increase during drawdown in I1. This could reflect that autotrophs were more affected by drawdown than heterotrophs, or that autotrophs had less Chl-*a* per biomass. Alternatively, it could be the result of biofilm carriers trapping organic sediment, thus increasing their AFDM, although visual inspection did not reinforce this possibility.

As expected, biofilm gross primary production (GPP) was also reduced due to the loss of primary producers (*i.e.,* lower Chl-*a*) during the drawdown of the reservoir. On the contrary, according to the increase in the AFDM, we could expect heterotrophs to be more resistant than autotrophs to the disturbances derived from the reservoir drawdown, and so, community respiration (CR) to be promoted, or at least, less affected than GPP. Based on our results, we are far from saying whether autotrophs were more affected than heterotrophs, but we hypothesize that in our case, CR was reduced, probably, due to the reduced autotrophic respiration as reported elsewhere (Uehlinger et al. 2003). Although metabolism was affected, drawdown exerted only subtle effects on nutrient uptake by the biofilm. During the Before period, SRP uptake was marginally higher in the reach closest to the dam and then decreased downstream. This longitudinal trend in SRP uptake was attenuated during the drawdown and the after periods. In contrast, NH_4^+ uptake showed no clear patterns. A potential explanation for these results is that the Enobieta Reservoir acted as a sink for phosphorus during its lifespan, as is reported for other impoundments (Ponsatí et al. 2015), as a consequence of sediment sequestering phosphorus (Maavara et al. 2015). This could result in phosphorus-starved biofilms below the dam during the before period, which under our experimental conditions, resulted in high uptake (Reddy et al. 1999). The presence of more P-rich sediment in the reaches located below the dam during the after period might have decreased this P uptake potential. On the other hand, the fact that nitrogen was likely never the limiting nutrient in the study reaches might explain the lack of significant changes in biofilm NH_4^+ uptake among reaches and periods.

Similar to biofilm SRP uptake, during the before period heterotrophic microbial activity linked to organic matter breakdown was marginally different between control and impact reaches. Indeed, as in the case of biofilm metabolism, metal toxicity may have impaired decomposition below the dam. For instance Lecerf & Chauvet (2008) showed metal pollution to reduce microbial decomposition of leaf litter and to depress spore production of aquatic fungi. Although we did not observe any clear pattern within the impact sites during and after reservoir drawdown, data revealed a slight increase of decomposition rates below the dam to the end of the experiment. This trend towards ecosystem functioning recovery may indicate that there was still a legacy effect of the previous degraded water quality state during the after period, and thus, that restoration to nearby undammed reaches conditions may take longer for microbial organic matter decomposition.

In summary, our results show that the slow drawdown of a large reservoir, a key step towards its final decommissioning, did not result in additional impacts to those caused by the operating reservoir. Furthermore, our findings indicate that biofilm biomass and activity recovered quickly afterwards, reaching values similar to those in control reaches that are among the best-preserved streams in the region (Elosegi et al. 2019). Given the key role biofilms play on stream ecosystem functioning (Battin et al. 2016) and the fact that the latter is the basis of essential ecosystem services, our results point to the beneficial effects of reservoir decommissioning on water quality and ecosystem services altogether, if carefully conducted to minimize impacts. This should be balanced with the efforts to restore the natural flux of other sediments such as gravel and cobbles, whose lack impairs ecosystems by "sediment starving" river sections below dams (Kondolf 1997; Kondolf et al. 2014). In general, managers should strive to minimize the export of fine sediment stored beyond the ancient channel of the stream, by using a means to immobilize the sediments as achieved through vegetation in this particular care.

4.3. Invertebrate communities

Decommissioning should mitigate the effects caused by dams in the long-term (Hansen & Hayes 2012), but it may also impair invertebrate communities in the short-term due to the downstream sediment and nutrient mobilization (Ahearn & Dahlgren 2005; Matthaei et al. 2010), resulting in an initial decline in macroinvertebrate density, especially for most environmentally sensitive taxa (Carlson et al. 2018; Mahan et al. 2021). There is also accumulating evidence that invertebrate communities can rapidly recover (< 1 to 2 years post-restoration) from the negative effects of dam decommissioning (Orr et al. 2008; Chiu et al. 2013; Mahan et al. 2021), but some authors report that they may need time periods over 3 years to recover from the pulse disturbance caused by dam decommissioning (Hansen & Hayes 2012; Renöfält et al. 2013). These diverging responses to dam decommissioning can be related to the varying site-specific conditions, for instance, the size of the dam, land use and catchment conservation status or mean annual discharge (Carlson et al. 2018).

The objective of the present was to analyze how stream invertebrates responded to reservoir drawdown in one of the largest dams decommissioned in Europe to date (Habel et al. 2020). We predicted that i) before drawdown, reduced water quality and streambed coarsening would result in low invertebrate density and diversity below the dam, these negative effects mitigating downstream with distance below the dam, ii) during drawdown, the mobilization of the sediment stored in the reservoir would further reduce invertebrate density and diversity, and iii) after drawdown, invertebrate communities in the reservoir and downstream would quickly resemble the communities found in nearby undammed tributaries.

Results

In the 135 benthic samples, we found 21,188 invertebrate individuals comprising 78 taxa (Table S3). The most abundant taxa were the amphipod *Echinogammarus* (21.3%), the caddisfly *Hydropsyche* (12.1%), and the mayflies *Baetis* (9.9%), *Habroleptoides* (9.1%) and Heptageniidae (4.8%).

Prior to drawdown, total invertebrate density was 48% lower in the impact than in control reaches (T_C = 1973.9 $\pm$ 236.3 ind. m^{-2} and T_I = 1030.6 $\pm$ 184.6 ind. m^{-2}) (Table S4). According to the effect size values, the influence of the dam was highest just below the dam (effect size$_{I1}$ = -1.94 and effects size$_{I2}$ = -0.98) and decreased downstream (effect size$_{I3}$ = -0.31 and effect size$_{I4}$ = -0.18) (Fig. 4.3.1). Although there was very weak evidence that the drawdown of the reservoir led to changes in the invertebrate density of the impact reaches (BDA:CI, $p = 0.08$; Table 4.3.1), we observed a substantial recovery of the density, especially in the sites closest to the dam (I1 and I2) (Fig. 4.3.1). During the drawdown period, differences in density between control and impact reaches disappeared ($T_c = 1985.6 \pm 250.6$ ind. m^{-2} and $T_I = 1978.9 \pm 266.6$ ind. m^{-2}), as shown by the significant before-drawdown / control-impact interaction (BD:CI, $p < 0.05$; Table S4). This trend in the community recovery was maintained during the after period, when invertebrate densities were similar in control and impact reaches ($T_c = 1644.4 \pm 258.4$ ind. m^{-2} and $T_I = 1617.2 \pm 234.0$ ind. m^{-2}) (BA:CI, $p = 0.05$; Table S4) (Fig. 4.3.1).

Evidence associates the drawdown of the reservoir with changes in both taxonomic richness ($BDA:CI_S$, $p < 0.01$) and diversity ($BDA:CI_{H'}$, $p < 0.05$) (Table 4.3.1). Before the drawdown of the reservoir, taxonomic richness and diversity were, in general, 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, $p < 0.01$; Table S3), the effect being highest in the site closest to the dam ($\text{effect sizes}_{S,I1} = -1.81$ and $\text{effect size}_{H',I1} = -0.97$) (Fig. 4.3.1). Despite richness and diversity increasing in the impact reaches during the drawdown period ($S_C = 20.8 \pm 0.7$ and $S_I = 18.0 \pm 1.4$; $H'_C = 2.2 \pm 0.1$ and $H'_I = 2.0 \pm 0.1$) ($BD:CI_S$, $p < 0.01$; $BD:CI_{H'}$, $p < 0.05$; Table S4), values in I1 were still below those in control sites (Fig. 4.3.1). It was only during the after period when all the impact sites reached values similar to those found in control sites (BA:CI, $p < 0.001$; $BA:CI_{H'}$, $p < 0.01$; Table S4). The IASPT biomonitoring index followed a similar pattern. During the before period IASPT index was 13% lower in impact reaches ($IASPT_C = 6.6 \pm 0.1$ and $IASPT_I = 5.8 \pm 0.2$) (BCI, $p < 0.05$; Table S4), especially in the site just below the dam ($\text{effect size}_{I1} = -0.40$) (Fig. 4.3.2). There was strong evidence that the drawdown promoted an increase in the presence of most pollution-sensitive taxa (BDA: CI, $p < 0.001$; Table 3), since IASPT values increased substantially during the drawdown and the after periods, as shown by the near-zero effect sizes and the significant BD:CI and BA:CI interactions (BD:CI, $p < 0.05$ and BA:CI $p < 0.0001$) (Fig. 4.3.2; Table S4).

During the before period, communities in sites I1 and I2 occupied a region of the NMDS biplot well separated from the communities found in control sites, but these differences in taxonomic composition decreased during the drawdown and the after periods, occupying the same region as the control sites during the latter (Fig. 4.3.3). Thus, there was strong evidence that the drawdown of the reservoir modified the composition of the invertebrate communities downstream from the dam, making them more similar to those of control sites (PERMANOVA BDA:CI, $p < 0.01$).

