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Exposed sediments in a temperate-climate reservoir under dam decommissioning contain large stocks of highly bioreactive organic matter

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ABSTRACT

Exposed sediments in a temperate-climate reservoir under dam decommissioning contain large stocks of highly bioreactive organic matter

Dam decommissioning (DD) is used to solve economic and social problems posed by old dams. However, we ignore the effect of DD on the content and reactivity of large stocks of organic matter (OM) buried in reservoir sediments. We explored temporal changes in the content and reactivity of sediment OM during the first 580 days after the drawdown phase of DD of a large reservoir in the N Iberian Peninsula. We determined the content of sediment OM as organic carbon (OC) in bulk sediment OM and water-extractable OM (WEOM). We estimated the reactivity of bulk sediment OM as its respiration rate and carbon-to-nitrogen ratio, and that of sediment WEOM as its respiration rate, percent biodegradable dissolved OC (%BDOC), and $SUVA_{254}$. The content of bulk sediment OM was 84 ± 5.1 (mean ± SE) mg OC/ g dry sediment, comparable to the values in the literature on sediment OM in dry sediments from lentic, but higher than in lotic ecosystems. The content of sediment WEOM was 0.81 ± 0.05 mg DOC/g dry sediment, higher than the values in the literature on sediment WEOM from lakes, soils, and rivers. On average, 41 % of WEOM was consumed by microorganisms in two days of incubation, showing the great reactivity of this OM fraction. The content of bulk sediment OM and the respiration rate of WEOM showed a nonlinear temporal trend, while %BDOC increased linearly with sediment exposure time. The labile OM produced by the vegetation that rapidly recolonized the reservoir and photoreactions may explain the temporal increase in %BDOC. Our results suggest that exposed sediments can be a source of labile OM and high C emissions in the river reach downstream of the reservoir after DD.

Key words: ageing dams, dam removal, exposed sediments, sediment organic matter, water reservoirs

RESUMEN

Los sedimentos expuestos tras el desmantelamiento de un embalse de clima templado contienen cantidades elevadas de materia orgánica altamente reactiva

El desmantelamiento de presas (DD) resuelve los problemas económicos y sociales que suponen las presas antiguas. Sin embargo, ignoramos el efecto del DD en la materia orgánica (OM) enterrada en los sedimentos del embalse, sobre todo su contenido y reactividad. En un experimento de incubación, exploramos cambios temporales en el contenido y reactividad de la OM del sedimento durante los primeros 580 días posteriores a la fase de vaciado de un gran embalse en el Norte de la Península Ibérica. Determinamos el contenido de OM del sedimento como carbono orgánico (OC) en sedimento y en materia orgánica extraíble en agua (WEOM) del sedimento. Determinamos la reactividad de la OM en el sedimento como su tasa de respiración y la ratio C:N, y la reactividad de la WEOM del sedimento como su tasa de respiración, el porcentaje de OC disuelto biode-

gradable (%BDOC), y $SUVA_{254}$. El contenido de OC en la OM en peso seco de sedimento fue de 84 ± 5.1 (promedio ± error estándar) mg OC/g de sedimento seco, comparable a los valores de la literatura de materia orgánica presente en el sedimento en lagos, estanques y presas, pero mayor que en los ríos. El contenido de WEOM del sedimento fue de 0.81 ± 0.05 mg DOC/g sedimento seco, superior a los valores de la literatura de WEOM del sedimento de lagos, suelos y ríos. En promedio, el ~41 % de la WEOM fue consumida por microorganismos en dos días, lo que demuestra la gran reactividad de esta fracción de OM. El contenido de OM del sedimento seco y la tasa de respiración de la WEOM mostraron una tendencia temporal no lineal, mientras que el %BDOC aumentó linealmente con el tiempo de exposición del sedimento. La OM lábil producida por la vegetación que rápidamente recolonizó el embalse y las fotoreacciones pueden explicar el incremento temporal de %BDOC. Nuestros resultados sugieren que los sedimentos expuestos pueden ser una fuente de OM lábil, que puede alterar las emisiones de C en tramos de río aguas abajo de las presas sujetas a desmantelamiento.

Palabras clave: *presas en envejecimiento, desmantelamiento de presas, sedimentos expuestos, materia orgánica del sedimento, embalses de agua*

INTRODUCTION

Ageing dams and the growing interest in river restoration have increased the practice of dam decommissioning (DD). Dam decommissioning is a widely hailed option to restore riverine connectivity, biodiversity, and ecosystem function (Allen et al., 2016; Bednarek, 2001; Magilligan et al., 2016). However, DD can also allow the downstream export and decomposition of organic matter (OM) buried in reservoir sediments (i.e., sediment OM) into greenhouse gases (GHGs) (Amani et al., 2022; Pacca, 2007). The decomposition rate of sediment OM depends on extrinsic environmental factors and the content and reactivity of sediment OM (Keller et al., 2020; Obrador et al., 2018; Paranaíba et al., 2021). Thus, DD can affect extrinsic factors of the decomposition of OM in sediments, and hence the content and reactivity of sediment OM by exposing the anoxic sediments to the atmosphere. For instance, exposed sediments in a large temperate reservoir under DD were reported to be a hotspot for carbon dioxide (CO_2) emissions (Amani et al., 2022). These CO_2 emissions decreased with sediment exposure time, hypothetically, due to a decrease in the content and reactivity of sediment OM. However, we lack empirical evidence of the effect of DD on the content and reactivity of the large stocks of OM buried in sediments of reservoirs during their life cycle (Downing et al., 2008; Maavara et al., 2017; Mendonça et al., 2012). The reactivity of sediment OM can affect its fate and shape the role of reservoirs in regional and global carbon (C) budgets (Kothawala et al., 2021). Reactive sediment OM can decompose into CO_2 in the reservoir or in the river reach downstream of the reservoir and, thus, remain in the short-term atmosphere-biosphere C loop. However, recalcitrant sediment OM may remain buried in the reservoir after terrestrialization (i.e., the transition from an aquatic to a terrestrial system) and/or reach coastal marine sediments and, thus, enter the long-term geological C pool. To include DD in the C footprint of reservoirs on a regional and global scale, it is necessary to test how the content and reactivity of sediment OM in reservoirs change over time after DD.

Reservoir sediments are hotspots for OM burial because, relative to lakes, they receive higher loads of sediment, OM, and nutrients from their relatively larger catchment area (Downing et al., 2008; Mendonça et al., 2017; Thornton et al., 1990). The catchment area to the waterbody area ratio is higher for reservoirs than lakes, implying higher inputs of terrestrial materials and a higher sedimentation rate in reservoirs (Thornton et al., 1990). The higher sedimentation rate in reservoirs creates better conditions for OM preservation because it potentially implies, compared to lakes, a shorter exposure time of sediment OM to oxygen (O_2) (Clow et al., 2015; Sobek et al., 2009, 2012). The shorter exposure time of sediment OM to O_2 and a large portion of allochthonous OM increase the burial efficiency of OM (i.e., the ratio of OM burial to OM deposition) and the areal burial

rate of OM in reservoir sediments (Sobek et al., 2009, 2012). The global areal burial rate of OM is six times higher in reservoirs than in lakes (Mendonça et al., 2017). The global burial rate of OM in reservoir sediments is estimated at 35.43 Tg C/yr, of which 75 % is contributed by allochthonous OM (Maavara et al., 2017). However, when this occlusion of OM in sediments is removed due to, for instance, DD, this sediment OM can become highly bioreactive (Bastviken et al., 2004; Freeman et al., 2001; Kothawala et al., 2021).

