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Effects of water abstraction on stream ecosystem functioning

Maite Arroita Azkarate

PhD Thesis

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Cover photo: Ugalde diversion scheme in the Añarbe Stream (Navarre), by Arturo Elosegi.

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CONTENTS

Summary

Water abstraction is a prevalent impact in streams and rivers worldwide, likely to further increase in the future to respond to the escalating demand for water, food and energy. Reduced discharge derived from water abstraction decreases the availability of instream habitats, can degrade water quality and affects fluvial communities. There is less information on the effects of water abstraction on stream ecosystem functioning, even though impacts are likely since all hydraulics, channel morphology and biodiversity are tightly linked to ecosystem processes. This dissertation explored the effects of water abstraction on stream ecosystem functioning, combining observational and manipulative, field and laboratory experiments.

We first assessed the impact of water abstraction on the storage and breakdown of coarse particulate organic matter by comparing these variables in reaches upstream and downstream from five low dams in mountain streams, and repeating the experiment in winter and in spring. Water abstraction did not affect water quality, but significantly reduced the width and depth of the wetted channel in both experiments, as well as the storage and breakdown of organic matter in winter. The number of shredders colonizing litter bags was also significantly lower in downstream reaches. These results point to an important effect of water abstraction on the storage and breakdown of organic matter in streams at least in some periods, which could impact the energetic basis of stream ecosystems.

Because the previous study was limited to surface organic matter breakdown and aquatic organisms have been shown to seek refuge in the hyporheos when stream channel dries out, we also analyzed the relative contribution of the hyporheic breakdown when the surface of the wetted channel is reduced and organic matter gets stranded in emerged sediments. We measured microbial and total breakdown rates of organic matter both on the surface and in the subsurface of the permanently wet channel and the parafluvial areas. Breakdown rates in all buried litter bags were very similar to the ones in the surface of the wet channel, showing that subsurface layers sustain breakdown activity even when the surface of benthos has dried out, a common feature of reaches impacted by abstraction.

Additionally, water abstraction can alter not only the frequency and severity of drying events, but also their timing, which could affect aquatic communities and processes showing marked temporal dynamics. Therefore, we studied how the degree of drought-related stress affects fungal activity and microbial decomposition, and whether the impacts depend on the timing of stress. In microcosms we recreated areas with flowing water,

stagnant water and dry beds. Combining these conditions and their sequence, we created 9 treatments (10 with the control) that differed in the stress level (low, medium, high) and the timing of peak stress (early, middle, late) and measured fungal biomass, sporulation, microbial respiration and decomposition of alder disks. The effects of drought-related stress levels were not consistent among response variables, which probably reflects that we recreated a small stress range. However, the effects of disturbances were systematically more detrimental in early stages of the decomposition process, and resulted in a lower fungal biomass and activity, and reduced litter decomposition. These results suggest that the effects of stress on breakdown-associated variables depend not only on the intensity and duration of stress, but also on its timing, early stress exerting greater impact than late stress on breakdown.

Finally, we experimentally abstracted water from a headwater mountain stream by putting in operation a long-unused diversion scheme and followed a Before-After/Control-Impact design in order to assess the effects of abstraction on biofilm biomass and activity, nutrient retention, and retention and breakdown of organic matter. Moreover, results were analyzed at the patch (i.e. per square meter) and the reach (i.e. per lineal meter) scales to determine which is the most meaningful way to measure the impact of water abstraction. At the patch scale abstraction reduced the biomass and the exoenzyme activity of biofilm, and the uptake of nutrients. At the reach scale all variables except benthic chlorophyll-*a* and leaf retention were significantly reduced by abstraction, as a consequence of the reduced surface of the wetted channel. Our results suggest that water abstraction has strong impacts on stream ecosystem functioning, being mainly associated to decreased wetted perimeter, which is a universal consequence of water abstraction.

Despite some spatial and temporal constraints, overall, this dissertation showed diversion schemes in the Basque Country to significantly reduce the rates of diverse key processes of stream ecosystem functioning. Therefore, our results cast doubt on the adequacy of the environmental flows, at least in our region, and reveal the urgent need of further investigation to address all the open questions, and develop and improve water abstraction practices that will effectively integrate human and ecosystem water needs in a timely and comprehensive manner.

Laburpena

Ur-detrakzioa mundu osoan zehar oso hedatuta dagoen jarduera da, handitzen jarraitzen duen ur-, jaki- eta energia-eskariari erantzuteko etorkizunean gehiago areagotzea espero dena. Ur-detrakzioak tarteko emari txikitzeak habitat lotikoen eskuragarritasuna murrizten du, uraren kalitatea andea dezake eta, ondorioz, ibaietako komunitateak kaltetu. Ur-detrakzioak ibaien funtzionamenduaren gainean dituen eraginei buruz, berriz, oso ezagumendu urria dugu, nahiz eta inpaktuak espero izatekoak diren, hidraulika, ubidearen morfologia eta biodibertsitatea estuki lotuta baitaude ibai-ekosistemetan gertatzen diren prozesuekin. Tesi honetan ur-detrakzioak ibai-ekosistemen funtzionamenduan duen eragina aztertu da, horretarako behaketa hutsetan oinarritutako lanak eta ekosistemen manipulazioak, laborategiko eta mendiko esperimentuak konbinatuz.

Hasteko, ur-detrakzioak ibai-ekosistemetako materia organikoaren metatze eta deskonposizioan duen eragina aztertu genuen, aldagai hauek alderatuz bost errekatako presetatik gorako eta beherako erreka-tarteetan, neguan eta udaberrian. Ur-detrakzioak ez zion ur-kalitateari eragin, baina adierazgarriki murriztu zituen ubide hezearen zabalera eta uraren sakonera bi esperimentuetan, eta, neguan, baita materia organikoaren metaketa eta deskonposizioa ere. Orbel-poltsak kolonizatu zituzten zatitzaileen kopurua ere txikiagoa zen presen azpian. Emaitza hauek adierazten dute, sasoi batzuetan behintzat, ur-detrakzioak eragin garrantzitsuak izan ditzakeela materia organikoaren metaketan eta deskonposizioan. Honek, era berean, ibai-ekosistemen oinarri energetikoa kalte dezake.