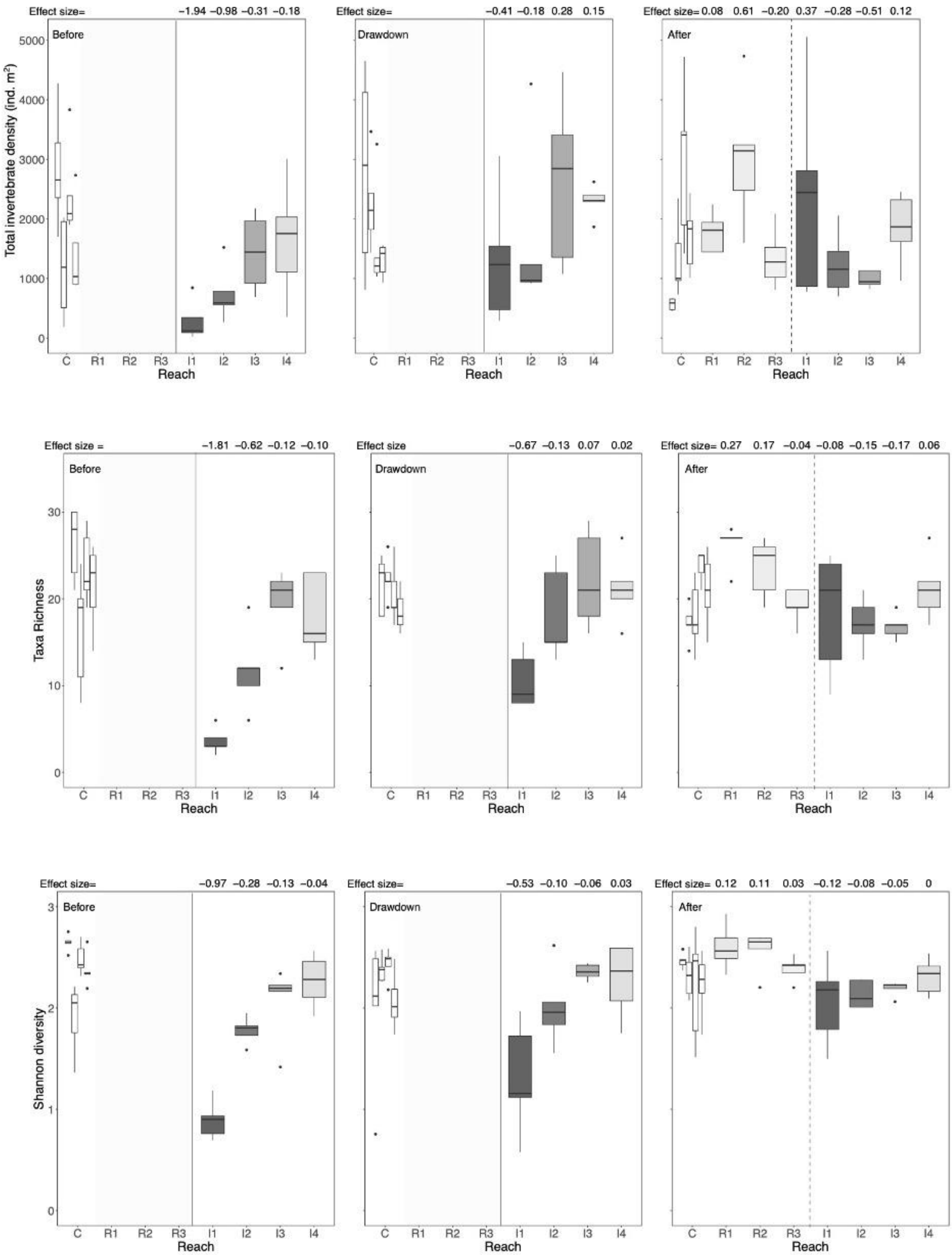

Figure 4.3.1. Total invertebrate density (ind. m^{-2}; top panels), taxa richness (S; middle panels) and Shannon diversity index (H´; bottom panels) in control (C), impact (I), and newly created sites (R) before, during, and after the drawdown of the reservoir. The box plots show the median, the interquartile 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 gray 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 gray 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.

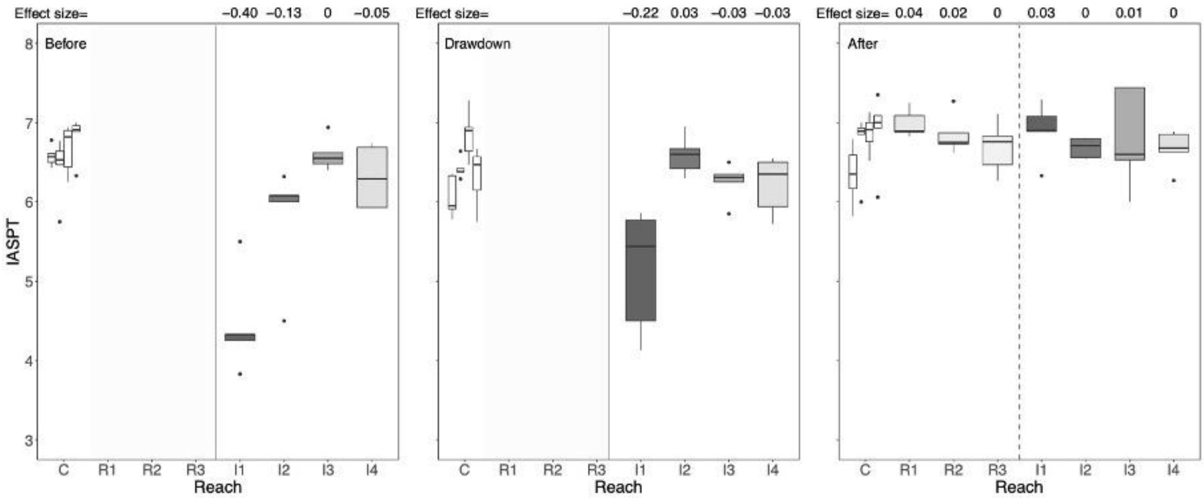

Figure 4.3.2. Values of the IASPT index in control (C), impact (I), and newly created sites (R) before, during, and after the drawdown of the reservoir. The box plots show the median, the interquartile range and the tails of the distribution, and dots represent outliers. C represents results for each control site (C1 to C4 from left to right). I1 to I4 represent results for each impact site. The gray scale of I sites reflects distance downstream from the dam. 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 gray 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.

Table 4.3.1. 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. Sampling site was used as a random factor. Bold values indicate statistically significant results with $p < 0.05$. Degrees of freedom were estimated with Satterthwaite´s method.

Variable	Source of variation	df	F value	p value
Invertebrate density (ind. m^{-2})	BDA	2, 108	2.24	0.11
	CI	1, 6	1.57	0.26
	BDA:CI	2, 108	2.60	0.08
Taxa richness	BDA	2, 108	1.83	0.16
	CI	1, 6	3.67	0.10
	BDA:CI	2, 108	6.63	**< 0.01**
Shannon diversity	BDA	2, 108	2.72	0.05
	CI	1, 6	2.31	0.16
	BDA:CI	2, 108	2.91	**< 0.05**
IASPT index	BDA	2, 108	2.90	**< 0.0001**
	CI	1, 6	2.14	0.19
	BDA:CI	2, 108	4.05	**< 0.001**

Reservoir colonization

During the drawdown period the stream channel newly formed as the reservoir level receded was devoid of invertebrates, but for the after period sampling, invertebrate community measures were similar in reservoir reaches and in control reaches (CR_T, $p = 0.47$; CR_S, $p = 0.28$; CR_{IASPT}, $p = 0.45$; Table 4.3.2). Diversity was an exception, being slightly higher in the reservoir reaches ($H'_C = 2.3 \pm 0.1$ and $H'_R = 2.5 \pm 0.1$) ($CR_{H'}$, < 0.05; Table 4.3.2) (Fig. 4.3.1). Although samples in the reservoir sites occupied a region of the NMDS biplot close to the ones that belong to the control sites, according to evidence (PERMANOVA CR, $p < 0.0001$), community composition in the reservoir reaches did not totally resemble those in control sites (Fig. 4.3.3).

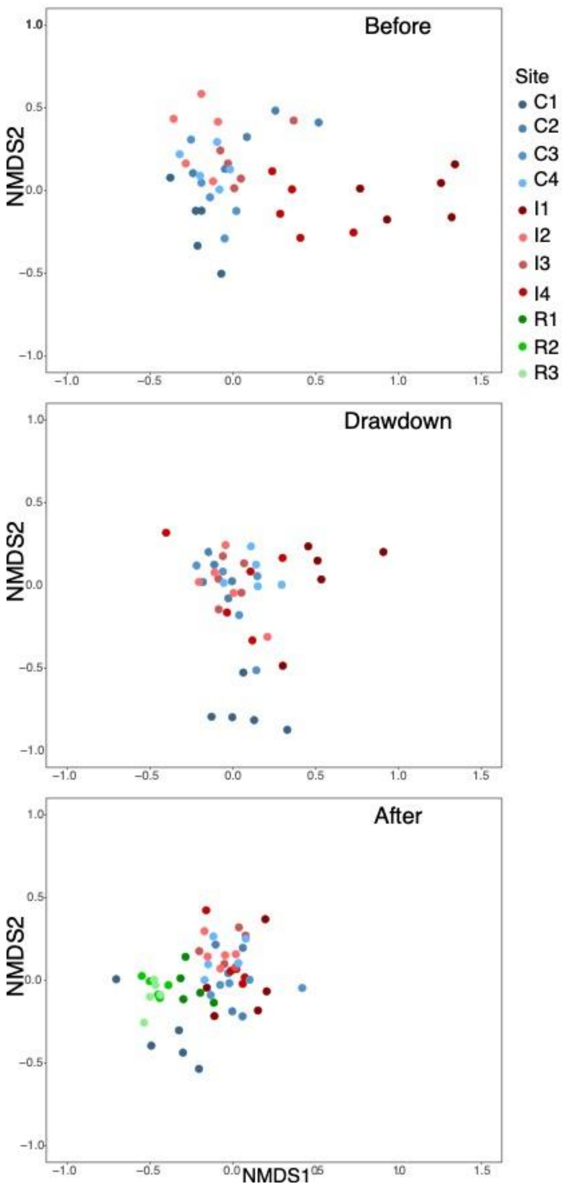

Figure 4.3.3. NMDS analysis of invertebrate community composition in control (C), impact (I), and newly created sites (R) before, during, and after the drawdown. Blue dots represent control sites. Red dots represent impact dots: the darkest dots represent I1 reach and the lightest ones I4 reach. Green 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.

Table 4.3.2. Results of the linear mixed-effects models using reach (control/reservoir) as a fixed factor and invertebrate community measurements as response variables. Sampling site was used as a random factor. Bold values indicate statistically significant results with $p < 0.05$. Degrees of freedom were estimated with Satterthwaite´s method.

Variable	Source of variation	df	F value	p value
Invertebrate density (ind. m^{-2})	CR	1, 5	0.62	0.47
Taxa richness	CR	1, 5	1.47	0.28
Shannon diversity	CR	1, 33	4.80	< 0.05
IASPT index	CR	1, 5	0.66	0.45

Discussion

Benthic invertebrate communities are useful indicators of the ecological responses to stream and river restoration projects (Miller et al. 2010; Jähnig et al. 2011), since they are highly sensitive to changes in the environment (Gore et al. 2001; Flores et al. 2017; Dolédec et al. 2021). Nevertheless, we are still far from predicting the response of invertebrate communities to restoration activities. First, because restoration projects aim at very contrasting goals, from improved water quality to flow modification or to habitat naturalization, and often lack proper monitoring of ecological outcomes (Bernhardt et al. 2005). Second, because some authors (Palmer et al. 2010; Griffith & McManus 2020) have shown that restoration projects often fail to trigger an increase in invertebrate diversity. This lack of desired response can be attributed to other limiting factors beyond the one addressed, or in some cases, 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 & McManus 2020). In our case, results showed that the drawdown of Enobieta Reservoir, the first step toward its decommissioning, caused no detrimental effects on the downstream invertebrate communities, and that one 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 the torrential characteristics of the local streams that made it easy to colonize the impact reaches and to minimize the legacy effect of the dam.