The bioreactivity of OM depends on its content and molecular composition and extrinsic environmental factors (Amani et al., 2019; Catalán et al., 2013; Webster & Benfield, 1986). The content of organic carbon (OC) is an important factor in the decomposition of OM because low concentrations of some molecules can be below the threshold of energetic requirements of decomposers and, thus, limit some catabolic reactions (Arrieta et al., 2015; Kothawala et al., 2021). The molecular composition of OM affects its decomposition by providing the energy and chemical elements required for the growth and reproduction of decomposers. Organic matter is a complex mixture of several molecules of different molecular size, structure, oxidation degree, hydrolysis degree, and aromaticity (Kellerman et al., 2014; Stubbins et al., 2014) and often characterized using optical techniques (Miller & McKnight, 2010; Stubbins et al., 2014; Weishaar et al., 2003). More bioreactive or labile OM contains molecules with low aromaticity, low carbon-to-nitrogen (C:N) ratio, and low molecular weight (Miller & McKnight 2010; Koehler et al., 2012; Gudasz et al., 2015). Water-extractable OM (WEOM: OM obtained by extracting a given mass of soil/sediment with an aqueous solution (Zsolnay, 1996)) represents only a small fraction of sediment OM, but it is often the most mobile, leachable, and biodegradable fraction (Bolan et al., 2011; Boyer & Groffman, 1996; Chantigny, 2003). Extrinsic environmental factors that affect the decomposition of sediment OM include temperature, O_2, the structure and function of microbial communities, the texture and moisture of the sediment, and exposure to solar radiation (Baumann et al., 2013; Keller et al., 2020; von Schiller et al., 2019; Walz et al., 2017). Dam decommissioning can alter some of these extrinsic environmental factors, and thus the content and reactivity of sediment OM during sediment exposure to the atmosphere.

Sediment exposure can affect the content and reactivity of sediment OM by mainly reducing sediment moisture, increasing sediment texture, increasing exposure to solar radiation, and promoting plant recolonization of exposed sediments. Low sediment moisture increases O_2 concentration in deeper layers of exposed sediments and the decomposition rate of sediment OM (Gómez-Gener et al., 2015; Kosten et al., 2018; Marcé et al., 2019). However, since extreme desiccation can reduce the decomposition rate of OM through a limited supply of OM to microorganisms (Schimel, 2018), the availability of C substrates, the activity of extracellular enzymes, and, thus, the decomposition rate of OM increase with sediment and soil moisture (Coulson et al., 2022; Manzoni et al., 2016; Manzoni & Katul, 2014). Since DD is a hot moment for the erosion of reservoir sediments (Duda & Bellmore, 2022; Ritchie et al., 2018), sediment texture may increase during sediment exposure due to the loss of fine-sized sediments, which are more susceptible to the erosion and transport downstream (Duda et al., 2022; Warrick et al., 2012). Furthermore, solar radiation (Granéli et al., 1996; Lindell et al., 1995; Wetzel et al., 1995) and plant recolonization can alter the content and reactivity of sediment OM by providing labile OM (Shaver et al., 1992; Shaver & Chapin III, 1986). Therefore, temporal changes in the content and reactivity of sediment OM can depend on the balance between the decomposition of OM and factors such as exposure to solar radiation and vegetation growth after DD. However, there is no clear characterization of how these factors affect the content and reactivity of sediment OM after DD in decommissioned reservoirs.

Here, we assessed whether the content and reactivity of the sediment OM changed during the first 580 days of sediment exposure after the drawdown phase of DD of the Enobieta Reservoir, a large (42 m high) temperate-climate reservoir in the North Iberian Peninsula. We collected sediment samples during six sampling campaigns between 2018 and 2020. We predicted that (1) the content of sediment OM would be high and high

-ly bioreactive, (2) sediment WEOM would be more bioreactive than bulk sediment OM, and (3) the content and reactivity of sediment OM would decrease with sediment exposure time because high precipitation in the region should support OM decomposition in exposed sediments after reservoir drawdown. To contextualize our results in a wider framework of environments, we compared the content and reactivity of sediment OM in the Enobieta Reservoir with literature data about dry soils and dry sediments of lentic and lotic inland waters.

METHODS

Study site

The Enobieta Reservoir (coordinates: 43º 13' 03'' N 1º 47' 15'' W, elevation: 345 m) was constructed in the Artikutza Valley (Navarre, N Iberian Peninsula) between 1947 and 1953 on the Enobieta Stream to regulate water supply to the municipality of Donostia-San Sebastián. The mean annual air temperature is 12.2 ºC with an average rainfall of 2604 mm/yr (period 1954–2019; Gobierno de Navarra 2019). This rainfall rate makes the Artikutza Valley, perhaps, the most humid region of the Cantabrian cornice. The hydrological network of the Artikutza Valley has a drainage basin of 3683 ha, with a geology dominated by acidic rocks, such as granite and schist (Atristain et al., 2022). The Artikutza Valley is mainly 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). The reservoir had an initial storage capacity of 2.66 hm^3 and an area of ~0.14 km^2. Geotechnic problems noticed during dam construction required the reduction of storage capacity to 1.63 hm^3 and the construction, downstream in the same catchment, of the Añarbe Reservoir in 1976. Subsequently, the Enobieta Reservoir was not used to provide water (Larrañaga et al., 2019) and was not maintained properly to the point that it became a safety problem. Due to the early structural instability and the conservation status of the Artikutza Valley (it is part of the Natura 2000 Network and a special conservation zone), the decommissioning of the Enobieta Reservoir began in 2017 and continued throughout 2018 and 2019 (Amani et al., 2022). The phase of reservoir drawdown of the Enobieta Reservoir ended on 25 February 2019.

Sampling strategy and treatment of sediment samples

We collected sediment samples during and after the drawdown of the Enobieta Reservoir during six sampling campaigns (C_1–C_6): on 10 September 2018, 22 October 2018, 21 January 2019, 09 April 2019, 02 July 2019, and 18 February 2020 (Table S1, available at https://www.limnetica.net/en/limnetica). To assess whether the content and reactivity of sediment OM changed over time, we used the sampling date minus the last inundation date of each site to find sediment exposure time (in days) for each site (Table S1). We determined the last inundation date for each site from the site elevation (Table S2, available at https://www.limnetica.net/en/limnetica), the reservoir bathymetry, and the daily evolution of water level in the reservoir (available in Amani et al. (2022)). The range of sediment exposure time was 9–580 days (Table S1). We collected sediment samples using six sites (A, B, C, D, E, and F), which were close to the tail of the reservoir, in the section exposed to the atmosphere for longer time (see Table S2 for coordinates). We collected three samples in a 1 × 1 m plot in each site when sediments were still bare and during the early recolonization of the bare sediments by vegetation. Thus, we collected 108 sediment samples: 6 sites × 3 replicate plots per site × 6 sampling campaigns. We lost one sample and, thus, we performed the incubation experiment and other analyses with 107 sediment samples.

