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Dam removal effects on carbon processing in a mountainous Mediterranean stream

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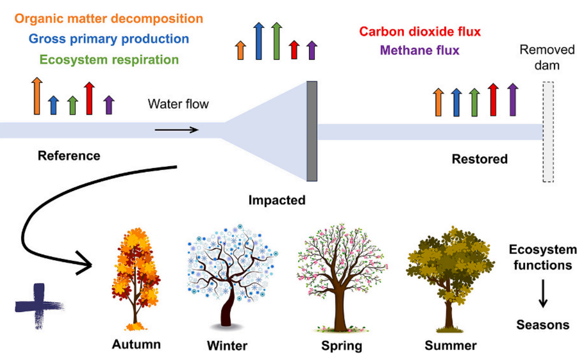
HIGHLIGHTS

- Functional metrics are useful indicators of dam removal restoration success
- Dam removal contributes positively to certain aspects of in-stream carbon processing
- Dam removal led to carbon dioxide fluxes akin to the reference conditions
- Decomposition and metabolic rates were not completely recovered after dam removal

GRAPHICAL ABSTRACT



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ABSTRACT

The global prevalence of obsolete or unsafe old dams necessitates the development of effective restoration approaches and expanded knowledge in this field. This study evaluates the effects of dam removal on carbon processing by measuring key ecosystem functions - organic matter decomposition, whole-reach metabolism, and gaseous carbon fluxes - in a mountainous Mediterranean stream. We compared these functions among three reaches: one where a dam was removed (restored), one with an intact dam (impacted), and one in natural conditions (reference). The measurements were conducted throughout the different seasons over the course of one year. Temperature-corrected organic matter decomposition rates and metabolic parameters in the restored reach showed intermediate values between those in the reference and impacted reaches. Additionally, dam removal resulted in carbon dioxide fluxes similar to those in the reference reach, whereas methane fluxes tended to be higher in the restored reach compared to the other reaches. Seasonal variation was high, and the observed effects were inconsistent across seasons for several functions. This inconsistency is likely due to uneven seasonal changes in the hydromorphological and physicochemical characteristics of the studied reaches. Our results indicate that, despite notable improvements, a longer timeframe is necessary for the restored reach to fully emulate the functional characteristics of the reference reach. While restoration by dam removal positively contributes to certain aspects of carbon processing, a more holistic approach, possibly encompassing broader

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hydromorphological and habitat enhancements, is needed to fully restore ecological processes in stream ecosystems. These insights are critical for informing future dam removal restoration projects, advocating the use of ecosystem function metrics as comprehensive indicators of ecological recovery and restoration success.

1. Introduction

Dam removal is nowadays considered a pivotal action for stream restoration, especially in developed countries, where many old and small dams have become obsolete or unsafe (American Rivers, 2020; Bellmore et al., 2017; Wagner and Moore, 2024). So far, around 2000 dams have been removed in Europe and in the United States, mostly small dams and low weirs (Habel et al., 2020). Despite the exact number of dams worldwide is unknown, the vast majority are small (i.e., < 10 m, but averaging around 3 m in height) (Duda and Bellmore, 2022). Dams disrupt the streams' natural course and flow, alter water temperatures, transform floodplains, interrupt stream continuity, and affect terrestrial and aquatic communities (Aristi et al., 2014). While dam releases are often timed to meet human demands for water supply, navigation, power production, and recreation, the needs of the stream's aquatic organisms and the overall influence of these operational rules are not always considered. Dam removal is an attempt to reverse the negative impacts, recovering the flow regime (longitudinal and lateral connectivity) and recreating habitat heterogeneity (Hart et al., 2002). This strategy has proven to be a highly effective stream restoration intervention to attenuate anthropogenic pressure on sediment release and transport (Bednarek, 2001), macroinvertebrate communities (Vasco, 2021; Wagner and Moore, 2024), stream connectivity (Magilligan et al., 2016), and migration of fish and other organisms (Barbarossa et al., 2020; Chen et al., 2023). Yet, the potential impacts of dam removal on ecosystem functioning caused by the mobilization of stored sediment, nutrients, and organic matter (OM), as well as their recovery, are still poorly understood (Amani et al., 2022; Atristain et al., 2023).

The accurate evaluation of stream restoration success, including dam removal, necessitates consideration of both (1) the physical features of the ecosystem and the associated biota and (2) the functional aspects related to the set of processes that regulate the fluxes of energy and matter (Baattrup-Pedersen et al., 2022; von Schiller et al., 2017). Despite the diversity of actions, stream restoration assessment typically focusses on physicochemical and biological features, such as the aquatic species diversity, water discharge and current velocity, sediment release and transport, and changes in water temperature or nutrient availability (Frainer et al., 2018; Furley et al., 2023; Lin et al., 2020). Including ecosystem functioning to evaluate the outcomes of these interventions is still uncommon (Cunha et al., 2022; Ferreira et al., 2020). Stream functioning can respond differently to environmental change or restoration strategies; thus, there can be a mismatch between functions (e.g., OM decomposition) and changes in more traditional indicators of ecosystem structure (e.g., benthic invertebrate community composition) (Cardinale et al., 2012; Mckie and Malmqvist, 2009; Sandin and Solimini, 2009).

Several biologically-mediated ecosystem functions can be used in stream restoration assessment. Among these, processes associated with carbon (C) dynamics, such as OM decomposition, whole-reach metabolism, and gaseous C fluxes, show high potential (Amani et al., 2022; Cunha et al., 2022; Ferreira et al., 2020). OM decomposition integrates riparian vegetation and aquatic communities via the instream cycling of energy and nutrients of terrestrial origin (Mancuso et al., 2023; Martinez-Sanz et al., 2024; Tiegs et al., 2019). Whole-reach metabolism represents the balance between the production and consumption of OM (Tank et al., 2010). Gaseous C fluxes, mainly in the form of carbon dioxide (CO_2) and methane (CH_4), are the result of metabolic processes acting in conjunction with other internal and external processes (Hotchkiss et al., 2015). These functions have been proposed in numerous studies as good proxies for ecosystem integrity and as an alternative to assess the health of stream ecosystems (Taniwaki et al., 2022; Tiegs et al., 2013; von Schiller et al., 2008). Despite the limited number of studies using a functional approach to evaluate stream restoration success, whole-reach metabolism and OM decomposition have proven to be valuable indicators (Ferreira et al., 2020). On the other hand, gaseous C fluxes have been significantly less implemented (Amani et al., 2022). Additionally, incorporating seasonal changes in ecosystem functioning is crucial, yet this aspect is often not addressed (Mancuso et al., 2023).

Here, we aimed to evaluate the effect of dam removal on stream C processing. We compared OM decomposition, whole-reach metabolism, and gaseous C concentrations and fluxes among three stream reaches in a mountainous Mediterranean stream: one where a dam was removed (restored), one with an intact dam (impacted), and one in natural conditions (reference) across different seasons. We hypothesized that C processing in the restored reach would deviate from that in the impacted reach and more closely resemble that in the reference reach. We further hypothesized that this effect would be consistent across seasons.