Aurreko ikerketa bentoseko deskonposiziora mugatu zenez eta ibaiak lehortu ahala organismo urtarrek babesa hiporreosean bilatzen dutenez, hiporreoseko deskonposizioaren garrantzi erlatiboa aztertu genuen, ibaien perimetro hezea txikitu eta materia organikoa sedimentu lehorretan pilatzen denean. Materia organikoaren deskonposizio-tasa mikrobiarrak eta guztizkoak neurtu genituen ubide hezeko eta gune paraflubialetako gainazalean eta azpi-geruzetan. Lurperatutako orbel-poltsa guztietako deskonposizio-tasak ubide hezeko gainazalean neurtutakoen oso antzekoak ziren. Hortaz, emaitzek erakusten dute azpi-geruzetan deskonposizio-jarduera manten daitekeela baita, ur-detrakzioak eragindako ibai-tarteetan gertatzen den bezala, bentoseko gainazala lehortzen denean ere.

Bestalde, lehorteen intentsitatea eta maiztasuna areagotzeaz gain, ur-detrakzioak lehorte-uneak ere asalda ditzake eta honek eragin garrantzitsuak izan ditzake dinamika tenporal markatuak dituzten ibai-ekosistemetako komunitate eta prozesuetan. Hortaz, lehorteekin erlazionaturiko estres-mailak onddo urtarren jardueran eta deskonposizio mikrobiarrean duen eragina aztertu genuen, eta baita eragina estres-unearen araberakoa den ere.

Laborategiko mikrokosmosetan ur-lasterrak, putzu isolatuak eta sedimentu lehorrak birsortu genituen. Egoera hauek eta euren segida konbinatuz 9 tratamendu sortu genituen (kontrolarekin 10), estres-mailan (txikia, ertaina, handia) eta estres-unean (hasieran, erdian, amaieran) desberdin zirenak, eta onddo urtarren biomasa, esporulazioa, arnasketa mikrobiarra eta haltz-hostoen deskonposizioa neurtu genituen. Aldagai desberdinek ez zioten era berean erantzun estres-mailari, ziurrenik estres-tarte txikiegia birsortu genuelako. Aitzitik, estresaren eragina sistematikoki kaltegarriagoa zen deskonposizio-prozesuaren hasieran gertatzean, eta aldagai guztiak murriztu zituen. Beraz, emaitzek erakusten dute deskonposizioarekin erlazionaturiko aldagaietan larriagoak direla estres goiztiarraren ondorioak eta iradokitzen dute estres-unea estresaren intentsitatea eta iraupena bezain garrantzitsua izan daitekeela.

Azkenik, aspaldi utzitako presa bat berrabiaraziz eta emariaren %90 deribazio-kanalera desbideratuz, BACI (Before-After/Control-Impact) esperimentu bat burutu genuen ur-detrakzioaren eragina aztertzeko biofilmaren biomasan eta jardueran, mantenugai-atxikimenduan, eta materia organikoaren atxikimenduan eta deskonposizioan. Horrez gain, emaitzak azalera unitateko eta metro linealeko aztertu genituen, ur-detrakzioaren eraginak neurtzeko modurik esanguratsuena zein den zehazteko. Azalera unitateko, ur-detrakzioak biofilmaren biomasa, jarduera entzimatikoa eta mantenugai-atxikimendua murriztu zituen. Metro linealeko, berriz, ubide hezearen perimetroa txikitzearen ondorioz, ur-detrakzioak adierazgarriki murriztu zituen aldagai guztiak, salbu klorofila-kontzentrazioa eta orbel atxikimendua. Gure emaitzek iradokitzen dute ur-detrakzioak inpaktu garrantzitsuak dituela ibai-ekosistemen funtzionamenduan, bereziki perimetro hezea txikitzearekin erlazionatuta daudenak, ur-detrakzioaren ondorio unibertsala dena.

Oro har, zenbait muga espazial eta tenporal alde batera utzita, tesi honetako emaitzek erakutsi dute Euskal Herriko detrakzio-jarduerek adierazgarriki murrizten dituztela ibai-ekosistemetako hainbat prozesu esanguratsu. Hortaz, zalantzan jartzen dute emari ekologikoen egokitasuna, gutxienez gure eskualdean, eta agerian uzten dute ikertzen jarraitzeko beharra, erantzunik gabe dirauten galderei erantzuteko, eta gizakiaren eta ibai-ekosistemen beharrizanak eraginkorki integratuko dituzten detrakzio-ereduak garatzeko.

Resumen

La detracción de agua es un impacto prevalente en ecosistemas fluviales de todo el mundo, siendo probable que aumente aún más para responder al incremento de la demanda de agua, alimentos y energía. La reducción del caudal derivada de la detracción de agua disminuye la disponibilidad de hábitats lóticos, puede degradar la calidad del agua y afectar a las comunidades fluviales. Aun así, y a pesar de que es esperable que haya impactos porque la hidráulica, la morfología del cauce y la biodiversidad están estrechamente ligadas a los procesos ecosistémicos, se tiene un conocimiento menor sobre los efectos de la detracción de agua en el funcionamiento de los ríos. En esta tesis se estudian los efectos de la detracción de agua en el funcionamiento de los ecosistemas fluviales, combinando experimentos observacionales y manipulativos, de campo y de laboratorio.