Contrary to what others reported (Gillespie et al. 2015; Dolédec et al. 2021), in Artikutza it seemed hard to link the differences between invertebrate communities at the site below the dam to changes in hydrology, since the Enobieta Reservoir had been out of use for almost three decades (see “Enobieta Dam decommissioning background” in the Methodology section), a period in which the bottom gate remained closed. Therefore, it had little or no effect on hydrology, as for most of the year it was full of water and the volume released from the spillway was roughly equivalent to the discharge it received from the basin. Rather, the decreased IASPT values suggest downstream impaired water quality, very probably linked to high metal concentrations, especially iron and manganese (Friedl & Wüest 2002; Bryant et al. 2011), which can be detrimental for the biota directly when dissolved and during chronic exposures (Cadmus et al. 2018), or indirectly when precipitated at circumneutral pH and well oxygenated receiving waters (Cadmus et al. 2018; Kotalik et al. 2019). We did not measure metal accumulation neither in biofilm nor in invertebrates, but we did observe black manganese precipitations as far as reach I4, although concentrations clearly decreased from I1 to I4, probably due to the decrease in metals transported, as well as to the dilution caused by the input of tributaries to the mainstem, as seen for other elements (Ellis & Jones 2013). Metal oxide deposits in streams can affect invertebrates by a variety of mechanisms (Wilson et al. 2019). Indeed, both Mn and Fe oxide coatings can clog the interstitial space among rocks (i.e., habitat for benthic organisms) or smother benthic organisms, thus reducing the abundance and the richness of benthic microbial biofilm and invertebrates (Cadmus et al. 2016; Kotalik et al. 2019; Wilson et al. 2019). Also, metals can affect community structure even in well preserved sites, where water quality is good and there are no other apparent impacts (MacCausland & McTammany 2007). Sediment starvation could also have been one of the drivers of impaired invertebrate communities downstream from the dam, since the lack of small particles such as sand and gravel alter the downstream channel morphology, consequently affecting community composition and lowering invertebrate density and diversity. For instance, Mellado-Díaz et al. (2019), in a research performed in Iberian reservoirs, reported that fluvial habitat alteration seemed to be the major disturbance for invertebrate community composition in most of their study sites.

One of the main goals of dam decommissioning is to recover connectivity and to restore sediment and biogeochemical fluxes (Grant & Lewis 2015). This should improve channel complexity and heterogeneity (Tullos et al. 2014; Magilligan et al. 2016) and water quality (Abbott et al. 2022; Atristain et al. 2022) in the long-term, important factors shaping benthic invertebrate communities (Boyero 2003; Astorga et al. 2014; García et al. 2017). In agreement with previous studies (Tullos et al. 2014; Magilligan et al. 2016; Peters et al. 2017), we observed that the drawdown of the reservoir not only reduced the median bed grain size in the impact sites, but it also improved water quality, especially in the reaches located closest to the dam. Dam decommissioning also triggered the transport of sediments and inorganic nutrients (Ahearn & Dahlgren 2005). Streams in the Artikutza valley have very low concentrations of suspended sediments because of the extensive forest cover, which prevents soil erosion (Elosegi et al. 2019), but drawdown caused high turbidity peaks. However, these peaks did rarely surpass 300 NTU, a common value during floods in other rivers in the area (Zabaleta & Antigüedad 2012), and seemed not to threaten the invertebrate communities. This result is in agreement with a mesocosm experiment where medium and low levels of sediment had no effect on invertebrate communities. (Davis et al. 2018). Moreover, although suspended sediment can cause anoxia in rivers, continuous records of oxygen during the opening of the bottom gate showed that oxygen saturation kept constantly over 90% (M. Atristain, unpublished data). Higher metal concentrations were also transported along with suspended sediment, but even the resuspension of Fe and Mn did not affect any of the invertebrate community metrics in the receiving waters. Hence, contrary to expected (Carlson et al. 2018), neither suspended solid nor higher metal concentrations impaired invertebrate community composition and structure. There are many possible explanations for this lack of impact on invertebrates. First, both Fe and Mn were released in a dissolved form because of aerated sediment and did not create metal oxide deposits in the benthos. Second, increased streambed complexity would favour invertebrates and, perhaps, counteract the effects of increased dissolved metals. So far, we cannot elucidate which was the main driver for changes on invertebrate communities before and during drawdown, or whether their response was a consequence of the co-occurrence of both factors (Ormerod et al. 2010). The literature shows that invertebrate communities can recover from the negative effects of dam decommissioning in less than 2 years (Carlson et al. 2018; Hansen & Hayes 2012), although the recovery time may vary among taxa (Renöfält et al. 2013). In our case, at the end of the study period, *i.e.,* barely a year after the main mobilization of sediments, the impact sites reached the same density, richness, diversity, and community composition as the control sites.

Remarkably, the invertebrate community in the area formerly drowned by the Enobieta Reservoir was by the end of the experiment very similar to the invertebrate 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, the taxa richness and Shannon diversity were even higher in the reservoir than in the rest of the sites. Indeed, some of the invertebrate taxa we collected, such as the hemiptera *Aphelocheirus*, were only found there. This taxon is typically found in vernal ponds and other stagnant bodies of water, which were quite abundant in the flattest areas of the emerged sediments, thus explaining its presence in nearby stream reaches. Whatever the case, the reservoir invertebrate community described here is likely transitory, and a fully mature community can only be expected after the stream has recovered its natural physical habitat, which will obviously require a longer time to develop.

Finally, we must highlight 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 take it down 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 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. On the other hand, it has been calculated that the volume of sediment mobilized with either the total or partial demolition of the dam would be smaller than that so far mobilized. Thus, it seems that the final decommissioning will cause no major impacts on biodiversity or water quality. 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 (*i.e.,* of one year), provided that, as in Enobieta, there is a nearby source of potential colonists.

5. Synthesis and Perspectives

The present dissertation examines the short-term effects of the decommissioning of a large headwater dam on stream structure and functioning, in what constitutes a whole-ecosystem manipulation. Following a mBACI design, which allows controlling spatial and temporal variability, we assessed both abiotic and biotic changes during drawdown and the first stages of ecosystem recovery after one of the largest dam decommissioning projects in Europe to date (Habel et al. 2020). Overall, our results show a positive effect of reservoir drawdown on stream structure and functioning, with no noticeable impacts, not even transient ones. We observed a quick recovery of water quality and biological communities in stream reaches located downstream from the dam, as well as a rapid recolonization of the new stream channel formed in the channel section of the formerly inundated reservoir. So far, these results point towards a successful dam decommissioning project in Artikutza Valley, although some steps remain for its final completion.

Main ecological effects of the dam presence and responses to its decommissioning

Our comparison between control and impact reaches revealed that during the before period, the reservoir increased downstream concentrations of heavy metals and ammonium. We also observed streambed coarsening and sediment starvation below the dam. These chemical and physical effects of damming seemed to affect biofilm community structure and functioning just below the dam. Indeed, contrary to what others reported (Morley et al. 2008; Aristi et al. 2014; Ponsatí et al. 2015) we did not observe higher chlorophyll-a concentrations or higher metabolic activity downstream from the dam. However, the Enobieta Reservoir was located in a headwater catchment, and thus, biofilm growth was limited by the shade provided by the riparian forest. We also observed slower microbial organic matter breakdown downstream from the dam. Although we did not measure microbial biomass in the wooden sticks, other authors (Colas et al. 2016) reported that river regulation by dams and high heavy metal concentrations could act synergistically to reduce fungal biomass, thus impairing microbial organic matter decomposition. Invertebrate community composition differed between control and impact reaches and, in concordance with other authors (Martínez et al. 2013; Mellado-Díaz et al. 2019; Wu et al. 2019), those in the impact reaches had lower density, richness and diversity. The IASPT index values, commonly used in Spanish biomonitoring assessments (Guareschi et al. 2017), showed invertebrates below the dam to be relatively pollution tolerant, thus pointing towards deteriorated water quality as a cause of community impairment. Overall, the ecological effects were stronger just below the dam, and were dampened downstream as tributaries joined the main stem, as has been also reported elsewhere (Ellis & Jones 2013; Mellado-Díaz et al. 2019).

The decommissioning of Enobieta Dam triggered the export of both suspended and bedload sediments to the downstream reaches, along with higher ammonium, iron, and manganese concentrations. In agreement with other studies (Sawaske & Freyberg 2012; Warrick et al. 2015), our results show that a staged dam decommissioning is a good strategy to reduce the volume of sediments exported. Besides, the comparison between our study and previous dam decommissioning literature (Sawaske & Freyberg 2012) also suggests that a good conservation status of the catchment promotes fast recolonization of the emerged sediments by terrestrial plants, thus further reducing sediment export. Indeed, although peaks of turbidity were common during reservoir drawdown, these were short-lived and in general below 300 NTU, which is not an unusual turbidity in streams in the region (Zabaleta & Antigüedad 2012). Due to these turbidity episodes, during most of the drawdown period the riverbed appeared covered by a mm-thin layer of fine sediments (personal observation) but changes in channel dimensions were almost unnoticeable and there was almost no channel aggradation.

Biofilm and invertebrates showed contrasting responses to the drawdown of the Enobieta Reservoir. Biofilm structure and functioning responded negatively to the export of the eroded sediment, probably due to the frequent turbidity episodes. Nevertheless, this negative effect was temporary, and disappeared quickly during the after period, except for microbial organic matter decomposition. This lack of recovery of decomposition is surprising given the significant recovery of water quality and macroinvertebrate communities below the dam, which also contribute to organic matter breakdown (Graça 2001). Muehlbauer et al. (2009) observed a similar pattern in the decommissioning of the Fossil Creek Dam (Arizona, US), where environmental characteristics and fungal and invertebrate communities improved below the dam after the restoration, but leaf litter breakdown did not. As we did not measure fungal biomass and the role of the invertebrates in wooden stick decomposition seems minor (Arroita et al. 2012), we can just speculate about metal contamination legacy being the factor affecting microbial organic matter decomposition.

Contrary to what has been observed elsewhere (Morley et al. 2020; Mahan et al. 2021), invertebrate communities improved during the drawdown period. This lack of negative responses of invertebrate communities, specifically of the most sensitive taxa (*e.g.,* Ephemeroptera, Plecoptera and Trichoptera), may have several possible explanations. First, physical habitat improved during the drawdown period, with median bed grain size quickly resembling that of nearby undammed reaches. Second, although metal concentrations were still high, metal oxide deposits disappeared (personal observation), and so would their potential indirect negative effect on invertebrates (Niyogi et al. 2001). Third, the good ecological status of nearby undammed reaches acted as a source of potential colonizers for impact sites. Fourth, fine sediment deposits were not thick enough to suffocate invertebrate communities and we found no evidence of anoxia in the sediments. Fifth, although we did not sample the hyporheic zone, during higher fine sediment transport episodes it may have acted as a refuge for invertebrates, as reported by other authors (Milner et al. 2022). Sixth, temporal sampling constraints. Indeed, contrasting recovery trends have been observed in macroinvertebrate communities, from short-term (*i.e.,* < 5 months) positive responses in densities (Orr et al. 2008) and taxa richness (Kil & Bae 2012), to long-term recovery (3-7 years) in taxa richness (Hansen & Hayes 2012), or long-term (*i.e.,* > 40 months) negative responses (Renöfält et al. 2013). We sampled invertebrates almost a year after the drawdown period started, and although several turbidity episodes happened within that period, one year may have been enough for macroinvertebrate communities to start to recover. In any case, there is accumulating evidence that invertebrate communities can recover rapidly (1 to 2 years post-restoration) from the negative effects of dam decommissioning (Chiu et al. 2013; Sullivan & Manning 2017; Carlson et al. 2018). Thus, as expected, during the after period descriptors of community composition and structure resembled those in nearby undammed reaches.