2. Material and methods

2.1. Study area and sampling design

The Riera Major stream originates in the Montseny mountain range (Catalonia, NE Spain) and is a tributary of the Ter River. The region has a Mediterranean climate (Csa), with hot and dry summers and mild and humid winters (Kottek et al., 2006). This second-order stream drains a 66-km^2 watershed that extends in an altitude range between 960 and 460 m above sea level. The watershed is dominated by siliceous geology. The stream has a sinuous morphology, and substrate is similar among the studied reaches with a higher percentage of fine substrate type (especially sand and silt) in the impacted reach. The Riera Major is located in the transition area between Temperate broadleaf forest and Mediterranean vegetation. Vegetation cover is dominated by oak (*Quercus ilex*) with chestnut (*Castanea sativa*) and spruce (*Picea abies*) (Sabater et al., 2000). The riparian forest is generally well developed and dominated by alder (*Alnus glutinosa*) (Marti and Sabater, 1996).

In 2017, a dam was removed in the Riera Major stream to restore connectivity along the watercourse (Supplemental Fig. S1). The dam was 3 m high, 0.8 m thick, and 29 m long and was completely clogged with sediment so it no longer had any functionality. It was removed by the companies Heura and Naturalea, promoted by the Diputació de Barcelona - Espai Natural Guilleries Savassona. The process consisted of four phases: (1) management of riparian forest; (2) removal of sediments; (3) dam disassembly; (4) environmental restoration; and (5) follow-up (more details are available in Naturalea, 2017). Specifically, in relation to the removal of sediments, the companies in charge of the project reported that a partial management was conducted. Efforts were made to stabilize the materials, which could not be completely removed due to budgetary constraints, and to allow them to slowly move downstream with the stream's natural flow.

For this study, three reaches (100-m each) were selected in this stream: one where a dam was removed as "restored" (41°54′44.3″ N, 2°23′12.6″ E), one with an intact dam as "impacted" (41°54′08.2″ N, 2°22′44.8″ E), and one in natural conditions as "reference" (41°54′01.8″ N, 2°22′44.5″ E) (Supplemental Fig. S2). All three reaches were located within 2.5 km of stream length. Comparisons between restored, impacted, and control reaches in the same stream are commonly used to evaluate restoration success (e.g., Anlanger et al., 2022; Levi and McIntyre, 2020). Nevertheless, many studies have assessed the effects shortly after the interventions. In this study, we investigated the outcomes of the restoration approximately six years after the dam removal. To examine potential differences in the effect of dam removal across seasons, we conducted four sampling campaigns, one in each season: autumn (October 2022), winter (February 2023), spring (April 2023), and summer (June 2023).

The discharge and average water velocity of the reaches were estimated through the pulsed release of a conservative solute [sodium chloride (NaCl)] (Gordon et al., 2004). Slopes were obtained empirically in-situ as the elevation difference over the length of each reach using a Bosch GOL 20 D Professional optical level. Canopy cover percentage was estimated as the average from eleven equally-spaced sampling transects distributed along each reach using a concave densiometer (Forestry Suppliers Inc., Jackson, MS, USA) (Lemmon, 1957; Lemmon, 1956). Wetted widths were measured at the same transects along the reaches. In-situ measurements of electrical conductivity were carried out at the very end of each studied reach in all samplings with a WTW handheld sensor. We collected water samples, always in triplicate, for determination of total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and total phosphorus (TP) analyses. Samples for TDN and DOC were filtered through GF/F glass fiber membranes, acidified, and refrigerated until analysis using a Shimadzu TOC Shimadzu (Tokyo, Japan) TOC-VCSH analyzer coupled to a TNM-1 Total Nitrogen Module. TP was determined by the colorimetric method, according to Grasshoff (1983).

2.2. Organic matter decomposition

Organic matter decomposition was measured with the cotton-strip technique (Tiegs et al., 2013). Two cotton-strips (Fredrix-brand without primer 12-oz. Style #548, Fredrix, Lawrenceville, GA, USA) were placed along each reach in five representative locations (i.e., a total of ten cotton-strips per reach) and were incubated in the stream bed anchored to an iron bar for 27 days in autumn, 22 days in spring, and 21 days in winter and summer. At the time of collection, each cotton-strip was immersed in ethanol (80 %) for one minute to stop microbial decomposition and was transported to the laboratory where it was dried at 60 °C until it reached a constant weight. The decomposition rate was calculated from the loss of tensile strength of the incubated material (as an indicator of microbial degradation of cellulose) compared to ten non-incubated cotton-strips. The measurements of tensile strength loss were carried out with a dynamometer (Mark-10, M5 series) coupled to a motorized test bench (ESM303, Mark-10) with a constant traction speed of 2 cm min^{-1}. The tensile losses indicate the OM decomposition rates expected in the stream and were normalized in relation to water temperature as it directly influences the OM decomposition. For this purpose, one temperature sensor (Onset-HOBO® MX2202, Onset Computer Corporation, Bourne, MA, USA) was deployed in each reach and data were collected during the whole incubation period at 10-min intervals.

2.3. Whole-reach metabolism

According to Demars et al. (2015), the two-station method is applicable to reach lengths 0.4 to 1.0 v/k (current velocity/reaeration coefficient). For our reaches, this range corresponds to 396–990 m (reference), 579–1447 m (restored), and 187–467 m (impacted). Thus, the quantification of metabolism using the two-station method was not suitable. Hence, daily rates of whole-reach metabolism [gross primary production (GPP) and ecosystem respiration (ER)] were estimated using the single-station method. This method involves measuring diel changes in DO concentration, water temperature, photosynthetically active radiation (PAR), and barometric pressure (Bott, 2006). Data loggers with sensors were deployed at the very end (100 m) of each studied reach to monitor changes in PAR (Onset-HOBO® UA-002-64, Onset Computer Corporation, Bourne, MA, USA), barometric pressure (Onset-HOBO® U20L-04), and DO and water temperature (Onset-HOBO® U26–001) at 10-min intervals over seven-day deployment periods. DO probes were calibrated to water-saturated air and anoxic concentrations prior to deployment. We estimated daily GPP, ER, and reaeration coefficient following procedures in Grace et al. (2015). For that, we used the BASE v2.3 (BAyesian Single Station Estimation) script available for R software. BASE is a daytime regression model (Kosinski, 1984). It describes the DO concentration (mg O_2 L^{-1}) at time step t + 1 from the GPP, ER, and reaeration at preceding time step t. By fitting the following equation (Eq. 1) to recorded data, parameter values of production, respiration, and reaeration rates were empirically obtained:

$$[DO]_{t+1} = [DO]_t + AI_t^p - R\left(\theta^{T_t-\overline{T}}\right) + k_{O2}\left(1.0241^{T_t-\overline{T}}\right)D_t \tag{1}$$

where AI_t^p is the volumetric primary production rate (mg O_2 L^{-1} d^{-1}), A is a constant representing the primary production per quantum of light, I is surface irradiance (μmol m^{-2} s^{-1}), p is an exponent reflecting the ability of primary producers to use incident light, R is the volumetric ecosystem respiration rate (mg O_2 L^{-1} d^{-1}), θ is the temperature dependence of respiration, T is water temperature (°C), $\overline{T}$ is mean water temperature over the 24-h period, k_{O2} is the reaeration coefficient (d^{-1}), and D is the oxygen deficit which corresponds to the difference between the measured DO concentration and the saturated DO concentration at a given temperature, salinity, and barometric pressure (mg O_2 L^{-1}).