Comenzamos evaluando el impacto de la detracción de agua en la acumulación y descomposición de materia orgánica, comparando estas variables en tramos aguas arriba y aguas abajo de cinco presas, en invierno y en primavera. La detracción de agua no afectó a la calidad del agua, pero redujo significativamente la anchura del canal mojado y la profundidad de la columna del agua en los dos experimentos, así como la acumulación y la descomposición de materia orgánica en invierno. El número de fragmentadores colonizando las bolsas de hojarasca fue menor debajo de las presas. Estos resultados un efecto importante de la detracción sobre la acumulación y la descomposición de materia orgánica al menos en algunos periodos, lo que podría impactar la base energética de los ecosistemas fluviales.

Dado que el estudio previo se limitó a la descomposición de materia orgánica superficial y que los organismos acuáticos buscan refugio en el hiporreos cuando los ríos se secan, también analizamos la contribución relativa de la descomposición hiporreica cuando la superficie del canal mojado se reduce y la materia orgánica se acumula en sedimentos expuestos al aire. Para ello, medimos la descomposición de materia orgánica microbiana y total en la superficie y en la subsuperficie del canal mojado y de zonas parafluviales. Las tasas de descomposición en todas las bolsas de hojarasca enterradas eran muy similares a las medidas en la superficie del canal mojado, mostrando que la subsuperficie mantiene actividad descomponedora incluso cuando la superficie del bentos se seca, característica común de los tramos de río afectados por la detracción.

Además de aumentar la intensidad y la frecuencia de eventos de sequía, la detracción de agua también altera su temporalidad, lo que podría afectar a comunidades y procesos que tienen dinámicas temporales marcadas. Por lo tanto, estudiamos cómo afectan distintos

grados de sequía a la actividad de los hongos acuáticos y a la descomposición microbiana, y si los efectos dependen de la temporalidad del estrés. En microcosmos, recreamos áreas con corriente, pozas aisladas y lechos secos. Combinando estas condiciones y su secuencia, creamos 9 tratamientos (10 con el control) que diferían en el grado de estrés (bajo, medio, alto) y en su temporalidad (inicio, medio, final), y medimos la biomasa fúngica, la esporulación, la respiración microbiana y la descomposición microbiana de discos de aliso. Las distintas variables no respondieron consistentemente al grado de estrés, lo que probablemente refleja que se recreó un rango de estrés demasiado pequeño. Sin embargo, los efectos fueron sistemáticamente más perjudiciales cuando el estrés ocurría en la fase inicial de la descomposición, reduciendo la biomasa de los hongos, su actividad, y la descomposición microbiana. Estos resultados sugieren que la temporalidad del estrés puede ser tan importante como su duración y su frecuencia a la hora de determinar los impactos sobre las variables asociadas a la descomposición de la materia orgánica.

Finalmente, detrajimos agua experimentalmente de un río de cabecera poniendo en marcha una presa de derivación abandonada, y mediante un experimento BACI (Before-After/Control-Impact) estudiamos los efectos de la detracción de agua en la biomasa y actividad del biofilm, en la retención de nutrientes, y en la retención y descomposición de materia orgánica. Adicionalmente, analizamos los resultados por unidad de superficie y por metro lineal, con el objeto de determinar cuál es la manera más representativa para evaluar los efectos de la detracción. Por unidad de superficie, la detracción de agua redujo la biomasa del biofilm, su actividad exoenzimática y la asimilación de nutrientes. Por metro lineal, todas las variables, excepto la concentración de clorofila-*a* y la retención de hojarasca, fueron reducidas significativamente por la detracción, a causa de la reducción de la superficie del canal mojado. En consecuencia, nuestros resultados sugieren que la detracción de agua tiene impactos importantes en el funcionamiento de los ecosistemas fluviales, principalmente asociados a la reducción del perímetro mojado, consecuencia universal de la detracción.

A pesar de las limitaciones espaciales y temporales, en general, los resultados obtenidos en esta tesis mostraron que las prácticas de detracción en el País Vasco reducen significativamente las tasas de procesos ecosistémicos cruciales. Por lo tanto, ponen en duda la suficiencia de los caudales ecológicos, al menos en nuestra región, y manifiestan la necesidad urgente de seguir investigando para responder a todas las incógnitas abiertas y desarrollar prácticas de detracción que integren eficazmente las necesidades de agua humanas y de los ecosistemas fluviales.

CHAPTER 1

General introduction

Water consumption, a rising environmental problem

A changing planet

The demographic and industrial development during the 20th century led to an accelerated increase in the demand of energy, water and other materials (Steffen et al. 2007), to the point that some of the boundaries for the resilience and sustainability of our planet seem to have been trespassed (Rockström et al. 2009; Steffen et al. 2011). The vast extent of these transformations led to proposing that a new geological epoch has begun, namely the Anthropocene (Crutzen 2002; Zalasiewicz et al. 2011), in which humans are the dominant geophysical force shaping the earth surface and determining the sedimentary record (Vitousek et al. 1997; Foley et al. 2005). The Anthropocene is characterized by a dramatic increase in the atmospheric concentration of carbon dioxide and methane, in global temperature, in erosion and the denudation of the continents, in sea level, together with accelerated extinctions and biotic population declines, which, overall, result in a distinctive stratigraphic signal (Crutzen & Stoermer 2000). Some scientists consider it started during the Industrial Revolution, in the latter part of the eighteenth century, whereas others link the beginning of the epoch to the Neolithic Revolution, closely synchronous with the Holocene, around 12,000 years BP (Zalasiewicz et al. 2008). Although it has not been formally established by the International Commission on Stratigraphy and there is still no consensus on the starting date, it is irrefutable that human activities are drastically changing the environment (Vitousek 1994; United Nations Environment Programme 2007), these changes affecting every ecosystem on Earth (Millennium Ecosystem Assessment 2005).