Other concomitant ecological responses

Concurrently to this study, other researchers have been collaborating with us in the monitoring of ecological changes within the Enobieta Dam decommissioning project. These include biofilm community composition (Garrastatxu et al. in *prep*), fish abundance (Ekolur 2017, 2020), distribution of the Pyrenean desman [*Galemys pyrenaicus* (É. Geoffroy Saint-Hilaire)] (Levy-Otheguy 2022), and reservoir greenhouse gas (GHG) emissions (Amani et al. 2022). Figure 5.1. shows some of the sites sampled by these researchers.

For biofilm community composition, we scraped 10 cobbles randomly in each site to obtain a biofilm slurry sample per site and period. In the laboratory, DNA was extracted, amplified, and sequenced with Illumina MiSeq (16s rRNA V3 and V4 bacterial gene region and rDNA ITS2 eukaryotic gene region) for the 19 biofilm samples obtained (before, n = 8, C & I reaches; after, n = 11 C, I & R reaches) (Fig. 5.1). Both bacterial and eukaryotic communities differed between before and the after-reservoir drawdown (Fig. 5.2). As reported in other studies (Ruiz-González et al. 2013), during the before period, downstream bacterial communities were different from those in control sites, the effect being highest in the site just below the dam (I1) and lowest in the farthest site (I4) (Fig. 5.2). During the after period, bacterial communities in control, impact and reservoir sites were closer to each other, although we could not observe any clear pattern in the recovery of the bacterial communities (Fig. 5.2). Eucaryotes followed the same pattern during the before period (Fig. 5.2). However, during the after period, instead of getting closer, differences among control and impact sites were higher than during the before period (Fig. 5.2). Further investigations on the composition and potential metabolism of these microbial communities are currently ongoing and will help understanding the functional consequences of these changes.

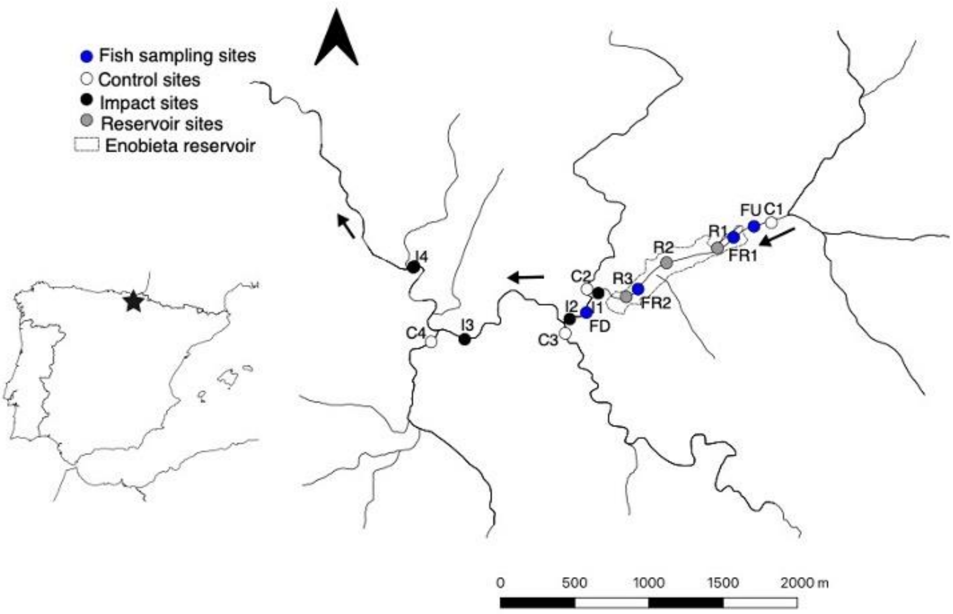

Figure 5.1. Study area showing the location of the 11 study sites [4 control sites (C1, C2, C3 & C4), 4 impact sites (I1, I2, I3 & I4) and 3 sites in the former reservoir (R1, R2 & R3)] in the Artikutza Valley (northern Iberian Peninsula). Blue colored dots (FC, FR1, FR2 & FI) indicate the electrofishing sites. The dashed line indicates the area drowned by the Enobieta Reservoir. Arrows mark flow direction.

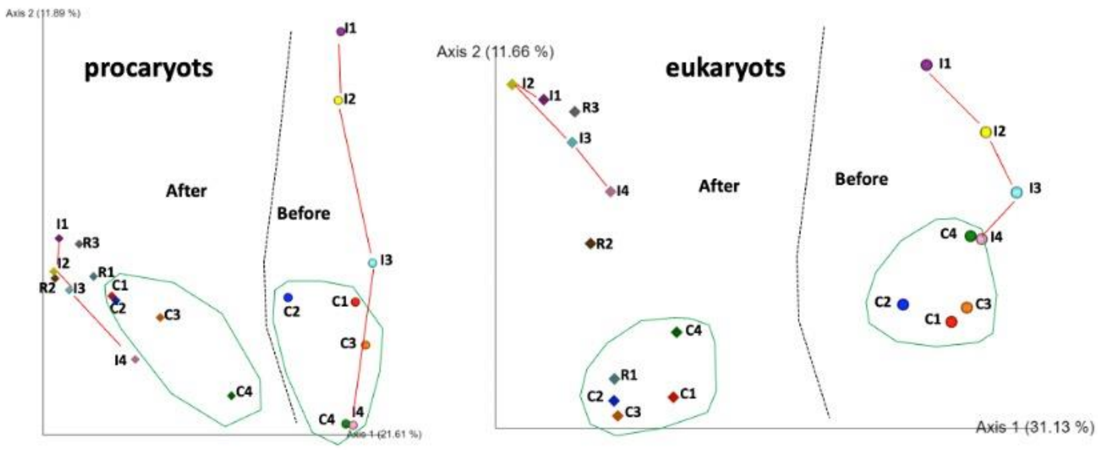

Figure 5.2. NMDS analysis of prokaryotic (left panel) and eukaryotic (right panel) community composition from DNA metabarcoding in control (C1 – C4), impact (I1 – I4), and newly created sites (R1 – R3) before (dots) and after (diamond) the drawdown of the reservoir. The red lines mark the trajectories of change in biofilm communities below the Enobieta Dam. Note that R reaches were sampled only during the after period.

In Artikutza, the fish community is mostly made up of brown trout (*Salmo trutta* L.) and the Adour minnow (*Phoxinus bigerri* Kottelat 2007), as is commonly found in headwater streams in the area (Ekolur 2017, 2020). Diadromous species such as the Atlantic salmon (*Salmo salar* L.) are missing, as the Añarbe Dam blocks their upstream migration. Surprisingly enough, a couple of eels (*Anguilla anguilla* L.) was electrofished in summer 2022 in Erroiarri Stream, at less than 300 m from Enobieta Dam (A. Elosegi, pers. comm.), in the context of a different project. Regarding the decommissioning of Enobieta Dam, electrofishing was carried out always in summer, in 3 sites (FU, FR1 & FD) prior to the reservoir drawdown (2017), and in 4 sites (FU, FR1, FR2 & FD) during (2019) and after (2020) the reservoir drawdown (Fig. 5.1). Trout populations were in good condition in all sites during the whole study period (Ekolur 2020). The drawdown of the reservoir did not cause any fish kill (personal observation) nor decreases in fish abundance (Fig. 5.3), and there was a rebound of the trout population in all sampling sites due to a strong recruitment (Table 5.1). Although trout was the dominant species in most sites, it seemed that minnows were more capable than trout to early colonize the newly created channel in the former reservoir area (*i.e.,* FR1 & FR2) (Fig. 5.3). This could be related to dietary preferences of each of these species. Indeed, minnows are omnivorous and can feed both on macroinvertebrates, as well as on detritus and periphyton (Killen 2014), the latter being especially abundant in the open channels newly created after drawdown. On the contrary, brown trout mainly feeds on invertebrates and fish (Rincón & Lobón-Cerviá 1999; Oscoz 2005), which took longer to recover in the newly created reaches.

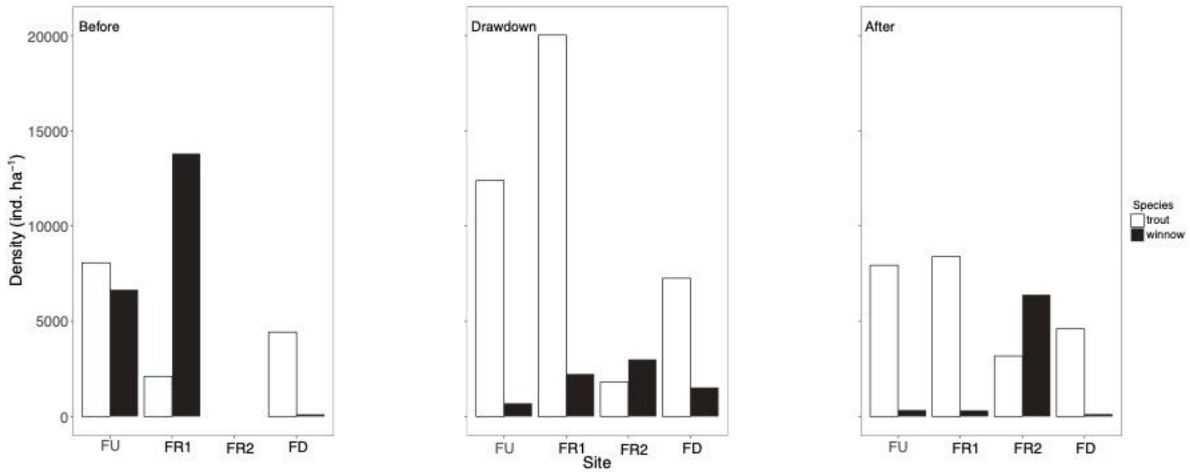

Figure 5.3. Density (ind. ha^{-1}) of brown trout (white bars) and common minnow (black bars) during the before, drawdown and the after periods upstream (FU), downstream (FD) and within the reservoir sites (FR1 and FR3). Note that site R3 could only be sampled during the drawdown and the after periods.

Table 5.1. Brown trout density (ind. ha^{-1}) per year class during the before, drawdown and after periods upstream (FU), downstream (FD) and within the reservoir sites (FR1 and FR2). Note that site FR2 was only sampled during the drawdown and the after periods.

Period	Site	Fry (ind. ha^{-1})	Young (ind. ha^{-1})	Adults (ind. ha^{-1})
Before	FU	6,557	1,054	459
	FR1	1,867	159	79
	FR2	-	-	-
	FD	1,443	1,394	1,591
Drawdown	FU	9,966	1,721	700
	FR1	16,497	2,859	669
	FR2	454	454	907
	FD	4,030	1,480	1,744
After	FU	4,523	2,366	1,077
	FR1	1,886	5,189	1,512
	FR2	197	2,293	684
	FD	788	2,189	1,622

Restoring the Enobieta Stream connectivity improved the distribution of the Pyrenean desman. This semiaquatic insectivorous mammal lives in mountain streams of the central-northern Iberian Peninsula and the Pyrenees. However its distribution has been severely reduced during recent decades and it is currently listed as vulnerable by the International Union for Conservation of Nature (Esnaola et al. 2021). This animal used to inhabit the Enobieta Stream upstream from the Enobieta Reservoir (Iñaki Aizpuru, Gipuzkoa Province Council, personal communication), but disappeared from it, apparently because of the disconnection with the rest of the river network. A study that monitored desman presence/absence thorough a year and a half based on artificial latrines (Fig. 5.4) showed that the desman colonized the basin shortly after the drawdown of the reservoir, and it is now present throughout all the fluvial network of Artikutza (Levy-Otheguy 2022).