Estimated reaeration coefficient values were highly correlated with gas transfer velocities calculated with eq. 7 in Raymond et al. (2012) [Pearson correlation coefficient (r) = 0.88; $p = 0.0001$] (see section 2.4). We assumed detection limits (GPP and ER) equal to 0.1 mg O_2 L^{-1} d^{-1}. Metabolic rates were estimated by BASE in mg O_2 L^{-1} d^{-1} and converted to g O_2 m^{-2} d^{-1} using the mean reach depth (m) calculated with discharge, current velocity, and mean reach wetted width. Further, reach lengths influencing the one-station diel DO change technique in our study were typically longer than the experimental reaches due to high current velocities and low reaeration, specifically in the restored and reference reaches [mean lengths: restored = 4.4 km, impacted = 1.4 km, and reference = 3.0 km; estimated according to Chapra and Di Toro, 1991]. This is a very common situation in this type of study. Following methods in Demars et al. (2015), metabolism estimates at the impacted reach's downstream sampling station were only approximately 20 % influenced by the restored reach. Conversely, metabolism estimates at the reference reach's downstream sampling station were approximately 20 % and 50 % influenced by the restored and impacted reaches, respectively.

2.4. Gaseous C concentrations and fluxes

We used the headspace equilibration method to measure the partial pressures of CO_2 (pCO_2) and CH_4 (pCH_4) in the three reaches. In all samplings, we took five water samples and two air samples at the very end of each reach. We rinsed the syringes (60 mL) three times with stream water, filled them up with stream water, emptied them to leave 30 mL of stream water within the syringes, and added 30 mL of air by pointing the syringe upwards (far from our breath) and pulling the plunger slowly. After these steps, we closed the stopcock and the syringes had 30 mL of stream water and 30 mL of air. They were shaken vigorously for 1 min and deposited horizontally in the stream shoreline for 10 min for final water-air equilibration. Temperature of equilibration was recorded with a WTW handheld sensor. Later, we inserted a needle into the end of the stopcock at each syringe tip. Pointing upwards, we opened the stopcock and immediately started pushing the plunger slowly to leave the equilibrated air out through the needle. When arriving at the 20 mL mark, we inserted the needle into the septum of a pre-evacuated 12-mL exetainer (Labco, UK) and pushed the plunger to the end in order to transfer the 20 mL of equilibrated air remaining in the syringe to the exetainer. For the air samples, we directly transferred 20 mL of ambient air to the exetainer following the same aforementioned procedure (no equilibration and shaking are needed in this case). The concentrations of CO_2 and CH_4 in water and air samples were determined on an Agilent 7820 A gas chromatograph equipped with a flame ionization detector. Aqueous CO_2 and CH_4 concentrations at field conditions were determined from measured headspace gas volume fractions and concentrations, based on the barometric pressure at the sampling site, field water temperature, laboratory equilibration temperature, and the appropriate Henry's law constants (Sander, 2015). Applying Fick's first law of gas diffusion (Eq. 2), we determined fluxes across the water-air interface [carbon dioxide flux (FCO_2) and methane flux (FCH_4); mmol m^{-2} d^{-1}] using the surface water and air partial pressures, the gas transfer velocities (Eq. 3), and Henry's constants adjusted for salinity and temperature (Millero, 1995; Weiss, 1974):

$$F = k\beta(p_w - p_a) \tag{2}$$

where F is the flux of CO_2 (FCO_2) or CH_4 (FCH_4) from lotic water (mol m^{-2} d^{-1}), k is the gas transfer velocity of CO_2 (kCO_2) or CH_4 (kCH_4) (m d^{-1}), β is the solubility coefficient of CO_2 or CH_4 (mol m^{-3} atm^{-1}), and p_w and p_a are, respectively, the partial pressures of CO_2 (pCO_{2w} and pCO_{2a}) or CH_4 (pCH_{4w} and pCH_{4a}) (atm) in water and air. Positive flux values represent gas evasion from the water to the atmosphere and negative values indicate gas uptake from the atmosphere to the water.

$$k = k_{600}\left(\frac{Sc}{600}\right)^{-\frac{2}{3}} \tag{3}$$

where Sc is the Schmidt number of CO_2 ($ScCO_2$) or CH_4 ($ScCH_4$) (dimensionless) and k_{600} (m d^{-1}) is k at a Schmid number of 600 calculated from measured slopes, water depth, discharge, and velocities following eq. 7 in Raymond et al. (2012).

2.5. Statistical analysis

We used two-way analysis of variance (ANOVA) with Tukey's post-hoc test to examine whether there were any statistically significant differences among reaches (three levels: restored, impacted, and reference) and across seasons (four levels: spring, summer, autumn, and winter), as well as their interactions, regarding the assessed ecosystem functions (OM decomposition rates, metabolism parameters, and gaseous C fluxes). Comparisons among the reaches allowed us to infer the effects of dam removal by comparing the values from the restored reach with those from the reference and impacted reaches. The underlying assumption was that similar rates of ecosystem functions between the restored and reference reaches would indicate successful restoration, while similar rates between the restored and impacted reaches would suggest that the restoration was unsuccessful. Furthermore, as mentioned previously, we conducted multiple function measurements in each reach across different seasons. Whole-reach metabolism was measured daily over a seven-day period, OM decomposition rates were determined using ten cotton-strips distributed along the length of the stream reach, and gaseous C fluxes were calculated from five water samples. This approach enabled us to evaluate both seasonal effects and the interaction between the factors. To ensure the validity of our analyses, we applied a ln-transformation to the data when necessary to meet the normality assumption (Shapiro-Wilk test, $p > 0.05$). Moreover, relationships among functions were explored using Pearson correlation coefficients. All statistical analyses were conducted in the Origin software, Version 2024 (OriginLab Corporation, Northampton, MA, USA). We set the significance level at $p < 0.05$.

3. Results

3.1. Environmental variables

The impacted reach was deeper and had lower water velocities in comparison to the others (Table 1). In addition, gas transfer velocities

Table 1

Environmental variables in the restored, impacted, and reference stream reaches. Data reported are means ± standard deviations. Abbreviations: Q, discharge; k_{600}, gas transfer velocity; k_{O2}, reaeration coefficient; CC, canopy cover; PAR, photosynthetically active radiation; Temp, water temperature; EC, electrical conductivity; DO, dissolved oxygen; DOC, dissolved organic carbon; TDN, total dissolved nitrogen; TP, total phosphorus.