Streams and rivers are among the most threatened ecosystems on Earth (Vörösmarty et al. 2010; Dudgeon 2013). They are complex and dynamic ecosystems that comprise not only the wetted channel, but also the floodplain, the riparian zone and the hyporheic zone (Sabater et al. 2009), and host a large biodiversity (Naiman & Décamps 1990; Meyer et al. 2007), including, among others, microorganism (e.g. bacteria, fungi, protozoa), algae, macrophytes, invertebrates and fish (Sabater et al. 2009). The main threats for streams and rivers and the biodiversity linked to them encompass degradation of the drainage basing by urbanization, agriculture or changes in vegetation cover, pollution, non-native species and climate change, which often act in concert (Dudgeon 2013). In addition, freshwater ecosystems are highly over-exploited, as the humanity makes extensive use of the resources they offer, such as freshwater, hydropower or fisheries. In many regions, water consumption even exceeds water availability (Sabater 2008), a situation that can only be maintained through extensive water transfers from other regions. As a consequence, the global water system has been transformed (Vörösmarty et al. 2004) with dams, diversion schemes, extensive waterways and systems for groundwater abstraction (Acreman et al. 2000; Poff & Hart 2002; Zarfl et al. 2015). Therefore, regulation and abstraction of water are prevalent impacts in freshwater ecosystems (Nilsson et al. 2005).

Water consumption on the rise

Nowadays, around 15% of the world's total runoff is retained in large dams (>15 m in height; Nilsson et al. 2005) and a further amount is directly diverted from streams and rivers by means of low weirs or other abstraction schemes (Vörösmarty & Sahagian 2000). According to the World Bank (2014a), 3,906.7 km^3 were withdrawn worldwide in year 2013, not counting evaporation losses from storage basins. Although this volume is only the 0.0003% of our planet water volume, it represents 10% of the global renewable freshwater resources and almost twice as much as the amount of water in rivers (Sabater & Elosegi 2009). Besides, there are large differences among countries (Fig. 1; FAO 2015a): abstraction is below 1.5% of water availability in Russia and many countries of South America (e.g. Brazil, Colombia and Bolivia) and central Africa (e.g. Gabon, Uganda, Democratic Republic of the Congo and Angola), ranges from 5% to 30% in the United States and many European countries (e.g. Spain, France, Germany and Poland), and reaches extreme values in countries such as Libya (615%), Saudi Arabia (936%) and United Arab Emirates (1,867%).

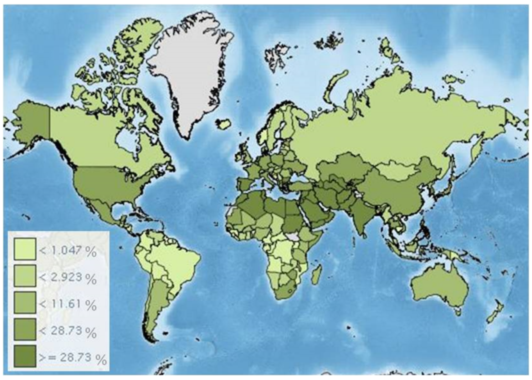

Figure 1. Percentage of renewable water resources withdrawn per country. From FAO 2015a.

Flow regulation and water abstraction are likely to increase even more in the near future, driven by the everlasting escalating demand −especially for irrigation and hydropower−, as well as to prevent and face global climate change (Poff et al. 2003; Palmer et al. 2008; Finer & Jenkins 2012). Worldwide, the surface of irrigated lands has doubled during the last 5 decades (Fig. 2; Gleick 2003; FAO 2009) due to the expansion of high-yielding crops that depend on irrigation and mechanization. Nowadays, the area under irrigation exceeds even the 75% of the arable land in semiarid regions such as the Mediterranean (Seibert et al. 2006), and future projections forecast further expansion to counterbalance rising temperatures (Gibelin & Déqué 2003), altered seasonality (Sánchez et al. 2004) and enhanced torrentiality (Räisänen et al. 2004).

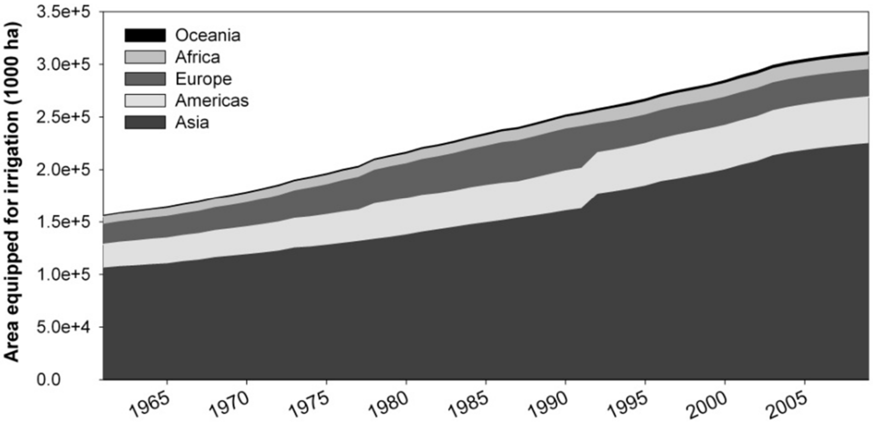

Figure 2. Irrigated area per each continent from 1960 to 2010. From FAO 2009.