In the field, we stored sediment samples in clean polyethylene falcon tubes that we transported in dark portable refrigerators to the laboratory. In the laboratory, we froze the sediment samples at -18 ºC. Before all analyses and the incubation experiment performed in this study (Fig. 1), we freeze-dried all sediment samples for 48

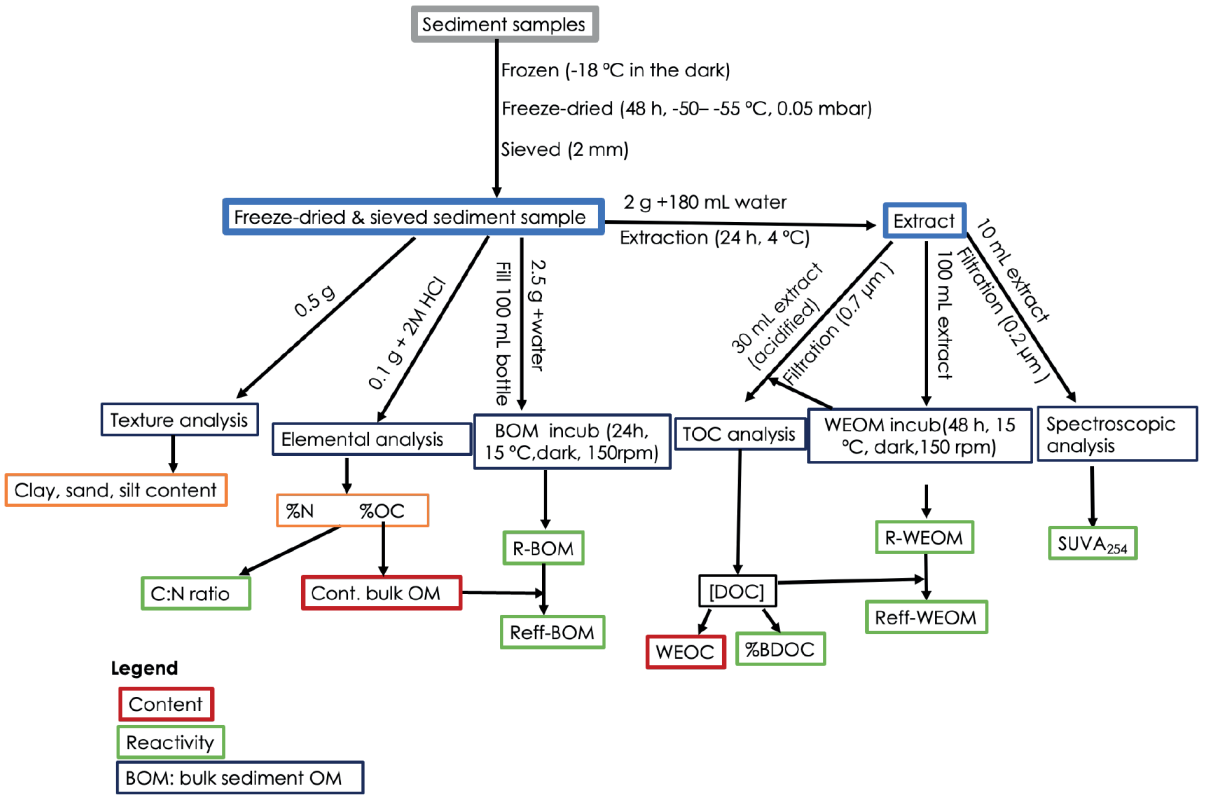

Figure 1. Schematic representation of the experiments conducted in this study. *Representación esquemática de los experimentos realizados en este estudio.*

h in a Telstar LyoQuest at a vacuum pressure of 0.05 mbar and a temperature between -50 and -55 ºC. We sieved the freeze-dried sediment samples with a steel sieve of a 2-mm mesh to retain the fine fraction of the sediments. We cleaned the steel sieve between samples with a plastic brush, taking maximum care to avoid contamination. We kept the sieved, freeze-dried sediment samples in clean polyethylene falcon tubes in the laboratory at -18 ºC until the incubation experiment and other analyses.

Sediment texture

We assessed the mean sediment size with 0.5 g of freeze-dried, sieved sediment using a laser light diffraction instrument (Coulter LS, 230, Beckman-Coulter, USA) after removing organic C (OC) with H_2O_2 (Arriaga et al., 2006).

Content of bulk sediment OM and sediment WEOM

We determined the content of bulk sediment OM as the amount of OC in the sediments. We determined the percentage of OC content (%OC) and the percentage of total nitrogen content (%N) on a 0.1 g dry sediment sample with an Elemental Analyzer (Model 1108, Carlo-Erba, Italy) after sediment acidification with 2M HCl to remove inorganic C and preserve OM. We reported the content of bulk sediment OM in mg OC/g dry sediment.

We determined the content of sediment WEOM as sediment water-extractable OC (WEOC: mg DOC/g dry sediment). We obtained WEOM by shaking a dry sediment aliquot of 2 g with 180 mL of mineral water (Font Vella) in 250-mL plastic bottles, in a dark incubator for 24 h at 4 ºC and 150 rpm. We filtered the sediment-water mixture

through glass fibre filters (0.7 µm pore size; Whatman GF/F, GE Healthcare, UK), pre-ashed for 4 h at 450 ºC, into clean polyethylene falcons of 50 mL. We used a different filter for each sample. We acidified the filtered samples to pH 2–3 with HCl 10 % to remove dissolved inorganic C and preserve OM. We used the high-temperature catalytic oxidation method to determine the concentration of DOC in a Shimadzu instrument (TOC-VCSH, Tokyo, Japan). We calculated WEOC as the product of [DOC] (mg/L) and the volume of water (L) used to extract WEOM divided by the mass (g) of each dry sediment sample:

$$\text{WEOC} = \frac{[DOC]\left(\frac{mg}{L}\right) \times water\ volume\ (L)}{mass\ dry\ sediment\ (g)} \quad (1)$$

Reactivity of bulk sediment OM and sediment WEOM

We assessed the reactivity of bulk sediment OM using three parameters: (1) respiration rate of bulk sediment OM, (2) respiration efficiency of bulk sediment OM, and (3) the mass ratio of %OC to %N (i.e., %OC/%N = C:N ratio, which was used as a proxy for reactivity). We determined the respiration rate of bulk sediment OM from the rate of dissolved O_2 consumption during incubation (von Schiller et al., 2019). We introduced 2.5 g of sediment samples into pre-washed 100 mL incubation glass bottles. We sealed the glass bottles with hexagonal glass stoppers (M-29/32, Scharlau, Spain) to avoid contamination of the samples. We left the sealed bottles on a laboratory benchtop for 24 h for the samples to acclimate to laboratory conditions. We aerated the water we used for incubation, Font Vella mineral water (spring: Sant Hilari Sacalm-Girona, Spain, [HCO_3^{1-}]: 143 mg/L, [Ca]: 42 mg/L, [Mg]: 11.3 mg/L, [Na]: 12.5 mg/L, and conductivity: 286 µS/cm), overnight in an open plastic jerrycan placed in a benchtop incubator (Optic Ivymen System, Spain) at 15 ºC and a rotation speed of 150 rpm. We used the air-saturated water to fill the bottles containing sediments and four control bottles without sediments (i.e., with mineral water only). We ensured that no air bubbles formed or stayed in the incubation bottles, which we sealed with the stoppers throughout the incubations.