Reach	Season	Width (m)	Depth (m)	Velocity (m s^{-1})	Q (L s^{-1})	k_{600} (m d^{-1})	k_{O2} (d^{-1})	CC (%)	PAR (μmol m^{-2} s^{-1})	Temp (°C)	EC (μS cm-1)	DO (mg O_2 L^{-1})	DOC (mg C L^{-1})	TDN (mg N L^{-1})	TP (mg P L^{-1})
Restored	Autumn	5.9	0.07	0.12	46	2.2	8.1	55	13.4	14.7	707	8.1	2.6	0.3	0.2
	Winter	7.7	0.10	0.18	124	3.6	10.8	6	62.36	8.8	523	10.5	2.9	0.8	0.3
	Spring	5.9	0.08	0.17	87	3.2	8.4	13	99.17	12.2	697	7.7	3.4	0.8	0.5
	Summer	4.5	0.10	0.21	127	5.0	13.3	18	83.91	15.2	454	8.2	3.7	1.5	0.3
	Mean	**6.0 ± 1.3**	**0.09 ± 0.02**	**0.17 ± 0.04**	**96 ± 38**	**3.4 ± 1.2**	**12.3 ± 3.5**	**23 ± 22**	**64.7 ± 37.4**	**12.7 ± 2.9**	**595 ± 126**	**8.6 ± 1.3**	**3.2 ± 0.5**	**0.9 ± 0.5**	**0.3 ± 0.1**
Impacted	Autumn	7.4	0.16	0.02	27	1.5	3.9	81	7.77	14.5	768	8.4	3.9	1.1	0.5
	Winter	7.5	0.19	0.05	70	2.5	7.5	52	32.4	7.41	550	9.6	3.5	0.6	0.3
	Spring	7.7	0.37	0.03	98	2.7	7.7	63	29.4	11.97	795	7.2	4.7	0.7	0.8
	Summer	7.1	0.28	0.06	106	3.8	10.5	79	67.2	15.16	454	7.8	3.7	1.3	0.4
	Mean	**7.4 ± 0.2**	**0.25 ± 0.09**	**0.04 ± 0.02**	**75 ± 36**	**2.6 ± 0.9**	**7.4 ± 2.7**	**75 ± 14**	**34.2 ± 24.6**	**12.3 ± 3.5**	**642 ± 166**	**8.3 ± 1.0**	**4.0 ± 0.5**	**0.9 ± 0.3**	**0.5 ± 0.2**
Reference	Autumn	4.2	0.06	0.10	22	2.9	11.7	70	5.4	14.6	705	8.5	4.7	1.1	0.4
	Winter	5.4	0.06	0.15	62	3.8	11.8	45	24.4	6.8	548	10.3	3.5	0.6	0.3
	Spring	5.0	0.09	0.11	45	3.6	9.3	53	31.1	12.0	808	7.6	4.3	0.6	0.9
	Summer	5.6	0.08	0.15	67	4.1	11.7	67	29.6	15.2	454	8.3	4.1	1.2	0.4
	Mean	**5.1 ± 0.6**	**0.07 ± 0.02**	**0.13 ± 0.03**	**49 ± 20**	**3.7 ± 0.5**	**11.1 ± 1.2**	**59 ± 12**	**22.6 ± 11.8**	**12.2 ± 3.8**	**629 ± 158**	**8.7 ± 1.1**	**4.2 ± 0.5**	**0.9 ± 0.3**	**0.5 ± 0.3**

and reaeration coefficients were lower in the impacted reach. Measured slopes were 0.006 (restored), 0.007 (impacted), and 0.009 m m^{-1} (reference). The impacted reach showed higher canopy cover and percentages varied across seasons, especially in the restored reach where the PAR was higher compared to the others. Stream discharge and water physicochemical variables were similar among reaches. Nevertheless, TP and DOC were lower in the restored reach.

3.2. *Ecosystem functions*

Tensile loss rates ranged between 0.87 and 4.71 % d^{-1} and 0.09 and 0.41 % dd^{-1} (Fig. 1). Results from the two-way ANOVAs showed that both stream reach and season had a statistically significant effect on tensile loss (Table 2). The interaction between the factors stream reach and season was not significant (Table 2). Pair-wise post-hoc comparisons of tensile loss among reaches showed that non-temperature-corrected rates in the restored reach (3.05 ± 0.83) were similar to those in the reference reach (3.22 ± 0.75) ($p = 0.47$) and higher than those in the impacted reach (2.37 ± 0.96 % d^{-1}) ($p < 0.0001$). Comparisons among seasons showed that decomposition rates were similar between spring (2.88 ± 0.80) and autumn (2.99 ± 0.70) ($p = 0.8995$), whereas the other pairs were statistically different [summer (3.79 ± 0.80) and winter (2.09 ± 0.65 % d^{-1})]. Nevertheless, when rates were corrected by water temperature, tensile losses in the restored reach (0.24 ± 0.05) were higher than those in the impacted reach (0.20 ± 0.08) ($p = 0.0086$) and lower than those in the reference reach (0.29 ± 0.06 % dd^{-1}) ($p = 0.0013$). Comparisons among seasons showed that temperature-corrected rates differed between winter (0.28 ± 0.10) and autumn (0.21 ± 0.05) ($p < 0.0001$), winter and spring (0.24 ± 0.07) ($p = 0.0483$), and autumn and summer (0.25 ± 0.05 % dd^{-1}) ($p = 0.0449$).

Metabolic parameters showed high spatial and temporal variation. Results from the two-way ANOVAs showed that both stream reach and season, as well as their interaction, had a significant effect on metabolic parameters (Table 2). GPP ranged from 0.07 to 6.08 (Fig. 2) and rates obtained in the restored reach (0.99 ± 0.49) were lower than those in the impacted reach (2.41 ± 1.92) ($p < 0.0001$) and higher than those in the reference reach (0.66 ± 0.46 g O_2 m^{-2} d^{-1}) ($p = 0.0001$). GPP was similar between spring (2.30 ± 2.09) and winter (1.55 ± 0.66) ($p = 0.0583$) and between summer (0.58 ± 0.45) and autumn (0.61 ± 0.45 g O_2 m^{-2} d^{-1}) ($p = 0.7580$). Post- hoc comparisons of GPP among reaches within each season showed that GPP differed among reaches in autumn ($p = 0.0102$) and spring ($p < 0.0001$) (impacted vs. restored), autumn ($p = 0.0038$), winter ($p = 0.0323$), and summer ($p = 0.0010$) (reference vs. restored), and winter, spring, and summer ($p < 0.0001$) (reference vs. impacted). In turn, ER varied between 0.77 and 15.26 (Fig. 2) and rates in the restored reach (2.72 ± 1.10) were significantly lower than those in the impacted reach (7.91 ± 3.47) ($p < 0.0001$) and higher than those in the reference reach (2.13 ± 1.02 g O_2 m^{-2} d^{-1}) ($p = 0.0007$). There was a significant difference across seasons in ER (Table 2), except between winter (3.66 ± 1.91) and autumn (3.82 ± 1.31 g O_2 m^{-2} d^{-1}) ($p = 0.6756$). Post- hoc comparisons of ER among reaches within each season showed that ER differed among reaches in winter, spring, and summer ($p < 0.0001$) (impacted vs. restored and reference vs. impacted) and summer ($p = 0.0025$) (reference vs. restored).

In all samplings, NEP rates were negative and GPP:ER ratios were lower than 1 (Fig. 2), indicating consistent net heterotrophic conditions. NEP in the restored reach (−1.73 ± 0.89) was similar to that in the reference reach (−1.47 ± 0.80) ($p = 0.3873$) and higher than that in the impacted reach (−5.50 ± 1.94 g O_2 m^{-2} d^{-1}) ($p < 0.0001$). There was a significant difference across seasons in NEP (Table 2), except between autumn (−3.20 ± 0.98) and spring (−3.71 ± 2.95) ($p = 0.2426$) and autumn and summer (−2.74 ± 2.51 g O_2 m^{-2} d^{-1}) ($p = 0.3046$). Post-hoc comparisons of NEP among reaches within each season showed that

Table 2
Results from the two-way ANOVAs on the effects of stream reach (restored, impacted, and reference), season (autumn, winter, spring, and summer) and their interaction on organic matter decomposition, whole-reach metabolism, and gaseous carbon concentrations and fluxes. Degrees of freedom: 2 (stream reach), 3 (season), and 6 (stream reach vs. season). Abbreviations: GPP, gross primary production; ER, ecosystem respiration; NEP, net ecosystem production; pCO_2, carbon dioxide partial pressure; pCH_4, methane partial pressure; FCO_2, carbon dioxide flux; FCH_4, methane flux.