Similarly, the use of water for hydropower is also expected to increase. Nowadays, more than 1.4 billion people still lack access to electricity, especially in rural Sub-Saharan Africa and Southern Asia, and the per capita demand of the rest is rising (UNEP 2012a). Therefore, securing the future energy demand and closing the electricity access gap are considered essential goals set for the society (Crousillat et al. 2010; UN-Energy 2010). However, the present global energy system is based on fossil fuels such as oil, coal and gas, which are limited resources unevenly distributed in the planet. In addition, they have detrimental environmental consequences, energy production and conversion accounting for 29% of global greenhouse gas emissions and, thus, being one of the main causes of global climate change (UNEP 2012b). In consequence, countries are required to meet their growing energy demand through the use of Kyoto-compliant energy resources (UNEP 2012a). Accordingly, new initiatives in the development and implementation of renewable energy sources are now under way. For instance, the 2009/28/CE Directive of the European Parliament and Council, part of the European 2020 climate and energy package, established that renewable energies must represent 20% of the gross energy consumption in the European Union. In the particular case of Spain, these politics resulted in a considerable increase in the use of renewable energy sources: they accounted for 6.3% of the primary energy consumption in 2004, for 11.3% in 2010 and are aimed at accounting for 20% by the end of 2020 (PER 2011-2020). Although renewable energy sources are very diverse, hydropower is notably prevalent, especially in countries with a large water availability, where it can produce more than 80% of the electricity requirements (Fig. 3; The World Bank 2014b).

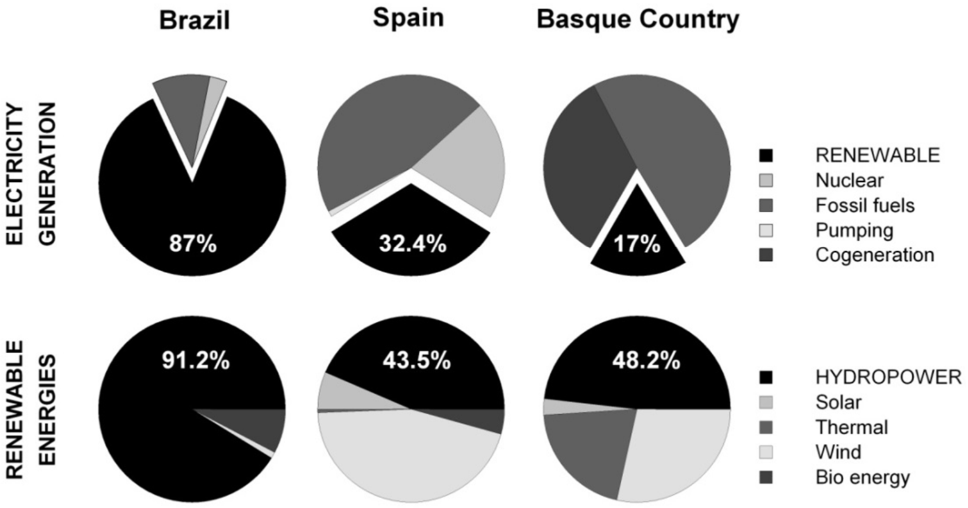

Figure 3. Sources of electricity generation in Brazil, Spain and the Basque Country (top). Contribution of each type of renewable energy sources to the electricity generated with renewables in Brazil, Spain and the Basque Country (bottom). Data provided by the International Energy Agency 2015, PER 2011-2010 and EVE 2013.

A dammed world

Overall, this situation led to a boom in infrastructures to retain, divert and abstract water from streams and rivers, especially reservoirs and conventional diversion schemes (also called run-of-the-river). Nowadays, there are ca. 45,000 large dams (>15 m in height) and over 800,000 low dams, retaining, as mentioned, over 15% of the world's total runoff (Nilsson et al. 2005) as well as 20% of the global sediment flux (Syvitski et al. 2005). Besides, at least 3,700 major dams are either planned or under construction primarily in countries with emerging economies, which will reduce the global number of remaining free-flowing large rivers by about 21% (Fig. 4; Zarfl et al. 2015). The main characteristic of dams is their capacity to regulate downstream flow, modifying the quantity, timing and variability of stream discharge (Poff & Allan 1995). Moreover, they retain all bedload and a large fraction of the suspended load (Vericat & Batalla 2006; Tena et al. 2011), thus promoting bed armoring and channel incision downstream (Brandt, 2000). They also affect water temperature (Olden & Naiman 2010) and chemistry (Friedl & Wüest 2002), as well as the growth, survival, dispersal and reproduction of native plants, macroinvertebrates and fish (Jansson et al. 2000; Santos et al. 2004; Mueller et al. 2011), altering the structure of riverine communities downstream from dams (Ward et al. 1999; Nilsson & Svedmark 2002; Martínez et al. 2013a). All these changes have been shown to affect stream ecosystem functioning, decreasing organic matter breakdown (Mendoza-Lera et al. 2012), increasing net nitrogen uptake capacity (von Schiller et al. 2015), and

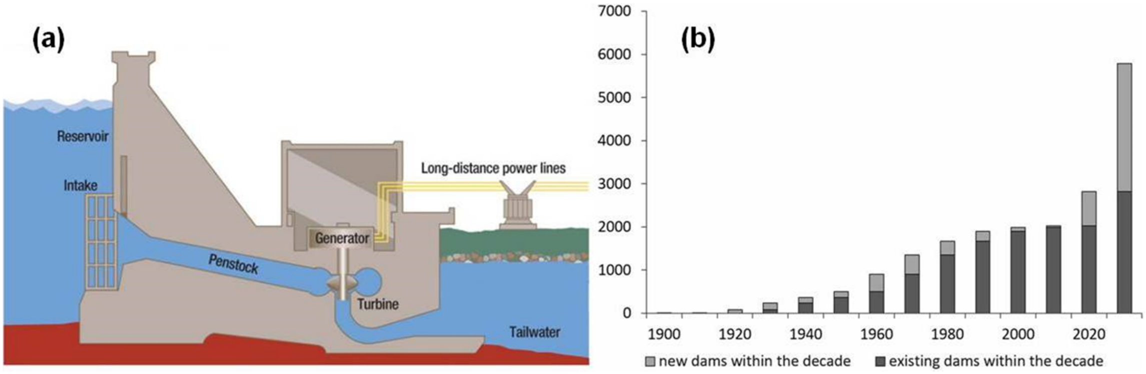

Figure 4. (a) Schematic picture of a reservoir. (b) Global pace of hydropower dam construction of existing hydropower dams (Lehner et al. 2011) and outlook for hydropower dams which are under construction or planned. Note that this compilation focuses on dams designed only for hydropower production, excluding dams designed primarily for water supply, flood prevention, navigation, recreation and very small hydropower dams. From Zarfl et al. 2015.

enhancing both biofilm (Ponsatí et al. 2014) and whole ecosystem metabolism (Aristi et al. 2014).