We incubated the samples and controls for 24 h at 15 ºC in the dark benchtop incubator at 150 rpm. The temperature of 15 ºC was close to the mean annual temperature of 12.2 ºC in the Artikutza Valley (Gobierno de Navarra, 2019). We conducted the incubation of bulk sediment OM for 24 h because preliminary experiments had shown that more time could result in anoxia. We measured the O_2 concentration four times during the incubations (at 2, 4, 8, and 24 h) with O_2 optode spots (model PSt3, PreSens) attached to the interior of each bottle using a standalone, portable, fiberoptic O_2 meter (Microx 4 trace, PreSens, Regensburg, Germany). We vigorously shook each incubation bottle before each measurement to ensure homogeneous O_2 concentrations inside the bottles. We calculated the respiration rate of the bulk sediment OM (R-BOM; µg O_2 g^{-1} dry sediment h^{-1}) as:

$$R-BOM = \frac{\frac{\left(o_{2sample}^{2h} - o_{2sample}^{24h}\right) - \left(o_{2control}^{2h} - o_{2control}^{24h}\right)}{incubation\ time\ (h)} \times volume\ resp.bottle\ (L)}{mass\ of\ dry\ sediment\ (g)} \quad (2)$$

where O_2 is [O_2] (mg/L), subscripts sample and control refer to each analytical replicate and the mean [O_2] in the four control bottles, and superscripts *2h* and *24h* correspond to the measurement times (respectively, 2 h and 24 h). The volume of the bottle was 100 mL, the incubation time was 22 h, the sediment mass was 2.5 g. To estimate the respiration efficiency of the bulk sediment OM (Reff-BOM; µg O_2 g^{-1} OC h^{-1}), we replaced mass of dry sediment in the equation (2) by the mass of OC in each sediment sample. The consumption rate of O_2 over incubation time was linear and, thus, we used the initial (2 h) and final (24 h) values, to estimate the decomposition rate of sediment OM.

We determined the reactivity of sediment WEOM using four variables: (1) respiration rate of sediment WEOM, (2) respiration efficiency of sediment WEOM, (3) biodegradable DOC (BDOC), and (4) a chromophoric index; $SUVA_{254}$. We determined the respiration rate of sediment WEOM by incubating the WEOM extract, which was not filtered. We used a syringe to carefully collect the supernatant, avoiding the

intake of the sediment and other particles. We conducted the incubation experiment for 48 h (the time it took to consume at least 1 mg O_2/L in our preliminary experiments) under the same conditions as for the bulk sediment OM; dark conditions, at 15 ºC and 150 rpm. We measured [O_2] at 2 h, 24 h, and 48 h using the same PreSens O_2 optodes. We calculated the respiration rate of sediment WEOM (R-WEOM; µg O_2 g^{-1} dry sediment h^{-1}) as:

$$R-WEOM=\frac{\frac{(O_{2sample}^{2h}-O_{2sample}^{48h})-(O_{2control}^{2h}-O_{2control}^{48h})}{incubation\ time\ (h)}\times resp.bottle\ volume\ (L)}{mass\ of\ dry\ sediment\ (g)} \quad (3)$$

We estimated the respiration efficiency of sediment WEOM (Reff-WEOM; µg O_2 g^{-1} of DOC h^{-1}) by replacing, in the equation (3), mass of dry sediment with the mass of DOC (g) in each WEOM extract. To determine the fraction of biodegradable DOC (BDOC), we measured [DOC] in the samples before and after incubation, and we filtered each WEOM extract using a different filter with a pore size of 0.7 µm before determining [DOC]. We then calculated BDOC as the difference in [DOC] before ([DOC_i]) and after incubation ([DOC_f]) and expressed it as % of [DOC_i], i.e., %BDOC as:

$$\%BDOC=\left(\frac{[DOC]_i-[DOC]_f}{[DOC]_i}\right)\times 100 \quad (4)$$

We analyzed the optical property of WEOM by filtering 10 mL of the WEOM extract with a 0.2 µm filter (Whatman GF/F, GE Healthcare, UK). We used a PharmaSpec UV-1700 spectrophotometer (Shimadzu, Tokyo, Japan) to obtain ultraviolet-visible (UV-Vis) spectroscopy (200–600 nm) using a 1 cm quartz cuvette (Obrador et al., 2018). We determined a qualitative property of WEOM: the specific ultraviolet absorbance at 254 nm ($SUVA_{254}$: L mg C^{-1} m^{-1}). We determined $SUVA_{254}$, which is a descriptor of DOC aromaticity (Shao et al., 2009), as in Weishaar et al. (2003):

$$SUVA_{254}=\frac{abs_{254}\times ln_{(10)}}{[DOC]\times l} \quad (5)$$

where *abs254* is the absorbance at 254 nm, *[DOC]* is in mg C/L, and *l* is the path length of the cuvette in m.

Meteorological and vegetation data

We evaluated how the accumulated precipitation (a proxy for sediment moisture) and temperature in the Artikutza Valley, and the vegetation growth in the Enobieta Reservoir after drawdown changed with time during our sampling period. We obtained daily precipitation and temperature data from the nearest meteorological station (Artikutza Station of Meteorology and Climate of Navarre). We assessed how the temperature changed during the sampling period using the mean daily temperature (ºC) that was recorded on our sampling dates. We used the sum of daily precipitation for seven days (six days preceding the sampling date plus the precipitation on our sampling date) to obtain the accumulated weekly precipitation (mm). We used the sampling date to assess the temporal changes in precipitation during the sampling period. We assessed the temporal change in vegetation recolonization of the exposed sediments using Sentinel 2-Multipectral Instrument (MSI) imaging data taken on the 15th of each sampling month, which was mostly 3–7 days before or after the sampling date, a maximum of 13 days. The Sentinel 2-MSI data were preprocessed using Google Earth Engine. We used these satellite images of the whole reservoir to obtain the normalized difference vegetation index (NDVI, dimensionless). We did not have NDVI values for the first and third sampling campaigns because we could not find satellite images for the two sampling campaigns. We determined sediment exposure time for NDVI, precipitation, and temperature using the sampling date for each variable minus the earliest last inundation date.