Function	Stream reach		Season		Stream reach * Season	
	F	P-level	F	P-level	F	P-level
Tensile loss (% d^{-1})	21.86	<0.0001	32.88	<0.0001	1.17	0.3295
Tensile loss (% dd^{-1})	19.80	<0.0001	7.67	<0.0001	1.75	0.1173
GPP	74.65	<0.0001	81.27	<0.0001	31.06	<0.0001
ER	181.63	<0.0001	27.23	<0.0001	23.58	<0.0001
NEP	178.28	<0.0001	19.09	<0.0001	22.79	<0.0001
GPP:ER	17.39	<0.0001	94.28	<0.0001	12.76	<0.0001
pCO_2	2.24	0.1177	159.24	<0.0001	13.44	<0.0001
pCH_4	43.20	<0.0001	32.92	<0.0001	20.42	<0.0001
FCO_2	4.76	0.0132	20.32	<0.0001	20.32	<0.0001
FCH_4	48.35	<0.0001	55.35	<0.0001	35.21	<0.0001

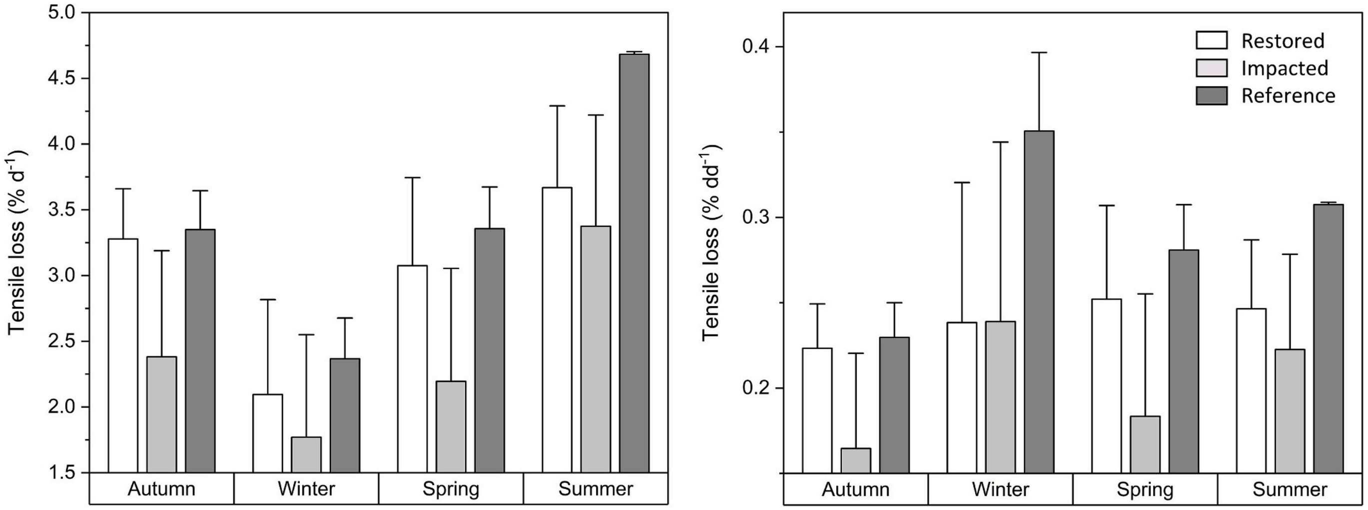

Fig. 1. Organic matter decomposition regarding tensile loss in % d^{-1} and % dd^{-1} in the restored, impacted, and reference stream reaches and their variation across seasons. Data reported are means ± standard deviations.

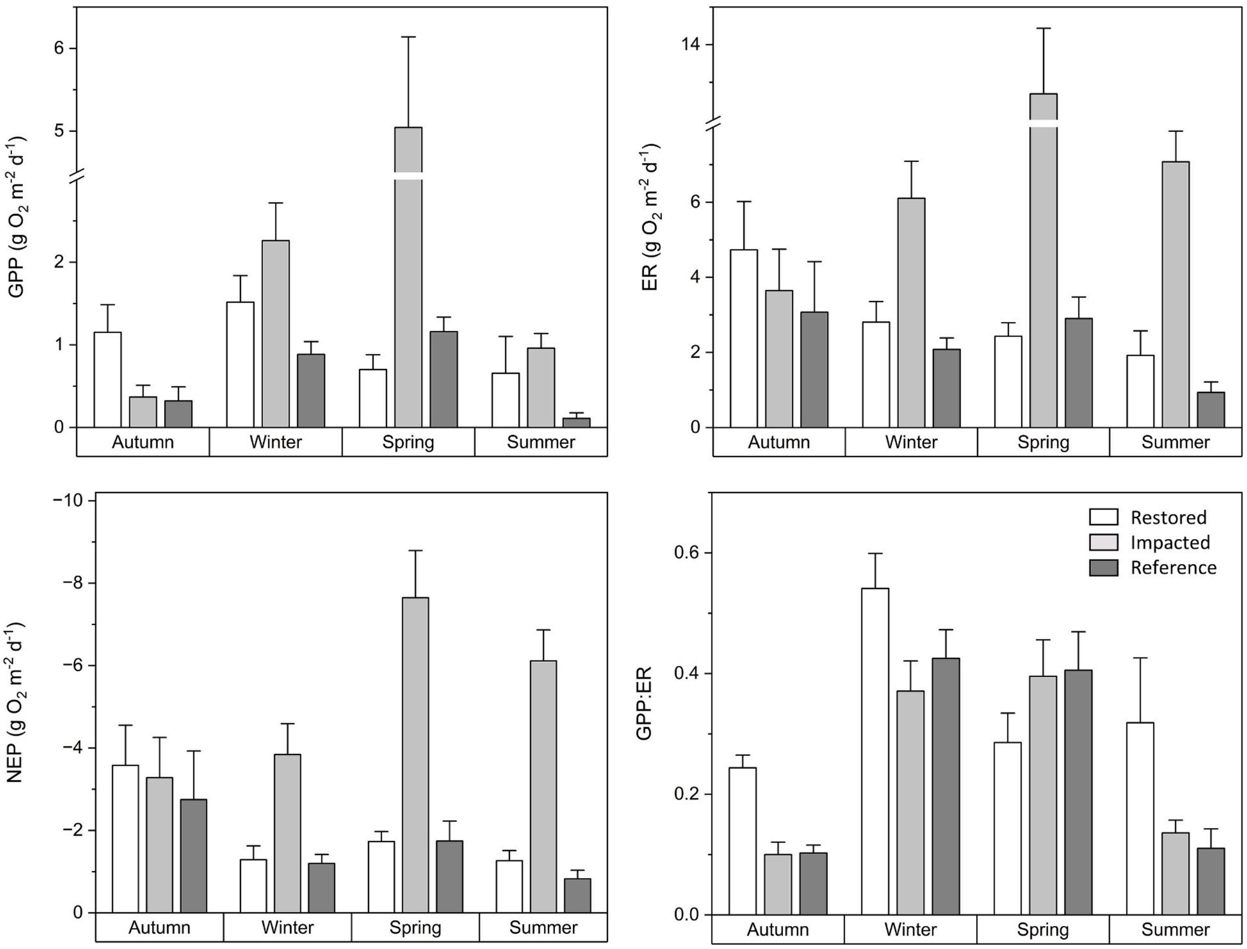

Fig. 2. Gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP), and GPP:ER ratios in the restored, impacted, and reference stream reaches and their variation across seasons. Data reported are means ± standard deviations.

rates differed among reaches in winter, summer, and spring ($p < 0.0001$) (impacted vs. restored and reference vs. impacted). GPP:ER ratios in the restored reach (0.36 ± 0.14) were higher than those in the impacted (0.27 ± 0.14) ($p < 0.0001$) and reference (0.28 ± 0.16) ($p < 0.0001$) reaches. GPP:ER ratios in summer (0.19 ± 0.11) and autumn (0.15 ± 0.07) were statistically similar ($p = 0.3177$) and lower compared to winter (0.46 ± 0.09) and spring (0.36 ± 0.08). Post- hoc comparisons of GPP:ER among reaches within each season showed that ratios differed among reaches in winter ($p = 0.0002$) and summer ($p < 0.0001$) (impacted vs. restored) and winter ($p = 0.0314$), spring ($p = 0.0223$), and summer ($p < 0.0001$) (reference vs. restored).