Diversion

Diversion or run-of-the-river schemes consist of a weir or dam that can provide little or no water storage and a canal that diverts water to nearby crops or a hydropower plant located some distance below (Fig. 5). Because these infrastructures are less impressive than large reservoirs, their effects have traditionally been perceived as less dramatic. Indeed, there is not such a detailed record as for large dams, although this type of scheme is extremely frequent in the world (Zarfl et al. 2015), even in small streams, where it can divert most of the water from the by-passed reaches (Arroita et al. 2015). For instance, in the Province of Gipuzkoa, the 22% of stream reaches are by-passed, a number that rises to 71.9% in extreme cases (Table 1; PGG 2006). Similarly to large dams, the number of diversion schemes is expected to increase in the future (FAO 2015b).

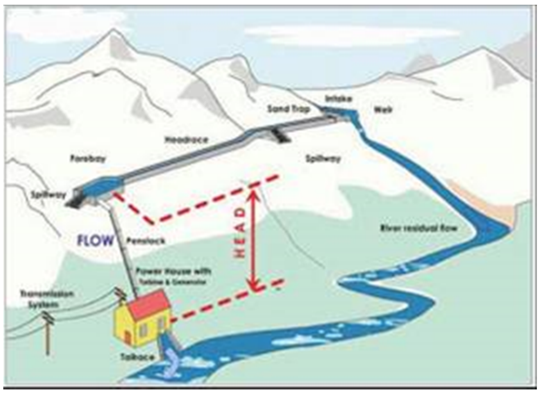

Figure 5. Schematic picture of a diversion or run-of-the-river scheme.

Table 1. By-passed and impounded stream length in streams from the Province of Gipuzkoa. From PGG 2006.

Stream	Stream length (m)	By-passed length (%)	Impounded length (%)
Amundarain	13,246	25	0
Añarbe	16,970	71.9	1.2
Aramaio	11,265	2.3	0.3
Arantzazu	14,792	64.7	5.9
Araxes	13,249	36.9	0
Berastegi	15,061	1.5	0.4
Deba	59,671	2.5	3.1
Leitzaran	31,601	70	4.1
Oiartzun	20,030	16.5	0.2
Oñati	15,531	10.9	4.8
Oria	77,254	7.6	5.3
Urola	64,221	10.6	3.4
Urumea	33,520	41.5	14.2
TOTAL	386,410	22.2	4.2

Water abstraction and river ecosystems

Although the overall impacts of water diversion could be important due to its prevalence, according to the literature published, this topic seems to have called relatively small attention among scientists. A search in Science Direct for articles with the terms "water abstraction" or "water diversion" in either the title, key words or abstract, published between 2005 and present yielded a total of 701 articles. Out of the 100 most relevant articles (ranked by Science Direct), 28 focused on water supply, mainly for drinking but also for irrigation or bathing. Most of these works analyzed the management of Chinese South-to-North Water Diversion Project, a huge project aiming to divert 44.8 km^3 from the Yangtze River in southern China to the more arid and industrialized north (http://www.nsbd.gov.cn/zx/english/). Other 28 articles were classified in the category “others”, most of them studying water diversion as a restoration tool for wetlands and estuaries, mainly in China and Louisiana. The next most abundant articles were the ones analyzing the effects of water abstraction on hydrogeomorphology (20). 12 of the studies assessed the impacts of abstraction on biological communities, including microorganisms, invertebrates, fish and the riparian vegetation. Only a small minority dealt with water quality (9) and ecosystem processes (3).

When assessing the impacts of human activities on ecosystems, one can look at either structural or functional aspects. Ecosystem structure refers to the scenario and the actors: the abiotic attributes that characterize the scenario, and the qualitative and quantitative composition of biological communities (e.g. channel morphology, water quality and invertebrate community composition; Gessner & Chauvet 2002; Sabater & Elosegi 2009). Ecosystem functioning refers to biophysical processes, which are determined by both abiotic attributes and organisms. These biophysical processes are diverse, including, among others, litter retention and decomposition (Pozo et al. 1998; Robinson & Gessner 2000; Larrañaga et al. 2003), secondary production of macroinvertebrates (Wallace et al. 1997), enzymatic activity of biofilms (Sabater et al. 1998; Hill et al. 2000; Romaní & Marxsen 2002), nutrient retention (Mulholland et al. 1985; Peterson et al. 2001; Arce et al. 2014), and ecosystem metabolism (Young & Huryn 1999; Mulholland et al. 2001; Uehlinger 2006). They change at different spatial and temporal scales, from individual components (e.g. biofilm metabolism, Ponsatí et al. 2014) to the whole ecosystem (e.g. stream metabolism, Aristi et al. 2014) and from a few hours (e.g. organic matter retention, Larrañaga et al. 2003) to years (e.g. wood decomposition, Díez et al. 2002). Besides, processes respond to environmental changes specifically (Bunn & Davies 2000; Young et al. 2008). For instance, organic matter retention is affected by channelization but not by eutrophication; organic matter breakdown is affected by eutrophication but not by channelization; and nutrient retention is affected by both (Elosegi & Sabater 2013). Moreover, they are key drivers of ecosystem services essential for the societal welfare (Costanza et al. 1997; Sweeney et al. 2004), ecosystem functioning being nowadays one of the main goals of freshwater ecosystems (Boulton 1999).