Statistical analyses

We determined temporal changes in the content and reactive of sediment OM during the first 9–580 days of sediment exposure after the drawdown phase of DD of the Enobieta Reservoir using generalized additive mixed models (GAMMs), with the R package mgcv (mixed GAM computational

vehicle) in R version 4.0.5 (R Core Team, 2021). We considered as response variable the content and reactivity of sediment OM, and as explanatory variable time as a fixed factor. We used site as a random factor. We visually explored temporal trends of precipitation, temperature, and NDVI during sediment exposure time. We additionally ran a correlation analysis to explore the direction and significance of the temporal trend in NDVI. We used the paired samples t-test to test the difference between the means of the respiration rates for bulk sediment OM and sediment WEOM and their respiration efficiency. Statistical tests were considered significant when the *p*-value was ≤ 0.05.

Table 1. Descriptive statistics of sediment texture and the content and reactivity of sediment OM in the Enobieta Reservoir. Bulk OM content is the content of bulk sediment OM and SE is the standard error of the mean. *Estadística descriptiva de la textura del sedimento y del contenido y reactividad de la materia orgánica del sedimento en el embalse de Enobieta. "Bulk OM content" es el contenido de OM en peso seco de sedimento y SE es el error estándar de la media.*

Factor	Variable	Mean	SE	Range
Sed. texture	Mean sediment size (μm)	33.7	1.0	21.0–43.3
Content	Bulk OM content (mg OC/g dry sediment)	84	5.1	20–143
	Sediment WEOC (mg DOC/g dry sediment)	0.81	0.1	0.29–1.6
Reactivity	R-BOM (μg O_2 g^{-1} dry sediment h^{-1})	2.8	0.2	0.5–5.1
	Reff-BOM (μg O_2 g^{-1} OC h^{-1})	32.1	2.4	9.5–78.4
	R-WEOM (μg O_2 g^{-1} dry sediment h^{-1})	2.4	0.1	0.6–8.1
	Reff-WEOM (μg O_2 g^{-1} DOC h^{-1})	1103	63	566–1860
	BDOC (%)	41.4	2.0	17.5–64.8
	$SUVA_{254}$ (L mg C^{-1} m^{-1})	2.91	0.17	1.23–5.7
	C:N ratio (dimensionless)	16.2	1.0	5.1–28.6

RESULTS

Sediment texture

The mean sediment size in the Enobieta Reservoir (Table 1) changed with sediment exposure time. The mean sediment size decreased between the beginning of our sampling campaign and ~200 days of sediment exposure, then increased from ~200 days to ~400 days before slightly decreasing and increasing again (Fig. S1, available at https://www.limnetica.net/en/limnetica).

Content of bulk sediment OM and sediment WEOM

The content of bulk sediment OM (Table 1) changed with sediment exposure time (Fig. 2a). The content of bulk sediment OM decreased between the beginning of our sampling period and ~200

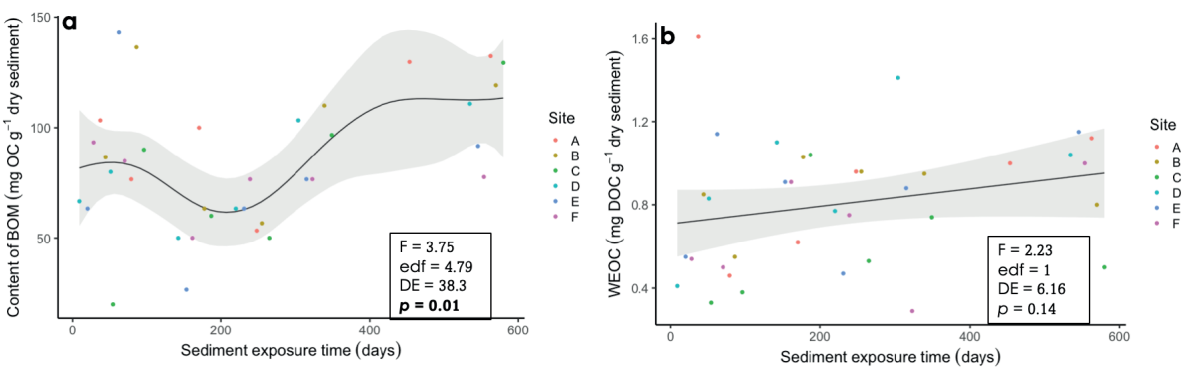

Figure 2. Temporal changes in the content of bulk sediment OM (a) and sediment WEOM (b) along sediment exposure time. The lines and shaded areas represent, respectively, the mean and 95 % confidence interval of GAMMs; each point represents the average of three sediment samples collected at each site for each sampling date; edf is effective degrees of freedom; DE is deviance explained (%); significant *p*-values are shown in bold. *Cambios temporales en el contenido de materia orgánica presente en el sedimento seco (a) y de la materia orgánica extraíble en agua (WEOM) del sedimento (B) durante el tiempo de exposición. Las líneas y espacios sombreados representan, respectivamente, la media y un intervalo de confianza del 95 % de los modelos aditivos generalizados mixtos; cada punto representa la media de tres muestras de sedimentos, recogidas en cada punto para cada día; edf hace referencia a los grados de libertad efectivos; DE a la desviación explicada (%); en negrita se muestran los* p-*valores significativos.*

days, increased between ~200 and 400 days, and then, between ~400 and 580 days of sediment exposure, it reached a plateau. Sediment WEOC (Table 1) did not change with sediment exposure time (Fig. 2b).

Reactivity of bulk sediment OM and WEOM

R-BOM and R-WEOM were not different (t(35.0) = 0.85, p = 0.40), while Reff-WEOM was 34.4 times higher than Reff-BOM (t(35.0) = 16.9, p < 0.01). Reff-WEOM, and %BDOC changed with sediment exposure time, while other parameters for the reactivity of sediment OM did not (Fig. 3 and 4). R-WEOM decreased between the beginning of our sampling and ~200 days, it also increased between ~400 days and 580 days of sediment exposure to form a nearly U-shaped curve (Fig. 3b). Reff-WEOM showed almost the same temporal trend as R-WEOM, but its increase between ~400 and 580 days was not as strong as for R-WEOM (Fig. 3d). Furthermore, %BDOC increased linearly with sediment exposure time (Fig. 4a).