Partial pressures of CO_2 and CH_4 also differed among reaches and seasons. Both CO_2 and CH_4 in water were generally oversaturated with respect to the atmosphere. Thus, streams were net emitters of CO_2 and CH_4, except in winter and just for CO_2. In the case of pCO_2, results from the two-way ANOVAs showed no significant effect of reach (range = 86.85–1551.81 ppmv) (Fig. 3) and a significant effect of season and the reach vs. season interaction (Table 2). Water pCO_2 differed among seasons, except between summer (869.28 ± 149.77) and spring (811.43 ± 205.33 ppmv) ($p = 0.5850$). Post- hoc comparisons of pCO_2 among reaches within each season showed that pCO_2 differed among reaches in autumn ($p = 0.0463$) (impacted vs. restored), autumn ($p < 0.0001$) and spring ($p = 0.0001$) (reference vs. restored), and spring ($p = 0.392$) (reference vs. impacted). In the case of pCH4, results from the two-way ANOVAs showed a significant effect of reach, season, and their interaction (Table 2). Water pCH_4 (range = 1.83–11.88) (Fig. 3) in the restored reach (5.11 ± 2.66) was higher than in the impacted (4.00 ± 1.10) ($p < 0.001$) and reference (2.82 ± 0.66 ppmv) ($p < 0.0001$) reaches (Table 2). Water pCH_4 differed among seasons, except between spring (4.14 ± 1.01) and autumn (4.00 ± 0.92 ppmv) ($p = 0.9600$). Post-hoc comparisons of pCH_4 among reaches within each season showed that pCH_4 differed among reaches in summer ($p < 0.0001$) (impacted vs. restored and reference vs. restored) and spring ($p = 0.0043$) (reference vs. impacted).

The fluxes of CO_2 and CH_4 also showed high spatial and temporal variation. FCO_2 and FCH_4 ranged between −63.65 and 234.74 and 0.01 and 1.92 mmol m^{-2} d^{-1}, respectively (Fig. 3). The negative FCO_2 was obtained in winter in the impacted (−15.22 ± 6.41) and reference (−43.91 ± 18.21 mmol m^{-2} d^{-1}) reaches, indicating that there was CO_2 uptake from the atmosphere to the water. Low FCO_2 was also found in the restored reach (5.44 ± 3.31 mmol m^{-2} d^{-1}) in winter. Results from the two-way ANOVAs showed that both stream reach and season, as well as their interaction, had a significant effect on the fluxes of CO_2 and CH_4 (Table 2). FCO_2 in the restored reach (88.77 ± 62.80) was similar to that in the reference reach (88.78 ± 108.18) ($p = 1.000$) and higher than that in the impacted reach (66.18 ± 59.42 mmol m^{-2} d^{-1}) ($p = 0.0165$). In addition, FCO_2 differed among seasons, except between summer (139.69 ± 37.04) and autumn (128.73 ± 66.01 mmol m^{-2} d^{-1}) ($p = 0.6145$). Post- hoc comparisons of FCO_2 among reaches within each season showed that FCO_2 differed among reaches in autumn ($p < 0.0001$) and spring ($p = 0.0023$) (reference vs. restored) and autumn ($p < 0.0001$) (reference vs. impacted). FCH_4 in the restored reach (0.47 ± 0.56) was higher than in the reference (0.10 ± 0.06) ($p < 0.0001$) and impacted (0.18 ± 0.12 mmol m^{-2} d^{-1}) ($p < 0.0001$) reaches. Moreover, FCH_4 was greater in summer (0.62 ± 0.60) compared to autumn (0.16 ± 0.08) ($p < 0.0001$), winter (0.06 ± 0.03) ($p < 0.0001$), and spring