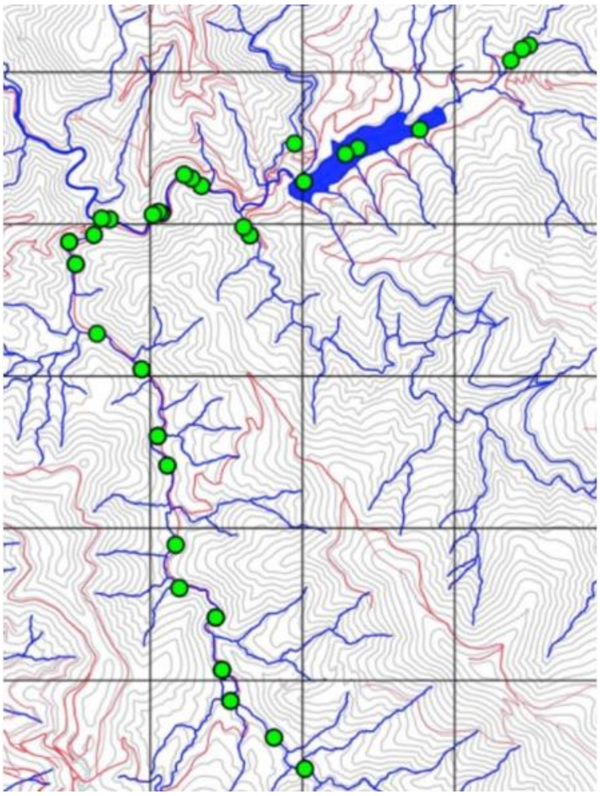

Figure 5.4. Location of the latrines throughout the Artikutza basin. Green color means positive presence of Pyrenean desman faeces.

Finally, Amani et al. (2022) shed some light on the short-term effects of dam decommissioning on carbon (C) fluxes through the transition from a lentic to lotic ecosystem. To do so, we measured CO_2 and CH_4 fluxes in impounded water, exposed sediment, and lotic water before, during, and after the drawdown of the reservoir. Prior to the drawdown, the Enobieta Reservoir acted as a net sink of atmospheric carbon dioxide (CO_2) and as a net source of methane (CH_4). Impounded waters are important emitters of CH_4 because of their increased anaerobic microbial functioning in anoxic conditions (Deemer et al. 2016). However, the Enobieta Reservoir was a net sink of carbon during the before period (Fig. 5.5). During the drawdown period, the reservoir area became a net source of C to the atmosphere, especially as CO_2 (Fig. 5.5). Exposed sediments emitted most CO_2 within the reservoir area, likely because of their increased CO_2 diffusivity, higher microbial respiration due to higher oxygen conditions, and lower CO_2 uptake by primary producers compared with inundated environments (Gómez-Gener et al. 2016; Marcé et al. 2019). During the after period, total C fluxes at the scale of the reservoir increased and peaked about 4 months after the reservoir drawdown, (Fig. 5.5). Thus, overall, the reservoir transformed from being a net carbon sink prior to the reservoir drawdown to being a net carbon source during the first 10 months after the reservoir drawdown. It is, nevertheless, to be expected that this trend will disappear as the forest colonizes the emerged sediments.

Oncoming changes

The fate of the Enobieta Dam

To date, we have only assessed the drawdown of the Enobieta Reservoir, which is the first step towards its final decommissioning. Indeed, although the dam allows water to flow freely, it cannot be kept as it currently stands. First, because the bottom gate, the main mechanism for regulating the reservoir, is only 1 m wide x 1.5 m high, what is too narrow for the heaviest rain episodes. Second, because it does not guarantee fish passage, since the bottom gate is 60 cm above the stream water level. Besides, the smooth bottom and the high speed of the water in the bottom gate conduit also complicates the passage of fish and other aquatic organisms. And third, because from a normative viewpoint, the Spanish Royal Decree 264/2021 of April 13 states, among other things, that the decommissioned dam cannot be abandoned without guaranteeing its own security and that of its surroundings. This Decree also states that the dam should not harmfully disturb the circulation of water. Furthermore, the current interpretation of this Decree by the Spanish Ministry for the Ecological Transition and the Demographic Challenge is that the owner of a dam that is to be decommissioned must revert the site to its previous status, i.e., remove the dam totally. The only acceptable reason not to do so would be that there are alternatives that, while ensuring the hydraulic safety for the future, are better for the natural values protected in Natura 2000 sites, as is Artikutza.

Therefore, the Municipality of San Sebastian, owner of the dam, commissioned a study to explore possible scenarios for the future of the dam, which ended with two alternatives: (i) partial removal of

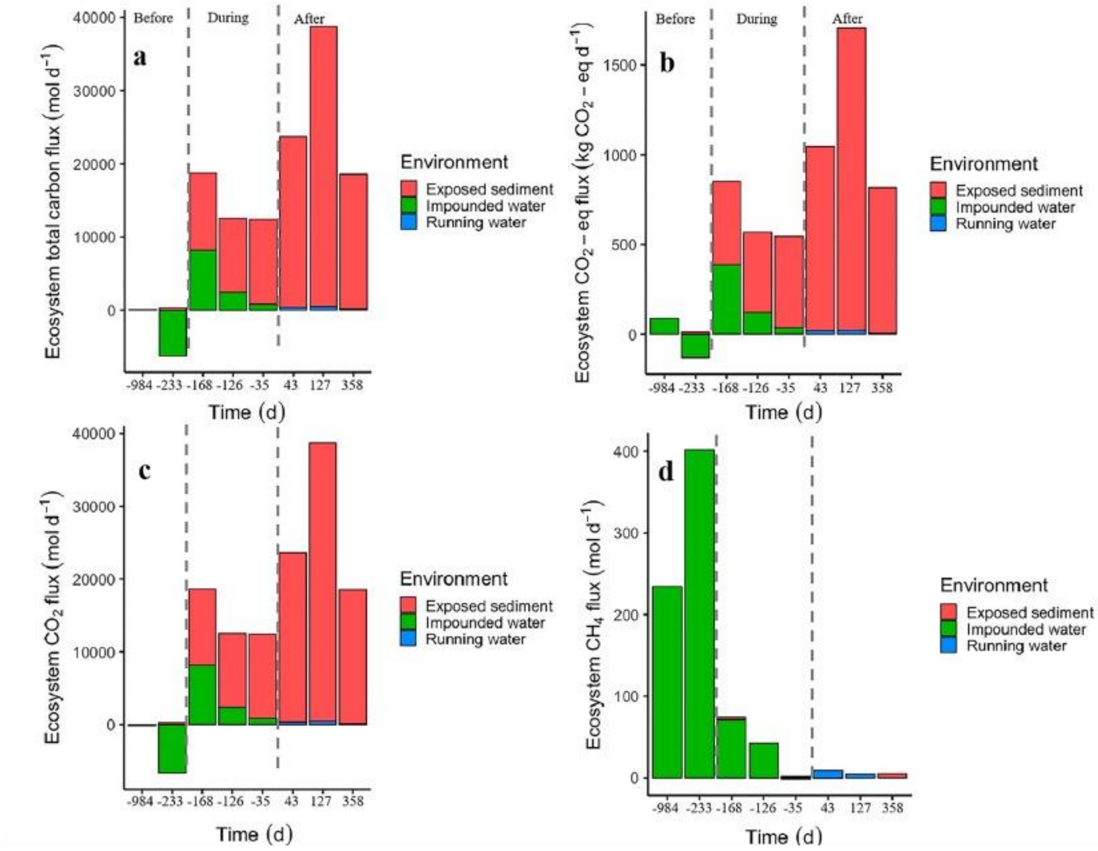

Figure 5.5 (a) Ecosystem total carbon flux, (b) carbon CO_2-eq flux, (c) ecosystem CO_2 flux, and (d) ecosystem CH_4 flux in exposed sediment, impounded water, and running water. Ecosystem CH_4 fluxes in impounded water are a sum of diffusion and ebullition but are only emitted via diffusion for exposed sediment and running water. The values below y = 0 indicate carbon uptake by the reservoir. Each vertical bar corresponds to a sampling campaign. The x-axis describes the 8 sampling campaigns, which are divided into 3 categories: before (days −984 and −233), during (days −168, −126, and −35), and after (days 43, 127, and 358) reservoir drawdown. Figure from Amani et al. (2022).

the dam by opening a 7-m wide notch from the left spillway to the bedrock, or (ii) total removal of the dam. According to this study by Elosegi et al. (2022), the second alternative would be more problematic than the first, because of the longer period of works (1 year vs 6 months), and because it would generate much more rubble and disturbance. Indeed, thousands of trucks would be needed to remove all the dam debris, affecting not only the stream but also all the surroundings (*e.g.,* the fauna inhabiting the Artikutza Valley). Consequently, the first alternative (i.e., partial removal) seems the best possible option to complete the decommissioning of the Enobieta Reservoir. Of course, opening a notch in the dam will lead to geomorphological adjustments upstream from the dam, but according to calculations by Elosegi et al. (2022), the total amount of eroded sediment volume would be less than 3795 m^3, which is *c.a.* 50% of the amount eroded during the drawdown. Thus, we would not expect a greater disturbance than the impact that we have already measured within our study period, and in any case, the whole ecosystem would recover in a short period of time. What is more important, the dam would not be an obstacle for fishes and other organisms, thus allowing mixing of previously isolated populations.

Long-term responses within the reservoir area

So far, we have only assessed short-term effects of the drawdown of the Enobieta Reservoir. Stream ecosystem structure and functioning in the sites located below the reservoir now resembles that of control sites. Therefore, we consider that the ecosystem is almost completely recovered. Nonetheless, the reservoir area will still undergo further changes in the next decades. Although the riparian forest is developing quickly (Fig. 5.6), it will still need some decades to reach the level of maturity of the riparian forest present in the control sites. Currently, it does not provide the Enobieta Stream neither with shade nor with enough allochthonous organic matter, which is the main energy source supporting food webs in temperate low order forest streams (Wallace et al. 1997). Indeed, most of the allochthonous organic matter entering forest streams in the region consists on leaves and other remains from riparian vegetation (Pozo et al. 1997). Thus, during its passage through the reservoir area, the Enobieta Stream now resembles in part a mid-order stream, in that primary producers are not light-limited, resulting in an autotrophic system. As the riparian forest matures, shading by vegetation will tend to limit primary producers (Acuña et al. 2005), and detritus forms will become the energetic basis of the food webs of the Enobieta Stream. In addition to leaf litter and shade, in several decades, a well-developed riparian forest will also provide dead wood to the stream (Chen & Wei 2008). Large wood is a key structural element in well-preserved streams of the Artikutza Valley (Fig. 5.7) and mature temperate forest streams elsewhere. Dead wood enhances habitat heterogeneity (Flores et al. 2013) and the retention of sediments (Scealy et al. 2007) and organic matter (Flores et al. 2011), and offers refuge for many species (Keim et al. 2000).