Meteorological and vegetation data

The accumulated weekly precipitation was 73 ± 11 (0.0–170) mm [mean ± SE (range)], the temperature was 11.7 ± 0.9 (5.5–18.5) ºC during the

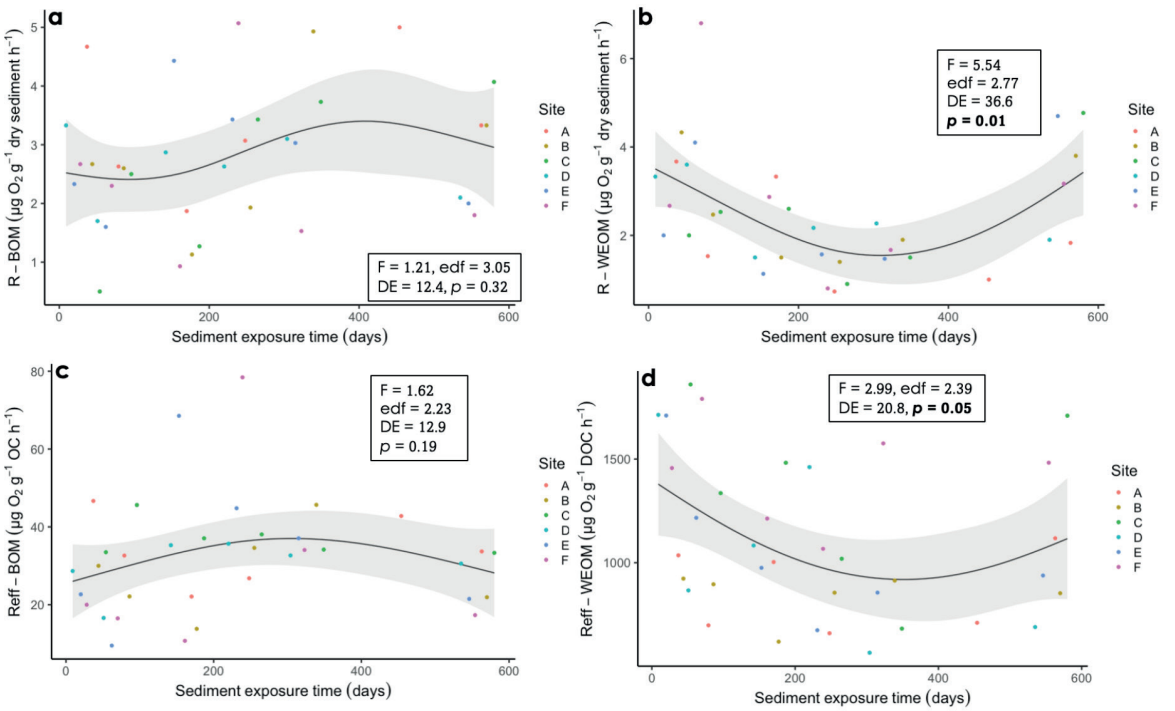

Figure 3. Temporal changes in the respiration rate for bulk sediment OM (R-BOM, a), the rate of microbial respiration for sediment WEOM (R-WEOM, b), respiration efficiency for bulk sediment OM (Reff-BOM, c), and respiration efficiency for sediment WEOM (Reff–WEOM, d) along sediment exposure time. The lines and shaded areas represent, respectively, the mean and 95 % confidence interval of the GAMMs; each point represents the average of three sediment samples collected for each sampling date at each site; edf is effective degrees of freedom; DE is deviance explained (%); significant p-values are shown in bold. *Cambios temporales en la tasa de respiración para la materia orgánica en el sedimento seco (R-BOM, a), tasa de respiración para la WEOM del sedimento (R-WEOM, b), eficiencia de la respiración para la materia orgánica en el sedimento seco (Reff-BOM, c), eficiencia de la respiración para la WEOM del sedimento (Reff-WEOM, d) durante el tiempo de exposición del sedimento. Las líneas y espacios sombreados representan, respectivamente, la media y un intervalo de confianza del 95 % de los modelos aditivos generalizados mixtos; cada punto representa la media de tres muestras de sedimentos, recogidas en cada punto para cada día; edf hace referencia a los grados de libertad efectivos; DE a la desviación explicada (%); en negrita se muestran los* p*-valores significativos.*

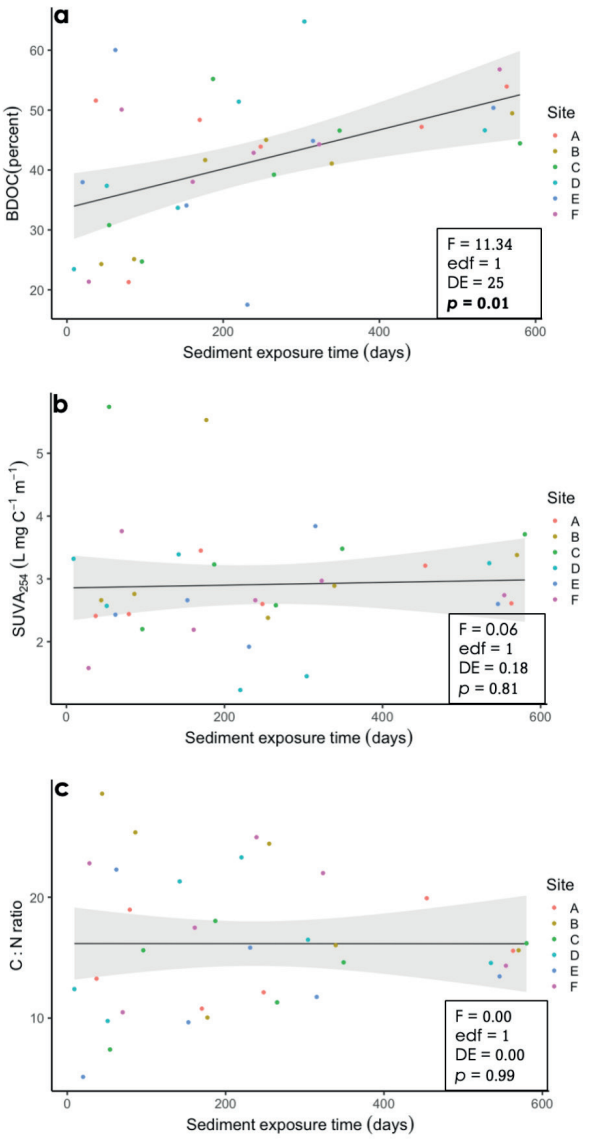

Figure 4. Temporal changes of BDOC (a), $SUVA_{254}$ (b), and C: N ratio (c) during sediment exposure time. The lines and shaded areas represent the mean and 95 % confidence interval of the GAMMs; each point represents the average of three sediment samples collected for each sampling date at each site; edf is effective degrees of freedom; DE is deviance explained (%); significant *p*-values are shown in bold. *Cambios temporales del carbono orgánico disuelto biodegradable (BDOC, a), $SUVA_{254}$ (b), y ratio C:N (c) durante el tiempo de exposición del sedimento. Las líneas y espacios sombreados representan, respectivamente, la media y un intervalo de confianza del 95 % de los modelos aditivos generalizados mixtos; cada punto representa la media de tres muestras de sedimentos, recogidas en cada punto para cada día; edf hace referencia a los grados de libertad efectivos; DE a la desviación explicada (%); en negrita se muestran los* p*-valores significativos.*