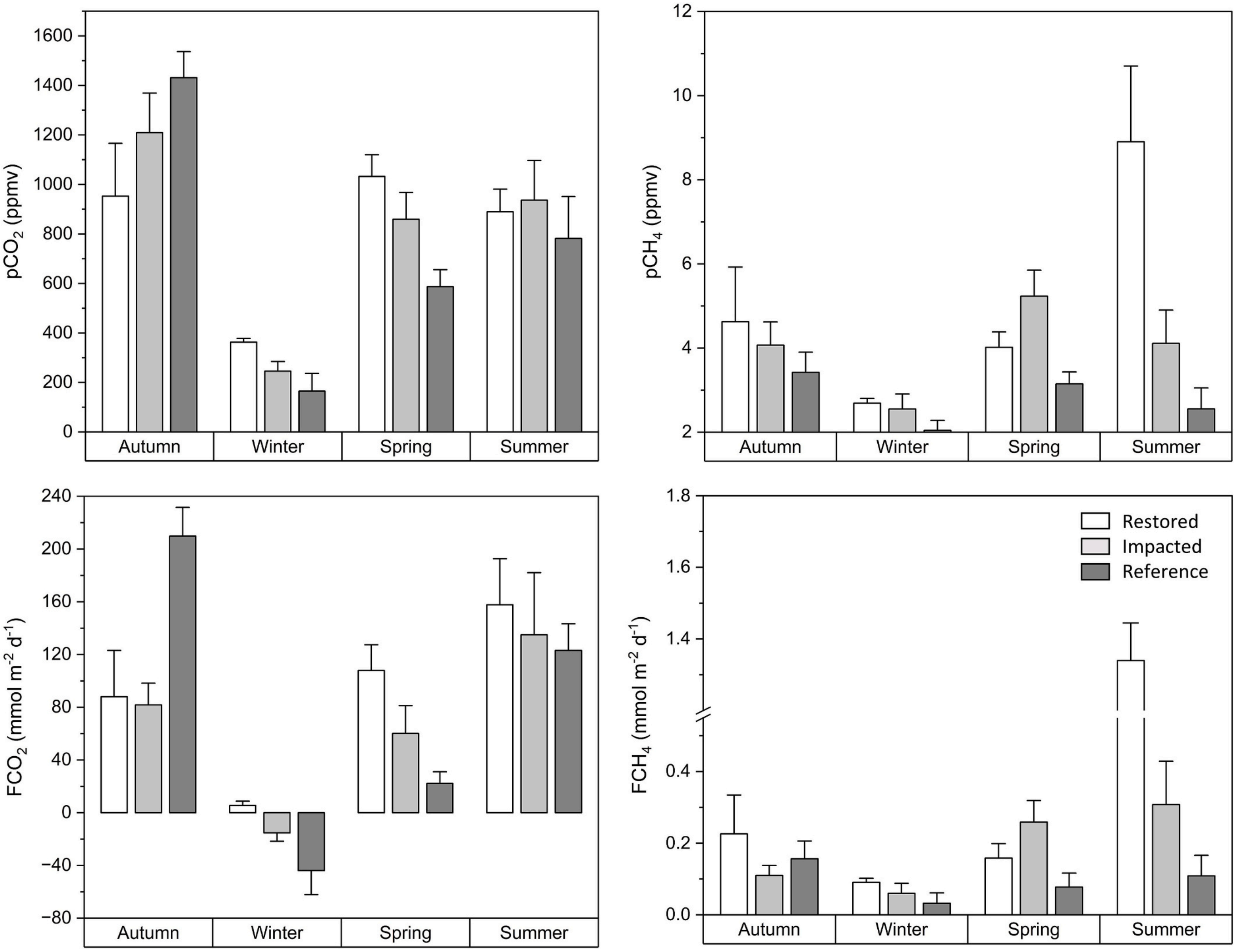

Fig. 3. Carbon dioxide partial pressure (pCO$_2$), methane partial pressure (pCH$_4$), carbon dioxide flux (FCO$_2$,) and methane flux (FCH$_4$) in the restored, impacted, and reference stream reaches and their variation across seasons. Data reported are means ± standard deviations.

(0.16 ± 0.09 mmol m^{-2} d^{-1}) ($p < 0.0001$). Post- hoc comparisons of FCH$_4$ among reaches within each season showed that FCH$_4$ differed among reaches in summer ($p < 0.0001$) (impacted vs. restored and reference vs. restored).

We observed significant correlations between gaseous C concentrations and fluxes for both CO$_2$ and CH$_4$. Tensile loss (temperature-corrected) and metabolic parameters presented distinctive behavior. Positive correlations were obtained between tensile loss and NEP ($p = 0.0453$; $r = 0.5859$), GPP and ER ($p = 0.0257$; $r = 0.6378$), GPP and GPP:ER ($p = 0.0011$; $r = 0.8193$), pCO$_2$ and pCH$_4$ ($p = 0.0452$; $r = 0.5862$), pCO$_2$ and FCO$_2$ ($p = 0.0004$; $r = 0.8547$), pCH$_4$ and FCO$_2$ ($p = 0.0139$; $r = 0.6855$), pCH$_4$ and FCH$_4$ ($p = 0.0007$; $r = 0.8385$), and FCO$_2$ and FCH$_4$ ($p = 0.0017$; $r = 0.8011$). Negative correlations were obtained between GPP and pCO$_2$ ($p = 0.0486$; $r = -0.5788$), GPP and FCO$_2$ ($p = 0.0139$; $r = -0.6854$), ER and NEP ($p = 0.0002$; $r = -0.8874$), GPP:ER and pCO$_2$ ($p = 0.0009$; $r = -0.8280$), and GPP:ER and FCO$_2$ ($p = 0.0021$; $r = -0.7936$). The complete correlation matrix is available in Supplemental Table S1.

4. Discussion

In this study, we compared C processing among a stream reach where a dam was removed (restored), another with an intact dam (impacted), and a reach in natural conditions (reference) across different seasons of the year. Differently from what we hypothesized, OM decomposition, metabolic parameters, and gaseous concentrations and fluxes measured in the restored reach after the dam removal intervention did not completely resemble those in the reference reach. Nevertheless, some functions presented values closer to the reference reach than those observed in the impacted reach, such as tensile losses normalized by temperature, GPP, and ER. Additionally, also deviating from our initial hypothesis, the effect of the restoration was not consistent across seasons for all the assessed functions, likely due to uneven variations in hydromorphological and physicochemical features. We argue that differences in environmental context, such as contrasting hydromorphological and physicochemical features among stream categories, may not be completely related to restoration in many projects, but could partially reflect indirect effects of reach differences. The environmental context (in combination with the restoration strategies) is also important to understand the outcomes of the interventions (Bega et al., 2024).

4.1. *Organic matter decomposition*

The tensile loss rates (not corrected for temperature) in the restored reach deviated from those in the impacted reach and resembled those in the reference reach. Anthropogenic changes to flow regimes in the form of dam constructions have the potential to alter OM decomposition rates. For example, litter decomposition has been documented to slow significantly in intermittent streams, isolated pools, and downstream dams compared to perennial streams (Arias-Real et al., 2020; Li et al., 2020; Martinez-Sanz et al., 2024; Mendoza-Lera et al., 2012; Menéndez et al., 2012). Indeed, greater current velocities and reaeration coefficients were measured in our restored and reference reaches. In addition, lower current velocities increase sedimentation, creating more suitable environments for biofilm overgrowth which can eventually prevent light from reaching the benthic communities and increase heterotrophic activity (Aristi et al., 2014). This also could explain the lowest tensile loss rates obtained in the impacted reach, especially closer to the dam. Nevertheless, when tensile loss rates were normalized by temperature, those in the restored reach deviated from the others and were in an intermediate position between the lowest and highest rates obtained in the impacted and reference reaches, respectively. These results suggest that OM decomposition was faster in the environment with minimal anthropogenic disturbance and that the intervention was not sufficient for decomposition rates to completely approach those observed in the reference reach, contradicting our hypothesis. A possible explanation for this observation is that not enough time passed since the restoration action (Moreno-Mateos et al., 2015). In the future, extra improvements in geomorphic recovery of the stream channel and flora and fauna recolonization are expected. Our results highlight the importance of the presence of continuous riparian vegetation to regulate stream water temperatures and, consequently, decomposition rates.

Variations in tensile loss rates across seasons were observed, but differences among reaches remained across seasons despite changes in magnitude. The effects of temperature changes on OM decomposition were further underscored when the differences across seasons were analyzed. Tensile loss rates without the temperature correction peaked in the warm summer and were lowest in the cold winter. However, this pattern was attenuated when decomposition was temperature-corrected and rates were then higher in winter and summer and lower in the other seasons. These outcomes highlight the role of intra-annual variation in stream temperature as a key driver of seasonal variation in decomposition rates (Mancuso et al., 2023). Apart from water temperature effects on tensile loss rates across seasons, increased discharges and current velocities have also been related to seasonal changes in OM decomposition (Cook and Hoellein, 2016; Ferreira et al., 2006). The effects of microbial activity can be masked by the losses in tension caused by the water turbulence in the cotton-strips (Tiegs et al., 2019; Tiegs et al., 2013). In our reaches, current velocities and discharges were similar between summer and winter. Our findings show that tensile losses corrected by temperature were less variable than those not corrected. This information must be taken into consideration when assessing the effects of dam removal interventions to improve their management and avoid hasty conclusions considering this important ecosystem function.

4.2. Whole-reach metabolism

Primary production and respiration were positively correlated in the studied reaches across seasons. This correlation suggests high autotrophic respiration where high rates of GPP yield higher ER because of the combined respiration of autotrophs and heterotrophic organisms present in the biofilms (Hall, 2016). In addition, all stream reaches presented heterotrophic conditions, consistent with a strong metabolic reliance on external organic matter inputs widely documented for small headwater streams (Giling et al., 2013; Whiles et al., 2013).