Figure 5.6. Young trees, mostly alder seedlings start to cover the banks of Enobieta Stream in the area formerly covered by the reservoir in October 2022. Note, nevertheless, that the canopy is still open. Picture: Miren Atristain.

Figure 5.7. One of the many large wood jams naturally formed in the Artikutza Valley. Urdallu Stream. Picture: Arturo Elosegi.

From the Serial Discontinuity Concept to the Serial Re-Continuity concept

During the 1980´s, theories such as the River Continuum Concept (RCC) (Vannote et al. 1980) and the Serial Discontinuity Concept (SDC) (Ward & Standford 1983) were developed to synthesize the factors that influence abiotic conditions and the resulting biotic responses over the longitudinal river profile. While the RCC viewed the natural river as an uninterrupted continuum, the SDC reminded that many rivers are affected by large dams, which break this continuum, thus disturbing the energy transfer patterns that the RCC proposed. For instance, headwater streams, typically characterized by narrow channels and coarse substrates, are strongly influenced by the surrounding riparian vegetation, which provides shade and coarse organic particulate matter (CPOM) in the form of leaf litter. According to the RCC, headwater stream communities would be mainly made up of shredders that feed on CPOM followed by collector-gatherers that consume shredded CPOM (*i.e.,* fine particulate organic matter, FPOM). On the other hand, the SDC predicts dams to interrupt the longitudinal transport of CPOM, thus altering the trophic relationships below the dam. Ward & Standford (1983) also stated that the effects of impoundments would differ depending on the location of the dam. Thus, some aspects that may be severely influenced in headwater streams may not respond in the same way in lowland streams. When comparing the results obtained in this dissertation with the predictions of the SDC for headwater streams, I found that my results often do not coincide with the SDC predictions (Table 5.2). More specifically, median substrate size was higher downstream from the Enobieta dam than in nearby undammed reaches, and nutrient levels varied depending on the compound, contradicting the SDC. Note that I only compare substrate size, nutrient levels, and invertebrate density because these were the only variables that coincided in both works.

Table 5.2. Comparison between the SDC predictions for substrate size, nutrient levels, and invertebrate density with the results obtained in this dissertation.

	SDC	Enobieta Dam
Substrate size	=	↑
Nutrient levels	↑	NH_4^+ ↑ / SRP ↓
Invertebrate diversity	↓	↓

The potential impact of the release of the sediment accumulated in reservoirs is a common management concern when removing dams (Tullos et al. 2016). Physical, numerical and conceptual models have been developed (Cui & Wilcox 2008; Downs et al. 2008; Bellmore et al. 2019) to predict the fate of the released sediment, but usually these models are case specific or do not consider the position of the dam along the river longitudinal profile. Because removing dams can cause different effects on downstream abiotic and biotic factors depending on its location along the stream longitudinal profile, here I present the Serial Re-Continuity Concept (SRC) in an attempt to gain insight into how dam removal may affect stream structure and functioning in low- and high-order streams. Following the SDC, the SRC makes predictions based on these premises: (1) The river continuum concept and the serial discontinuity concept hypotheses are conceptually sound, and their underlying assumptions valid. (2) The watershed is free of pollution and other disturbance, except the dam. (3) Unless otherwise stated, the dams are large and are removed in a non-staged work. Because the main impacts of dam removal seem to be associated with changes in the geomorphological setting of the stream and the former impounded area, I base my predictions on those changes, and try to link them to changes in ecosystem structure and functioning.

Imagine we have two reservoirs, one in the headwaters and the other in the lowlands, both partially filled with sediment. The sediment deposited in both reservoirs would differ, being coarser in the headwater reservoir, finer in the lowland one (Fig. 5.8). These differences, together with distinct flow rates, would drive contrasting dynamics of sediment erosion and transport. According to the review conducted by Sawaske & Freyberg (2012), the erodibility of coarse sediment is higher than the erodibility of fine sediment. Based on this information, one may think that larger amounts of sediment would be eroded in the headwater reservoir than in the lowland reservoir. Besides, as reported by Curran & Coveleski (2021), the coarser fraction of the sediment will not initially travel further downstream unless high flows occur, what would result in local channel aggradation below the dam. Thus, organisms living in the reach just below the dam would be buried, and these changes would in turn affect ecosystem functioning. For instance, a strong reduction in macroinvertebrate diversity would impair leaf litter decomposition, whereas the lack of interaction with the hyporheic zone would affect nutrient spiraling. Conversely, when removing a lowland reservoir, a minor fraction of sediment would be eroded, and it would be transported far away, thus avoiding large deposits of sediment below the dam. On the other hand, the turbidity caused by the transported fine sediment would reduce light availability and affect negatively the macrophytes that the SDC forecasted downstream from lowland dams. Therefore, the dam removal would soon lead to a situation close to what the RCC described for lowland reaches: limited primary production by benthos due to turbidity and water depth (Vannote et al. 1980). Consequently, removing a large dam would be expected to cause stronger geomorphologic and biologic impacts in the headwaters than in the lowlands. Moreover, although the SDC does not consider fish migration, the SRC does, and removing a lowland dam would also restore fish passage to a greater extent than removing an upstream dam.

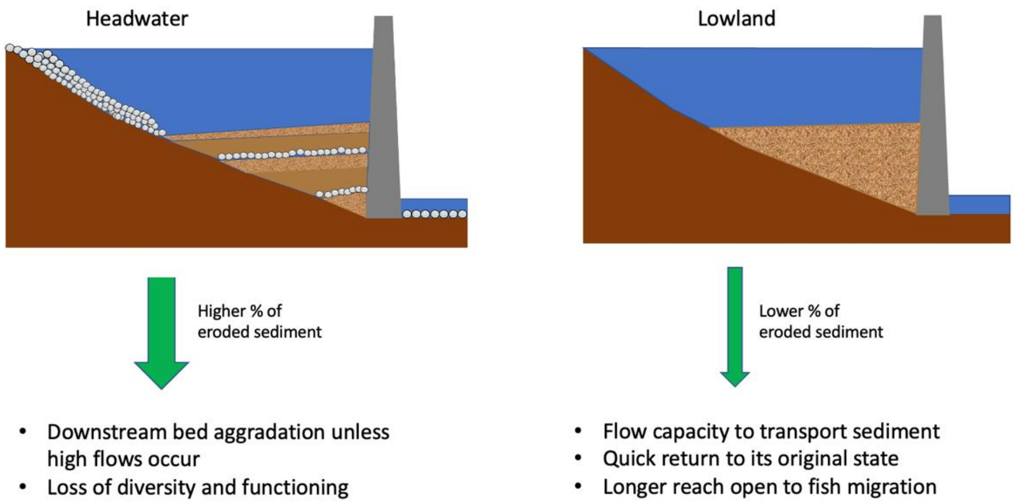

Figure 5.8. Conceptual model of the Serial Re-Continuity Concept. The reservoir in the left panel represents a headwater reservoir, whereas the one in the right panel represents a lowland reservoir. Green arrows represent the sediment eroded from the reservoir. The thicker the arrow, the greater the amount of eroded sediment.

The future of dams

It is unclear the direction that the management of dam infrastructures will follow in the future. On the one hand, within the global change scenario, the rising global human population and the intensification of economic activities have led to higher water demand (Crist et al. 2017; Ripple et al. 2017), which is projected to increase 50% by 2050 (Leflaive 2012). In order to satisfy this water demand for domestic, agricultural, industrial and energetic purposes (Albert et al. 2021), it is expected that the number of regulated rivers will increase even more (Belletti et al. 2020). Furthermore, dams will be increasingly important to face the uncertainties associated to rising drought risk under global climate change (Ehsani et al. 2017; Boulange et al. 2021). On the other hand, with many dams aging worldwide (Perera & North 2021), dam removal already outpaces their construction in some parts of the world, especially in North America and Europe (Beatty et al. 2017), where the median age of large dams is highest (between 50 and 100 years) (Perera et al. 2021). Considering that nearly 50% of the global rivers are already fragmented (Grill et al. 2015) and that many of the regulation infrastructures are ageing and do not fulfil the purpose for which they were built, what could water managers do to face rising water regulation demand and deteriorating dams? In my opinion, the key point for success is the prioritization of the dam candidates to be decommissioned (Garcia de Leaniz & O'Hanley 2022) and the candidates to be repaired or to be newly constructed. This decision would highly depend, among others, on ecological, safety, economic and society reasons. It is important that when making decisions, each dam is considered individually, and as reported by Kondolf & Yi (2022) "while, in some cases, dam removal is a practical way to improve river condition and to resolve safety problems of aging dams, the reality is that most dams in existence today will remain for the foreseeable future". Thus, our priority should be to improve the performance of dams while we try to reduce their environmental impacts, for instance, by constructing fish ladders and sediment bypass structures. One way of improving the performance of the dams and their associated reservoirs is to avoid sediment accumulation by managing the basin in a conservationist way as in Artikutza, or else, restoring the reaches above the reservoirs with woody debris to retain the sediments before entering the reservoir, as proposed by Elosegi et al. (2017).

The future of dam removal science

Despite being a case study, we showed that a slow reservoir drawdown could minimize the erosion and the downstream transport of stored sediment, thus causing little impact on stream ecosystem structure and functioning. However, the present dissertation left many questions unanswered, which constitute important topics for future research and must be addressed to optimize future dam removals.

Our field study assessing the effects of a large dam decommissioning was limited to a nearly pristine catchment; therefore, our results are not directly transferrable to other scenarios with other stressors acting at the same time. Indeed, we must bear in mind that dam decommissioning is not panacea, as it can cause impacts associated, for instance, to the dispersal of toxic sediment (Ashley et al. 2006), (Ashley et al. 2006), as happened in the Edward Dam removal in New York (USA), where sediments were contaminated with polychlorinated biphenyls. Similarly, the presence of invasive species can be a problem for dam removal (Foley et al. 2017). Besides, streams and rivers are subjected to other multiple pressures (Dudgeon 2019), such as agriculture or urban pollution, that might limit their response to dam removal (Fig. 5.9). Therefore, an essential question to be addressed is how other stressors can modulate the response to this major restoration work.

Presently, no standardized methods are available for analyzing stream ecosystem responses to dam removal, what makes it hard to rate projects as successful or not. Indeed, finding general patterns is difficult because project monitoring is scarce and too often based on contrasting metrics and sampling methods. Considering the importance of data availability and the transmission of scientific information, policymakers should enforce managers to use standardized metrics such as the guidelines of the EU Water Framework Directive.