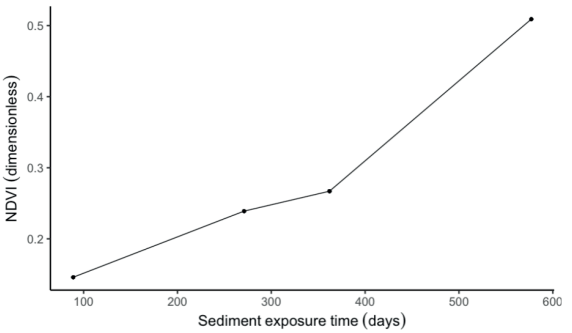

Figure 5. Temporal changes in NDVI (dimensionless) with sediment exposure time. *Gráfico de líneas de los cambios temporales en el índice de diferencia normalizada de vegetación (adimensional) durante el tiempo de exposición del sedimento.*

study period. Precipitation decreased from 18.8 to 0.0 mm between 54 and 96 days, increased from 0.0 to 148 mm between 96 and 265 days, decreased from 148 to 20.9 mm between 265 and 349 days, and increased from 20.9 to 170 mm between 349 and 580 days of sediment exposure (Fig. S2a, available at https://www.limnetica.net/en/limnetica). Temperature decreased from 18.5 to 5.5 ºC between 54 and 187 days, increased from 5.5 to 8.7 ºC between 187 and 265 days, between 256 and 349 days it increased from 8.7 to 18.2 ºC, and then decreased from18.2 to 7.0 ºC between 349 and 580 days of sediment exposure (Fig. S2b, available at https://www.limnetica.net/en/limnetica). Correlation analysis showed that NDVI increased with sediment exposure time ($r = 0.9$, $p < 0.01$). Vegetation continuously increased during sediment exposure, but the growth rate was greater between 362 and 577 days of sediment exposure (Fig. 5).

DISCUSSION

As expected, we report a high content of highly bioreactive bulk sediment OM and sediment WEOM in the Enobieta Reservoir. However, in contrast to what we expected, the content and reactivity of sediment OM did not decrease with sediment exposure time. For instance, %BDOC increased linearly with sediment exposure time, while the content of bulk sediment OM, R-WEOM, and Reff-WEOM showed complex

temporal trends. A common trend for R-WEOM and Reff-WEOM is that they began to increase when vegetation became abundant between 362 and 577 days, while the content of bulk sediment OM reached a plateau at ~400 days of sediment exposure. The linear increase in %BDOC with sediment exposure time and the late increases in R-WEOM and Reff-WEOM may be due to the input of labile OM produced by plants recolonizing the reservoir and the conversion of high molecular, recalcitrant OM to low molecular, labile OM through photodegradation.

The content of bulk sediment OM in the Enobieta Reservoir (84 ± 5.1 mg OC/g dry sediment) was comparable to the global content of sediment OM in ponds (mean ± SD in mg OC g^{-1} dry sediment), 180 ± 200, lakes, 140 ± 170, and reservoirs, 100 ± 110, but higher than in streams, 30 ± 40 (Keller et al., 2020). However, sediment WEOC (0.81 ± 0.05 mg DOC/g dry sediment) in the Enobieta Reservoir was higher than WEOC in lakes (mean ± SE in mg C/g dry sediment), 0.52 ± 0.06 (Table S3, available at https://www.limnetica.net/en/limnetica), soils, 0.35 ± 0.03 (Table S4, available at https://www.limnetica.net/en/limnetica), and rivers, 0.29 ± 0.02 (Table S5, available at https://www.limnetica.net/en/limnetica). The mean content of sediment OM in the Enobieta Reservoir may be comparable to the global mean content of sediment OM in ponds due to a high perimeter-to-area ratio of ponds that may lead to higher input and burial of OM in the sediments of ponds (Keller et al., 2020). Since the areal C burial rate in natural lakes is 4–12 times lower than in reservoirs (Mendonça et al., 2017), the content of bulk sediment OM in the Enobieta Reservoir should be higher than in lakes. However, our findings are consistent with those of Keller et al. (2020) who found no difference between the content of sediment OM in lakes and reservoirs worldwide. Furthermore, as found in this study, a previous study reported a higher content of sediment OM in reservoirs than in streams (Keller et al., 2020). High inputs of sediment and OM from the catchment increases C burial and content in reservoir sediments.

The content of bulk sediment OM decreased between the first sampling campaign and ~200 days of sediment exposure, which may be due to a rapid decomposition of labile OM contained in sediments that were mostly bare (with almost no vegetation) (Gómez-Gener et al., 2015; Kosten et al., 2018; Marcé et al., 2019). The content of bulk sediment OM increased between ~200 and 400 days of sediment exposure, which may be due to the input of OM produced by plants recolonizing the exposed sediment. However, the content of bulk sediment OM reached a plateau at ~400 days of sediment exposure. At this stage, we do not have a clear explanation of why the content of bulk sediment OM reached this plateau, especially, because vegetation continued to grow. We can speculate that there may have been a developing microbial community associated with root development. These microorganisms could have compensated for the effect of vegetation regrowth, a potential new source of OM, on the content of bulk sediment OM by increasing heterotrophic respiration. The balance between the supply of OM by plants and the loss through respiration could have led to a plateau of bulk sediment OM at ~400 days of sediment exposure. However, the role of vegetation recolonization in C content and microbial structure and function in exposed sediments after DD deserves further research.

Sediment OM in the Enobieta Reservoir was highly bioreactive. The mean O_2 consumption rate for bulk sediment OM (mean ± SE in μg O_2 g^{-1} dry sediment h^{-1}: 2.76 ± 0.20) was lower than the global mean of the O_2 consumption rate of bulk soil OM in dry soils of wetlands, 3.74 ± 0.39 (Table S6, available at https://www.limnetica.net/en/limnetica), but was ~2 times higher than the global mean of the O_2 consumption rate in dry sediments of streams, 1.43 ± 0.31 (Table S7, available at https://www.limnetica.net/en/limnetica). The mean decomposition rate of OM in dry soils of wetlands may be higher than in dry sediments of reservoirs because wetlands are more likely to bury large stocks of bioreactive OM due to high primary productivity and low O_2 concentration (due to soil water saturation), which inhibits the decomposition of OM in wetlands (Freeman et al., 2001; Mitsch et al., 2013). Carbon buried in wetlands comprises ~33 % of wetland soils (Villa & Bernal, 2018), and the decomposition of OM increases with the content of OM (Keller et al., 2020; Kothawala et al., 2021; Paranaíba et al., 2021). Thus, the lower amount of sediment OM may explain its

lower decomposition rate in streams than in the Enobieta Reservoir. By comparing the C:N ratio, we may also infer that sediment OM in the Enobieta Reservoir (C:N ratio = 16.2 ± 1.0) was more bioreactive than sediment OM in streams, C:N ratio: 26.0 ± 2.2 (von Schiller et al., 2019). The C:N ratio in the Enobieta Reservoir was, however, higher than in lakes (Dean & Gorham, 1998). In addition, we report %BDOC for a two-day incubation, 41.4 ± 2.0 %, which is 1.4 times lower than %BDOC in dry sediments of three reservoirs in the Three Gorges Reservoir region in China and dry soils from a wetland in Southeastern China, which were, however, incubated for an average time of 28 days at 28 ºC, mean: 58.0 % (Table S3). Since the decomposition of sediment OM increases with temperature (Gudasz et al., 2010, 2015), %BDOC in the Enobieta Reservoir would be comparable or even higher than %BDOC in the three reservoirs and the wetland if the incubation temperature and time were equal. Furthermore, %BDOC in the Enobieta Reservoir was ~2 times higher than the global mean %BDOC in dry soils incubated for an average time of 50 days at 16.9 ºC, 22.1 ± 1.4 % (Table S4). Thus, although the experimental approaches adopted to estimate %BDOC differ among studies, our results highlight that reservoir sediments may be hotspots of highly biodegradable OM.