The dam removal was not sufficient for the metabolic rates in the restored reach to approach those observed in the reference reach. The impacted reach showed greater GPP and ER compared to the other reaches. The presence of the dam resulted in a decrease in current velocities, which has been related to biofilm stabilization and increased heterotrophic activity due to a lower abrasive effect (Benson et al., 2013; Saltarelli et al., 2018). Removing dams promotes increasing in-stream current velocities and therefore scouring of algae, responsible for decreasing in-stream GPP and ER rates. A key explanation here is probably the incomplete recovery of the riparian vegetation in the restored reach which was young and less complex, affecting light availability as well as the qualitative and quantitative features of allochthonous OM inputs. In the first years after dam removal and recovery of riparian vegetation, light availability often drives metabolism dynamics through still greater GPP rates, although lower than those before vegetation restoration (Reisinger et al., 2019). As the riparian vegetation and hydrological connectivity within streams develop, heterotrophic processes may become more important (Gift et al., 2010; Harrison et al., 2011). Piscart et al. (2024) reported a rapid recolonization by invertebrates, but a still low phytobenthic primary production in restored river reaches after dam removal. The authors stated that three years after intervention, there was a still significant time lag between the recovery of communities and the expected ecosystem functioning restoration. Long-term monitoring is necessary to elucidate the temporal evolution of metabolic rates following dam removal and the surrounding riparian vegetation restoration (Bott and Newbold, 2023; Henry et al., 2002; Wu et al., 2013). It is worth mentioning that even being shadier than the other reaches, the impacted reach did not present the lowest GPP and ER rates, suggesting that the negative influence of the dam regarding stream metabolism outweighs the benefits generated by riparian vegetation.

Differences in metabolic rates were observed across seasons as well among reaches within seasons. The highest GPP rates occurred in spring and winter. Higher GPP during these periods is expected because canopy cover is mostly absent (Bernhardt et al., 2018; Bott and Newbold, 2023; Vannote et al., 1980) (Supplemental Fig. S2). McTammany et al. (2007) and Giling et al. (2013) measured reductions in GPP rates due to increases in riparian shading in temperate streams. Hart (2013) reported early spring and late winter GPP peaks as well, which were positively associated with leaf abscission and light availability. The decrease in canopy cover can also promote greater biofilm and algae growth in streams (Mosisch et al., 2001) (Supplemental Fig. S3). Regarding ER, rates in our reaches were greater in the early spring as well and were associated with GPP. The predominant base flow during this season promotes stream bed stability and biofilm accumulation, which can support greater GPP and ER (Chowanski et al., 2020). In addition, the seasonality of ER seems mainly driven by changes in water temperature (Acuña et al., 2004). Stream respiration has been documented to increase in warmer seasons and waters (Perkins et al., 2012). However, the lowest water temperature in our reaches were measured in the spring (and winter). At last, Chowanski et al. (2020) highlighted that timing and duration of periods with elevated GPP and ER differed among temperate reaches following changes in river management. Accordingly, these fluctuations should be considered in future dam removal projects.

4.3. Gaseous C concentrations and fluxes

Our initial hypotheses regarding gaseous C concentrations and fluxes were not confirmed. We observed relevant changes in these variables across the studied reaches and seasons. Whereas water pCO_2 was similar among reaches, FCO_2 was lower in the impacted reach. Somewhat contrastingly, water pCH_4 was higher in the impacted and restored reaches, but FCH_4 was lower in the impacted and reference reaches. These results can be explained by the lower gas transfer velocities measured in the impacted reach. Gaseous C fluxes depend on these velocities and partial pressures (Eq. 2). Lotic waters are expected to present greater FCO_2 than impounded waters as shallower streams with higher water velocities are often associated with higher interfacial turbulence (Gómez-Gener et al., 2015). Conversely, turbulence favors more oxic conditions due to the mixing of the water column. Therefore, CH_4 production is less likely as higher DO concentrations interfere with methanogenesis and also promote its oxidation (Robison et al., 2022). Hence, impounded waters are considered important CH_4 emitters because of their increased anaerobic microbial functioning (Amani et al., 2022; Bastviken et al., 2004; Deemer et al., 2016). In our studied reaches, pCH_4

and gas transfer velocities were always similar or higher in the restored reach with respect to the other reaches. As a consequence, FCH_4 was higher in the restored reach. As the restoration was not executed so long ago, there is probably still the influence of all the remaining organic material that sedimented over the time the dam operated and was later released by its removal (Bellmore et al., 2019). Major et al. (2017) highlighted that removing dams can release stored sediments for decades, which significantly affect the habitat structure upstream and downstream for long periods. Initial deposition of sediments, for example, can bury benthic and riparian organisms, but as this initial sediment pulse is eroded in the long-term, new habitats for organisms are created and decreased FCH_4 can be expected.

Regarding the seasonal variation, we observed that gaseous C fluxes were higher in autumn (for FCO_2) and summer (for both FCO_2 and FCH_4). On the other hand, negative or very low FCO_2 was found in late winter, indicating net uptake or negligible emission of CO_2. This pattern can be explained by the climatic conditions of Mediterranean regions, resulting in a highly seasonal regime (Bernal et al., 2013; Gasith and Resh, 1999). During the wet period (late autumn to early spring), the hydrological longitudinal connectivity increases, and most of the fluvial network area is covered with surface water. On the other hand, during the dry period (from late spring to early autumn), the hydrological longitudinal connectivity decreases, and the area covered with surface water is drastically reduced. The reduction of the stream flow as a consequence of seasonal drought prolongs the residence times of the water in impoundments, which favor C processing through the promotion of the interaction between OM and biological actors (Acuña and Tockner, 2010). Hence, gaseous C fluxes from impounded waters might increase during hydrological contraction (Gómez-Gener et al., 2015). Clear seasonal patterns in FCH_4 were also observed in temperate agricultural streams, with higher values in autumn and summer which were negatively correlated with stream flow (Smith and Böhlke, 2019).

5. Conclusions

Our study indicates that OM decomposition, whole-stream metabolism, and gaseous C fluxes were not completely recovered after dam removal. Tensile losses corrected by temperature and metabolic parameters in the restored reach were in an intermediate position between those obtained in the reference and impacted reaches, despite closer to the reference reach. In addition, higher CH_4 fluxes were measured in the restored reach. Among other factors, a possible explanation for these observations is that not enough time passed since the restoration action which led to an incomplete recovery of riparian vegetation (affecting light availability and water temperature) and the presence of remaining materials that sedimented over the time that the dam operated. Moreover, in addition to great variations across seasons regarding the evaluated ecosystem functions, there were significant differences among reaches within seasons for metabolic parameters and gaseous C concentrations and fluxes. This was likely due to uneven variations in hydromorphological and physicochemical features of the studied reaches across seasons which adds complexity to stream management. These effects need to be considered in restoration interventions in which the values of functional indicators in reference and impacted reaches can be compared with those in restored reaches and a natural seasonal fluctuation is expected. Finally, while the effectiveness of dam removal is often gauged by responses in physical features and biodiversity, important aspects of the ecological and environmental benefits of these strategies may be detected more effectively by monitoring ecosystem processes. Rates of OM decomposition, metabolic parameters, and gaseous C fluxes hold great potential to be incorporated in the set of response variables monitored to offer a comprehensive assessment of stream restoration effectiveness.

CRediT authorship contribution statement

João Miguel Merces Bega: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Davi Gasparini Fernandes Cunha:** Writing – review & editing, Validation. **Margarita Menéndez López:** Writing – review & editing, Supervision, Methodology, Investigation. **Alba Camacho-Santamans:** Writing – review & editing, Investigation, Data curation. **Daniel von Schiller:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176672.

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