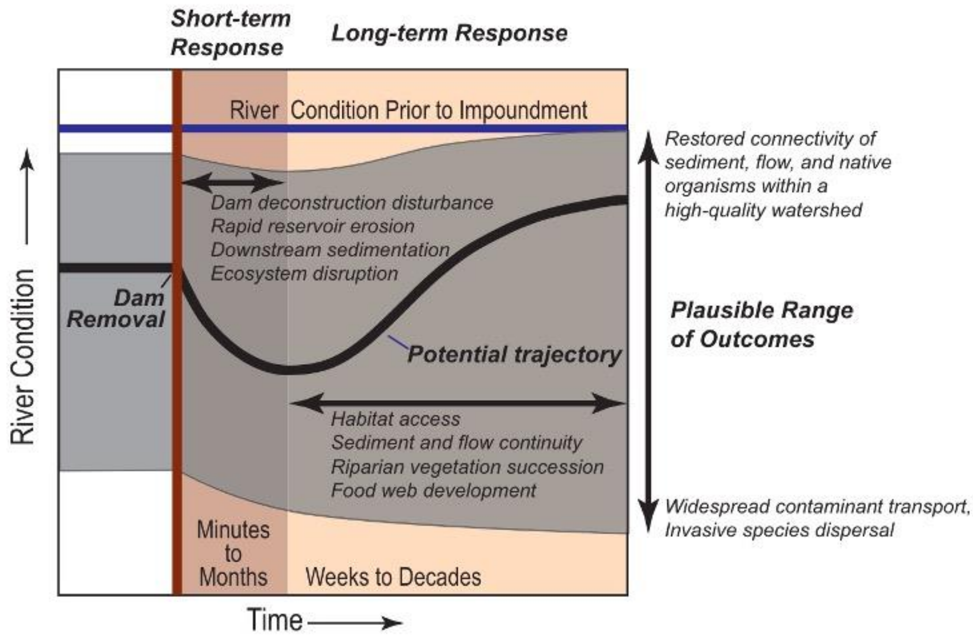

Figure 5.9. Conceptual river response to dam removal. Prior to dam removal, physical and ecological river condition is likely altered to some degree from pre-impoundment conditions by changed flow, sediment regime and aquatic connectivity. Dam removal will typically result in short-term disturbance, but the system will approach a new steady state dictated by overall watershed conditions. The indicated potential trajectory is just one of many possible outcomes within the gray shaded area depending on the original effects of the dam and reservoirs, their sizes, removal strategy, and regional environmental conditions. From Foley et al. (2017).

It is also indispensable to gather the published empirical data and conduct systematic reviews and meta-analyses to shed some light on the main drivers of the responses of stream ecosystem structure and functioning to dam removal. This information could also be valuable to build general models that may allow to predict and thus minimize the impacts of this restoration work. For instance, fish dispersal models (*e.g.,* Radinger & Wolter 2014; Radinger et al. 2017) can be adapted to predict invasive species redistribution after dam removal. Moreover, by modelling the erosion rate and fate of sediments, we could reduce the dispersal of contaminated sediments, for example confining them. Models could also be used to predict the gains and losses in ecosystem services, thus raising the awareness on the importance of healthy stream and river ecosystems within the society. Certainly, dam removal scientists have still many questions to answer, but this is what makes science such an exciting challenge. I hope this dissertation will add a small piece in the giant puzzle of dam removal science.

6. General conclusions

1. The Enobieta Dam created sediment starvation in downstream reaches. Dam decommissioning triggered the erosion and the downstream transport of the sediment accumulated in the reservoir. This sediment transport resulted in turbidity peaks in downstream reaches, mostly during rain events. However, in the long term, median bed particle size decreased and nowadays resembles the particle size observed in control reaches.

2. During the before period, the hypoxic conditions in the hypolimnion during stratification resulted in high concentrations of manganese and iron, although these concentrations diminished with distance. Ammonium concentrations followed a similar pattern. During the drawdown period we observed peaks of the three compounds, but water quality swiftly recovered during the after period, and nowadays water physicochemical characteristics are similar in control and impact reaches.

3. Before dam decommissioning the structure and functioning of biofilm was similar in all analyzed reaches, except for organic matter decomposition, which was lower in impact reaches. Sediment transport during drawdown reduced Chl-*a*, biofilm metabolism and microbial organic matter decomposition, but these differences disappeared in the after period.

4. As expected, benthic macroinvertebrate density, taxa richness and diversity were lower below the dam before decommissioning. Surprisingly, the differences in macroinvertebrate communities between control and impact reaches decreased during the drawdown period. The communities fully recovered, and the differences disappeared by the end of the study.

5. Overall, the Enobieta Dam constituted a black spot in the Artikutza valley, fragmenting the river and altering its geomorphology, water quality and the structure and functioning of biological communities. One year after the start of the decommissioning all variables but one were similar in control and impact reaches, manifesting the success of this restoration project. Therefore, this study evidences a positive effect of reservoir drawdown on stream structure and functioning.

6. The impact and the recovery process of the decommissioning highly depend on site-specific conditions such as the catchment conservation status or the decommissioning procedure. In

particular, the success of this project is partly attributed to the excellent conservation status of the Artikutza Valley and the slow drawdown carried out in the Enobieta Reservoir.

Ondorio orokorrak

1. Enobietako presa hustu baino lehen, sedimentu falta somatzen zen urtegitik behera. Presa hustean, urtegian metatutako sedimentuen erosioa eta garraioa gertatu ziren. Garraio horren ondorioz, uhertasun gorakadak behatu ziren inpaktu tramuetan, batez ere euri jasa handietan. Sedimentu partikulen tamainaren mediana txikitu egin zen, kontrol tramuetan aurkitzen denaren antzekoa izan arte.

2. Presa hustu aurretik, estratifikazioak hipolimnionean eragindako hipoxia zela eta, manganeso eta burdin kontzentrazio handiak behatu ziren presatik behera, nahiz eta kontzentrazio horiek txikitu egiten ziren errekan behera joan ahala. Amonio kontzentrazioek antzeko patroia jarraitu zuten. Hustuketa fasean, hiru konposatuon kontzentrazioa emendatu zen. Hala ere, errekuperazio fasea uraren kalitatea azkar hobetu zen, uraren ezaugarri fisikokimikoak antzekoak izanik kontrol eta inpaktu tramuetan.

3. Presa hustu aurretik, biofilmaren egitura eta funtzionamendua antzekoak ziren kontrol eta inpaktu tramuetan, materia organikoaren deskonposaketa izan ezik, hau geldoagoa baitzen inpaktu tramuetan. Hustuketa fasean garraiatutako sedimentua zela eta, klorofila kontzentrazioa, metabolismoa eta materia organikoaren deskonposaketa murriztu egin ziren. Hala ere, desberdintasun horiek desagertu egin ziren errekuperazio fasean.

4. Espero bezala, presa hustu aurretik, makroornogabeen dentsitatea, taxoi aberastasuna eta Shannon dibertsitate indizea baxuagoak presatik behera. Hustuketa fasean, harrigarria suertatu bazen ere, desberdintasunak murriztu egin ziren. Komunitateak erabat berreskuratu ziren errekuperazio fasean, behatutako desberdintasunak erabat desagertu zirelarik.

5. Oro har, Enobietako presa Artikutzako haranean puntu beltza zen, ibaia zatitu eta geomorfologia, uraren kalitatea eta funtzionamenduan eragiten baitzuen. Presa hustu eta urtebetera, aldagai ia guztiek antzeko balioak izan zituzten kontrol eta inpaktu tramuetan. Hori da, hain zuzen, proiektu honen arrakastaren adierazle, presaren hustuketak eragin positiboa izan baitu ekosistemaren egitura zein funtzionamenduan.

6. Itxuraz, hustuketaren eragina zein errekuperazioa, bertako baldintzen menpe daude, hala nola, arroaren kontserbazioa edo eraisketa moduaren menpe. Hein handi batean,

errestaurazio proiektu honen arrakasta Artikutzako haranaren kontserbazio bikainari eta urtegia poliki hustu izanari dagokie.

Conclusiones generales

1. Previo al inicio del desmantelamiento de la presa, se observó la falta de sedimento de tamaño más fino aguas abajo de la presa. El desmantelamiento de la presa provocó la erosión y el transporte aguas abajo del sedimento acumulado en el embalse. Este transporte de sedimentos resultó en picos de turbidez, principalmente durante eventos de lluvia. A medio? plazo, disminuyó la mediana del tamaño de partículas del lecho de los tramos localizados aguas abajo del embalse, y hoy en día se asemeja al tamaño de las partículas observadas en los tramos control.

2. Antes del vaciado, las condiciones hipóxicas del hipolimnion durante la estratificación resultaron en concentraciones altas de manganeso y hierro, aunque esas concentraciones disminuyeron conforme la distancia a la presa aumentaba. Las concentraciones de amonio siguieron un patrón similar. Durante el período de vaciado observamos picos de concentración de los tres compuestos, pero la calidad del agua se recuperó rápidamente tras el vaciado. Hoy en día las características fisicoquímicas del agua son similares en los tramos control e impacto.

3. Antes del desmantelamiento de la presa, la estructura y el funcionamiento del biofilm eran similares en los tramos control e impacto, excepto para la descomposición de la materia orgánica, que era menor en los tramos impacto. El transporte de sedimentos durante la fase de vaciado redujo la concentración de clorofila y el metabolismo y la descomposición del biofilm, pero las diferencias desaparecieron al final del estudio en la fase de recuperación.

4. Las variables relacionadas con la estructura de la comunidad de macroinvertebrados, incluyendo la densidad, la riqueza taxonómica y el índice de diversidad de Shannon, mostraron los valores más bajos por debajo de la presa. Sorprendentemente, las diferencias en las comunidades de invertebrados entre los tramos control e impacto se redujo durante el período de vaciado. Las comunidades se recuperaron completamente al final del estudio.

5. En general, la presa de Enobieta constituyó un punto negro en el valle de Artikutza, fragmentando el río y alterando la geomorfología, la calidad del agua y la estructura y el funcionamiento de las comunidades biológicas. Un año después del comienzo del desmantelamiento, la mayoría de las variables llegaron a ser similares en los tramos control e impacto, manifestando el éxito de este proyecto de restauración. De hecho, este estudio

evidencia un efecto positivo del vaciado de un embalse en la estructura y el funcionamiento de los ríos.

6. Tanto el impacto como el proceso de recuperación después del desmantelamiento dependen en gran medida de las condiciones específicas del lugar y el estado de conservación de la cuenca en la que se encuentra el embalse. En particular, el éxito de este proyecto se atribuye por un lado al excelente estado de conservación del valle de Artikutza y al vaciado lento que se ha realizado en el embalse de Enobieta.

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8. Supplementary material

Geomorphology and water physicochemistry

Figure S1. Photograph of one of the riverbanks excavated by the Enobieta Stream due to the erosion of the sediment accumulated in the bottom. Notice a gravel-dominated layer at the bottom, and two thick leaf litter layers at the top, separated by a thin reddish silt layer.