Reff-WEOM was 34.4 times higher than Reff-BOM. This result reinforces that WEOM is the most bioavailable fraction of OM (Boyer & Groffman, 1996; Chantigny, 2003), and that most of the degradation of OM in bulk sediments is based on WEOM. Furthermore, our results suggest that C burial in reservoir sediments is due to conditions not favorable for C decomposition, rather than the inherent C recalcitrance (Catalán et al., 2016; Kellerman et al., 2015; Kothawala et al., 2021). If the OM buried in the sediments of the Enobieta Reservoir was inherently recalcitrant against microbial decomposition, we should have reported low decomposition rates in our incubation experiment. Since we conducted our incubation experiment with the native microbial community under dark conditions, at a temperature close to the temperature in the region of the Enobieta Reservoir and without the addition of nutrients, we may speculate that the key factor that restricted the decomposition of sediment OM during the operational phase of the Enobieta Reservoir was anoxia. The high sedimentation rate and the limited exposure time of sediment OM to O_2 (Sobek et al., 2009, 2012) can result in the burial of inherently bioreactive OM in reservoir sediments. However, we expected that the content and reactivity of sediment OM would decrease with sediment exposure time, as increased availability of O_2 would increase the microbial decomposition of OM during sediment exposure.

Interestingly, %BDOC increased linearly with sediment exposure time, while the content of bulk sediment OM, R-WEOM and Reff-WEOM exhibited complex temporal trends during the first 9–580 days of sediment exposure. The linear increase in %BDOC with sediment exposure time may be explained by the rapid recolonization of exposed sediments by vegetation and the effect of photodegradation. As shown by the NDVI values, vegetation rapidly recolonized the reservoir after reservoir drawdown. Growing plants may supply an important amount of fresh and labile OM. For instance, depending on plant species, roots release 10–250 mg C/g root produced as root exudates (McNear, 2013; Vranova et al., 2013). Root exudates comprise labile, low molecular weight organic compounds, such as amino acids, peptides, and sugars (Rovira, 1969). These root exudates can also increase microbial biomass (Eisenhauer et al., 2017; Sung et al., 2006; Wang et al., 2012), which can contribute to the labile C pool. However, the labile OM of microbial biomass and plants that recolonize exposed sediments after drawdown can also increase the bioreactivity of old recalcitrant OM buried in sediments, a process called the priming effect (Bianchi et al., 2015; Guenet et al., 2010, 2014). Thus, the priming effect due to labile OM produced by microorganisms and regrowing plants could lead to a decrease in the content and reactivity of sediment OM. Furthermore, high-molecular weight, recalcitrant molecules in sediment OM of exposed sediments may also be converted into low-molecular weight, bioreactive molecules, due to sediment exposure to solar radiation (Granéli et al., 1996; Lindell et al., 1995; Wetzel et al., 1995). Though photoreactions produce mainly inorganic C (CO_2), they also produce

organic compounds of low molecular weight and low aromaticity called biologically available photoproducts (Backlund, 1992; Catalán et al., 2013; Kieber et al., 1989; Mopper & Stahovec, 1986). Since sediment exposure is a hot moment of OM decomposition, aromaticity should have increased with sediment exposure time (Hansen et al., 2016). Thus, we expect photodegradation to be one of the reasons sediment exposure time did not affect the aromaticity of sediment OM. However, future studies should assess the specific effect of solar exposure on the molecular weight of sediment OM after DD.

Other parameters of the content and reactivity of sediment OM showed non-linear temporal trends. R-WEOM and Reff-WEOM showed almost the same temporal trend as the content of bulk sediment OM but did not reach a plateau at ~400 days of sediment exposure. The effects of terrestrialization and associated development of the microbial community and solar radiation may explain why R-WEOM and Reff-WEOM continued to increase with sediment exposure time. With current data, we cannot, beyond speculation, explain why other factors, such as the decomposition rate for bulk sediment OM and its respiration efficiency, $SUVA_{254}$, sediment WEOC, and the C: N ratio did not change with time. However, $SUVA_{254}$ in sediment WEOM of the Enobieta Reservoir was in the range of $SUVA_{254}$ of dissolved OM reported from sediments of different types of inland waters (0.2–3.7 L mg C^{-1} m^{-1}, Chen & Hur (2015)), but lower than $SUVA_{254}$ of dissolved OM in waters collected from a range of aquatic systems, 3.2–10.6 L mg C^{-1} m^{-1} (Helms et al. 2008).

The observed temporal trend of the sediment texture was not expected since water withdrawal should result in rapid transport of fine-sized sediment, which would increase the mean size of the sediment during the early sampling campaigns. The late increase in mean sediment size may be explained by a higher transport of fine sediment and the accumulation of coarse sediment in the reservoir. Furthermore, sediment texture did not affect the content and reactivity of sediment OM in the Enobieta Reservoir, and previous studies also reported conflicting results on the role sediment texture in the reactivity of sediment OM (Mendoza-Lera et al., 2017; von Schiller et al., 2019).

Amani et al. (2022) hypothesized that the areal CO_2 fluxes in exposed sediments decreased with the sediment exposure time due to a decrease in the content and reactivity of sediment OM in the Enobieta Reservoir after the drawdown phase of DD. This study rejects the hypothesis that the content and reactivity of sediment OM in the Enobieta Reservoir decreased with sediment exposure time. Decreasing areal CO_2 fluxes in exposed sediments due to reduced C availability and microbial activity due to sediment drying should not be expected in a humid region, such as the Artikutza Valley with a rainfall of 2604 mm/yr (Atristain et al., 2022). However, a decrease in temperature over the last two sampling campaigns shown in this study may explain why areal CO_2 emissions in exposed sediments and running water decreased during the sampling period in Amani et al. (2022).

CONCLUSION

This study explored the content and reactivity of bulk sediment OM and sediment WEOM in a reservoir under DD. We reported a high content of highly bioreactive sediment OM, with the respiration efficiency of sediment WEOM being higher than that of bulk sediment OM. Sediment OM in exposed sediments during and after DD is susceptible to erosion and lateral transport downstream of the reservoir. Our results suggest that exposed sediments may be a great source of labile OM in downstream river reaches. Lateral transport of labile OM from the reservoir can imply higher C respiration and CO_2 fluxes in the river network downstream of the reservoir, therefore, interfering in the final OM delivered to the coastal ocean after DD. It is necessary to know how the lateral transport of C from the reservoir alters C dynamics in the river segments downstream from the removed reservoir. Future studies should also examine the effects of vegetation recolonization on C dynamics in the reservoir and the lateral transport of C downstream of the reservoir after DD.

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CONFLICT OF INTEREST

The authors claim no conflict of interest.

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