Impacts on ecosystem structure

Water abstraction reduces discharge up to the point that it can convert perennial streams into intermittent, which strongly reduces their longitudinal connectivity (Malmqvist & Rundle 2002). Indeed, although most abstraction schemes have set environmental flows, these are often close to disrupting the superficial flow and shrinking the channel into a series of isolated pools (Arroita et al. 2015). Even when it is not so dramatic, reduction in discharge results in a contraction of river ecosystems, decreasing the surface and quality of instream habitats (Stanley et al. 1997). Therefore, water abstraction can exacerbate the effects of global climate change, affecting the occurrence, the severity, the frequency and also the timing of drying events (Milly et al. 2005; IPCC 2014). Abstraction by low dams can also alter water quality, increasing temperature (Meier et al. 2003, Bae et al. 2015) and pH (Rader & Belish 1999; McIntosh et al. 2002) and decreasing dissolved oxygen concentration (James et al. 2008). Changes in water physico-chemical properties are even more accentuated in isolated pools, which enhance the accumulation of organic matter as well as the concentration of nutrients and potentially toxic leachates, increase water temperature and often result in hypoxia (Lake 2003; Canhoto & Laranjeira 2007). Although these conditions are detrimental for most organisms (Acuña et al. 2005; Foulquier et al. 2014), it must be noted that isolated pools, together with the hyporheos, can constitute an important refuge for communities and processes when most of the discharge is being diverted. Indeed, during strong abstraction, many benthic invertebrates move to the remaining pools where they can accumulate in large densities (Dewson et al. 2007a; Verdonschot et al. 2015), enter the hyporheos (Stanley et al. 1994; Stubbington 2012), or alternatively, they can abandon the reach through drift (James et al. 2008). Water abstraction also affects biofilms (Mosisch 2001) and the reproduction, condition and growth of fish (Magoulick & Kobza 2003), forcing many fish to migrate downstream (Keaton et al. 2005), and thus, affecting fish communities (Xenopoulos et al. 2005; Benejam et al. 2010, 2014). Diversion schemes include other impacts, such as barriers to dispersal (Nislow et al. 2011) or drowning of both aquatic and terrestrial organisms in diversion canals (Benstead et al. 1999; Roberts & Rahel 2008), thus threatening biodiversity within the hydrographic network.

Impacts on ecosystem functioning

Contrasting with the studies on ecosystem structure, there is relatively little information on the effects of abstraction on ecosystem functioning (but see Dewson et al. 2007b), even though impacts are likely since all hydraulics, channel morphology and biodiversity are tightly linked to ecosystem processes (Gücker & Boëchat 2004; Elosegi et al. 2011; Elosegi & Sabater 2013; Hall et al. 2002). The retention, storage (Pozo et al. 1997) and breakdown (Gessner & Chauvet 2002) of allochthonous organic matter are key processes on which stream ecosystem productivity depends (Tank et al. 2010; Wallace et al. 1997), especially in streams running through forested catchments (Webster & Benfield 1986; Abelho 2001) where shading by the riparian vegetation limits primary production (Vannote et al. 1980; Wallace et al. 1999). Indeed, detritic organic matter forms the energetic basis of complex food webs (Hall et al. 2000; Woodward 2009) and modulates important ecosystem processes such as nutrient retention and stream metabolism (Crenshaw et al. 2002). In low order streams, organic matter is mainly constituted by leaf litter (Abelho 2001), which gets into the stream channel through vertical or lateral inputs (Webster & Meyer 1997). Retention and storage of organic matter entering streams control the availability for aquatic organisms (Bilby & Likens 1980) and can be strongly affected by water abstraction. On the one hand, dams of all size, from debris dams and low weirs to large dams, can trap organic matter (Flores et al. 2011; Gurnell 1998; Sanchez-Vidal et al. 2013) and thus, reduce inputs into downstream reaches. On the other hand, water abstraction reduces discharge and slows down current velocity, which can promote retention and accumulation of organic matter (e.g., Brookshire & Dwire 2003; Dewson et al. 2007b).

Organic matter retained in streams suffers a complex set of changes until it is finally decomposed to inorganic matter, this detritus pathway being essential for recycling chemical elements and thus for sustaining life on Earth (Zimmer 2008; Gessner et al. 2010). These changes result from the complex interaction of several abiotic and biotic processes, such as leaching, mechanical abrasion, microbial degradation, and fragmentation by invertebrates (Graça 2001; Hieber & Gessner 2002), which are overlapping over time (Wantzen et al. 2008). Leaching dominates at the early stages of leaf litter decomposition and is defined as the rapid loss of soluble compounds (Bärlocher 2005a). The activity of microbial decomposer is considered one of the most important mechanisms of leaf litter decay (Gessner & Chauvet 1994), in which aquatic fungi play a predominant role (Hieber & Gessner 2002; Pascoal & Cássio 2004). Fungi rapidly colonize submerged leaves, degrade plant cell polymers (Chamier 1985) and increase the palatability of leaves for invertebrates (Graça & Canhoto 2006). Some shredding aquatic insects and crustaceans are the most common invertebrates that consume organic matter, using leaf litter as a food resource and incorporating leaf material into secondary production (Graça & Canhoto 2006; Canhoto & Graça 2008).

All these processes can be sensitive to water abstraction. In particular, lower discharge and velocity reduce abrasion (Chauvet et al. 1993; Heard et al. 1999), whereas increased temperature could accelerate chemical reactions and biological activity (Yvon-Durocher et al. 2010). Impaired fungal and/or macroinvertebrate communities could also result in slower decomposition (Death et al. 2009; Schlief & Mutz 2009). The effects of water abstraction could be especially detrimental when a large proportion of the discharge is diverted, since emersion has been shown to significantly slow down organic matter breakdown (Bruder et al. 2011). Although breakdown of organic matter is also slower in isolated pools (Schlief & Mutz 2011) as well as in the hyporheic zone (Cornut et al. 2010; Flores et al. 2013), the relative contribution of these storage zones to nutrient recycling might be relevant during these periods of strong diversion, because aquatic organisms might seek refuge in these zones keeping water.