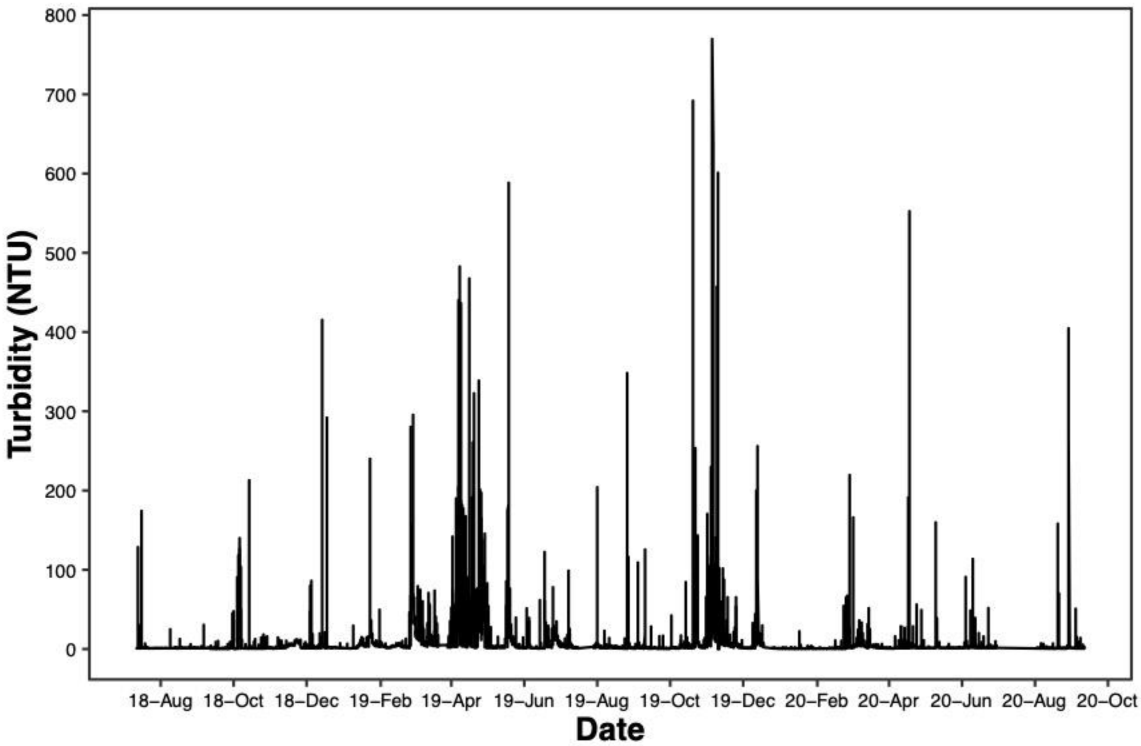

Figure S2. Turbidity (NTU) time series data in the impact site (I2) during the before, drawdown and after periods.

Table S1. Full output of the results of the linear mixed-effects models for water physicochemical attributes. The intercept for the fixed factors is control reaches during the before period, and BCI, BD:CI and BA:CI refer to the control-impact comparison during the before period and the before-drawdown/control-impact and before-after/control-impact interactions, respectively.

Variable	Source of variation	Estimate	t value	p value
T (°C)	Intercept	2.40	26.70	< 0.0001
	BCI	0.10	3.44	< 0.01
	BD:CI	-0.05	-2.10	< 0.05
	BA:CI	-0.06	-1.75	0.08
EC (µS cm^{-2})	Intercept	68.54	6.43	< 0.001
	BCI	16.27	1.16	0.29
	BD:CI	3.92	1.35	0.18
	BA:CI	9.12	2.28	< 0.05
pH	Intercept	7.29	65.44	< 0.0001
	BCI	0.23	2.26	< 0.05
	BD:CI	-0.18	-1.62	0.11
	BA:CI	-0.22	-1.41	0.16
DO sat. (%)	Intercept	101.24	171.95	< 0.0001
	BCI	0.26	0.43	0.68
	BD:CI	-0.32	-0.68	0.50
	BA:CI	-0.24	-0.36	0.72
SRP (µg L^{-1})	Intercept	2.06	5.21	< 0.001
	BCI	-0.36	-1.29	0.24
	BD:CI	0.33	1.92	0.06
	BA:CI	0.36	1.68	0.10

	Intercept	1.39	4.92	< 0.001
NH_4^+	BCI	0.78	3.20	< 0.01
(μg L^{-1})	BD:CI	-0.22	-0.84	0.40
	BA:CI	-0.78	-2.21	< 0.05
	Intercept	2.47	7.90	< 0.0001
Fe	BCI	1.54	4.43	< 0.01
(μg L^{-1})	BD:CI	-0.01	-0.044	0.96
	BA:CI	-1.09	-4.01	< 0.001
	Intercept	1.61	4.61	< 0.001
Mn	BCI	1.90	4.36	< 0.01
(μg L^{-1})	BD:CI	-0.30	-1.03	0.31
	BA:CI	-1.23	-4.24	< 0.0001

Biofilm structure and functioning

Table S2. Full output of the results of the linear mixed-effects models of for biofilm structural and functional attributes. The intercept for the fixed factors is control reaches during the before period, and BCI, BD:CI and BA:CI refer to the control-impact comparison during the before period and the before-drawdown/control-impact and before-after/control-impact interactions, respectively.

Variable	Source of variation	Estimate	t value	p value
	Intercept	0.39	2.80	< 0.05
Biomass	BCI	-0.07	-0.74	0.47
(g AFDM m^{-2})	BD:CI	-0.01	-0.06	0.95
	BA:CI	0.06	0.73	0.47
	Intercept	0.50	1.76	0.15
Chlorophyll-*a*	BCI	0.02	0.181	0.86
(mg m^{-2})	BD:CI	-0.29	-3.05	< 0.01
	BA:CI	-0.11	-1.11	0.27
	Intercept	1.61	7.86	< 0.0001
GPP	BCI	0.10	0.68	0.51
(mg O_2 h^{-1} m^{-2})	BD:CI	-0.69	-5.26	< 0.0001
	BA:CI	-0.26	-1.95	0.06
	Intercept	5.20	5.79	< 0.001
CR	BCI	1.12	1.59	0.14
(mg O_2 h^{-1} m^{-2})	BD:CI	-4.03	-5.61	< 0.0001
	BA:CI	-1.26	-1.81	0.07
	Intercept	93.12	3.42	< 0.01
SRP uptake	BCI	42.415	2.06	0.07
(µg h^{-1} m^{-2})	BD:CI	1.48	0.08	0.93
	BA:CI	-15.11	-0.77	0.44

	Intercept	80.81	2.34	0.05
NH_4^+ uptake	BCI	5.59	0.24	0.82
($\mu g\ h^{-1}\ m^{-2}$)	BD:CI	-3.03	-0.15	0.88
	BA:CI	-1.84	-0.09	0.93
	Intercept	4.98×10^{-3}	9.22	< 0.0001
	BCI	-1.18×10^{-3}	-2.90	< 0.01
k (day^{-1})	BD:CI	-8.40×10^{-4}	1.97	0.05
	BA:CI	5.92×10^{-4}	1.23	0.22

Invertebrate communities

Table S3. List of the taxa found in 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.

Upper taxonomic levels	**Order**	**Family**	**Genus**
Acari			
Annelida			
Hirudinea	Arhynchobdellida	Erpobdellidae	*Erpobdella*
Oligochaeta			
Crustacea	Amphipoda	Gammaridae	*Echinogammarus*
		Niphargidae	
Insecta	Coleoptera	Dytiscidae	*Laccophilus*
		Elmidae	*Dupophilus*
			Elmis
			Esolus
			Limnius
			Oulimnius
			Potamophilus
			Riolus
			Stenelmis
		Gyrinidae	*Orectochilus*
		Hydraenidae	*Hydraena*
		Hydrophilidae	
		Scirtidae	*Elodes*
			Hydrocyohon
	Diptera	Athericidae	*Atherix*
		Ceratopogonidae	
		Chironomidae	
		Dixidae	*Dixella*
		Empididae	
		Limoniidae	
		Psychodidae	
		Rhagionidae	
		Simulidae	

	Tabanidae	
	Tipulidae	*Tipula*
Ephemeroptera	Baetidae	*Baetis*
	Caenidae	*Caenis*
	Ephemeridae	*Ephemera*
	Ephemerellidae	*Ephemerella*
	Heptagenidae	
	Leptophlebiidae	*Habroleptoides*
Hemiptera	Aphelocheiridae	*Aphelocheirus*
	Mesoveliidae	*Mesovelia*
Odonata	Calopterygidae	*Calopteryx*
	Cordulegastridae	*Cordulegaster*
	Gomphidae	*Gomphus*
		Onycogomphus
Plecoptera	Capniidae	*Capnioneura*
	Chloroperlidae	*Chloroperla*
		Siphonoperla
	Leuctricidae	*Leuctra*
	Nemouridae	*Amphinemura*
		Nemoura
		Protonemura
	Perlidae	*Dinocras*
		Marthamea
		Perla
	Perlodidae	*Isoperla*
		Perlodes
Trichoptera	Brachycentridae	
	Glossosomatidae	*Glossosoma*
	Goeridae	*Silo & Lithax*
	Hydropsychidae	*Hydropsyche*
	Lepidostomatidae	*Lepidostoma*
	Leptoceridae	
	Limnephilidae	
	Odontoceridae	*Odontocerum*
	Philopotamidae	*Philopotamus*
	Phryganidae	
	Polycentropodidae	*Holocentropus*

			Plectronemia
			Polycentropus
		Rhyacophilidae	*Hyperrhyacophila*
			Hyporhyacophila
			Pararhyacopila
			Ryacophila
		Sericostomatidae	*Sericostoma*
Mollusca	Basommatophora	Planorbidae	
	Mesogastropoda	Hydrobiidae	*Bythinella*
	Sphaeriida	Sphaeriidae	*Pisidium*
Rhabditophora	Tricladida	Dugesiidae	*Dugesia*
		Planariidae	*Polycelis*

Table S4. Full output of the results of the linear mixed-effects models for invertebrate assemblages. The intercept for the fixed factors is control reaches during the before period, and BCI, BD:CI and BA:CI refer to the control-impact comparison during the before period and the before-drawdown/control-impact and before-after/control-impact interactions, respectively.

Variable	Source of variation	Estimate	t value	p value
Total density (T, inv.m^{-2})	Intercept	1973.89	7.43	< 0.0001
	BCI	-943.33	-2.51	< 0.05
	BD:CI	936.67	2	< 0.05
	BA:CI	916.11	1.95	0.05
Taxa richness (S)	Intercept	21.95	12.02	< 0.0001
	BCI	-8.75	-3.39	< 0.01
	BD:CI	6	2.85	< 0.01
	BA:CI	7.15	3.39	< 0.001
Shannon diversity (H´)	Intercept	2.35	15.08	< 0.0001
	BCI	-0.60	-2.72	< 0.05
	BD:CI	0.37	2.31	< 0.05
	BA:CI	0.46	2.91	< 0.01
IASPT index	Intercept	6.62	32.52	< 0.0001
	BCI	-0.84	-2.90	< 0.05
	BD:CI	0.47	2.14	< 0.05
	BA:CI	0.89	4.05	< 0.0001