Other processes potentially sensitive to water abstraction include biofilm activity and nutrient retention (Elosegi et al. 1995; Sweeney et al. 2004). Biofilms are complex mixtures composed of algae, bacteria, protozoa and fungi, which are embedded in a matrix of polysaccharides and other polymers (Lock et al. 1984). These organisms produce exoenzymes that cleave macromolecules derived from both autotrophic production and allochthonous inputs (Jones & Lock 1993; Chappell & Goulder 1994; Lock 1990), hydrolyzing high-molecular-weight organic compounds to low-molecular-weight molecules, which are available for microbial uptake (Chróst 1991). Therefore, biofilms play crucial roles in carbon and nutrient dynamics in stream ecosystems (Fischer 2002; Hall & Tank 2003; Allan & Castillo 2007). Indeed, biofilms significantly contribute to transforming and retaining up to 50–75% of nitrogen and 30% of phosphorous entering streams from the watershed (Peterson et al. 2001; Mulholland 2004). Likewise, nutrient and carbon retention are key determinants of resource availability for many consumer groups in forested streams, biofilms occupying a key position at the base of food webs (Reddy et al. 1999; Peterson et al. 2001; Rowe & Richardson 2001). Besides, nutrient retention is the basis of the self-purification capacity of streams and rivers, one of the most important ecosystem service provided by these ecosystems (Costanza et al. 1997). Both biofilm activity and nutrient retention can also be affected by water abstraction. Low flow decreases water depth and increases water residence time, thereby enhancing its contact with the sediments (Argerich et al. 2008), and promoting nutrient retention (Wollheim et al. 2001; Hall et al. 2002). However, reduced discharge can increase the thickness of the biofilm boundary layer, restricting the advective transport (Bishop et al. 1997) and the diffusion of molecules (de Beer et al., 1996), what can limit the renewal of nutrients and other substances within the biofilms and, thereby, reduce their activity. Additionally, less nutrients enter by-passed reaches because part of them is directly diverted together with water and, therefore, it is likely that the amount of nutrients retained in streams is reduced by abstraction. Other potential impacts of water abstraction on biofilm and, thus, on nutrient retention include the concentration of benthic invertebrates in response to the contraction of the wetted channel (Acuña et al. 2005; Dewson et al. 2007a), which could increase their grazing pressure (Hillebrand 2009).

Two important points to be considered when assessing the consequences of water abstraction on stream ecosystem functioning are the timing of the impact and the scale at which impacts are analyzed. In fact, the structure and activity of biological communities as well as ecosystem processes show marked temporal dynamics, and their sensitivity, resistance and resilience to disturbances might differ depending on their stage. Moreover, stressors like droughts have been reported to have legacy effects (Datry et al. 2011; Dieter et al. 2011, 2013; Martínez et al. 2015), suggesting impacts in early stages of a process could be more detrimental than impacts in later stages, especially for cumulative processes showing a clear succession of steps in which the last outcome integrates the entire sequence, such as organic matter decomposition. Concerning the scale at which the impacts of water abstraction are analyzed, as mentioned before, the most evident effect of abstraction is the reduction of the surface covered by water. Therefore, even if water abstraction would not affect a variable at the patch scale (i.e. measured per square meter of stream bed), it could have significant effects at the reach scale (i.e. measured per linear km of channel length), as shown by Sweeney et al. (2004) in streams narrowed due to forest clearing. Moreover, from the point of view of global change, as well as from the perspective of ecosystem services, the reach scale is more meaningful than the patch scale (Battin et al. 2009).

Objectives

This dissertation studies the effects of water abstraction on stream ecosystem functioning, by combining field and laboratory experiments. More specifically, we try to answer the following questions:

1. What are the effects of water abstraction on the storage and breakdown of organic matter?
2. What is the relative contribution of the hyporheic breakdown when the surface of the wetted channel is reduced and organic matter gets stranded in emerged sediments?
3. How does the degree of drying related stress affect fungal activity and microbial decomposition? Do impacts differ depending on the timing of stress?
4. What are the effects of water abstraction on biofilm activity and nutrient retention? What is the most meaningful way to assess these impacts?

CHAPTER 2

Impact of water abstraction on storage and breakdown of coarse organic matter in mountain streams

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Abstract

Water abstraction is a prevalent impact in streams and rivers, which is likely to increase in the near future. Because abstraction reduces discharge, the dimensions of the wetted channel and water depth and velocity, it can have strong influence on stream ecosystem functioning. Although the impacts of large dams on stream and river ecosystems are pretty well known, the effects of diversion schemes associated to low dams are still poorly understood. Furthermore, the remote location of many diversion schemes and the lack of collaboration by power companies often make it difficult to know the volume of water diverted and its environmental consequences. To assess the impact of water abstraction on the storage and breakdown of coarse particulate organic matter in streams we compared reaches upstream and downstream from five low dams that divert water to hydropower plants in mountain streams in N Spain. We measured the storage of organic matter and the breakdown of alder leaves in winter and spring, and calculated the results at the patch (i.e. per square meter of bed) and at the reach scale (i.e. per lineal meter of channel). Water diversion significantly reduced discharge, and the width and depth of the wetted channel, but did not affect water quality. Diversion reduced significantly the storage and breakdown of organic matter in winter but not in spring. The number of shredders colonizing litter bags were also significantly reduced. The results point to an important effect of water abstraction on the storage and breakdown of organic matter in streams at least in some periods, which could affect downstream reaches, global carbon fluxes, and associated ecosystem services.

Keywords: abstraction, diversion, low dam, organic matter, decomposition, ecosystem functioning

Introduction

Demographic and industrial development led to a significant increase in the demand of energy, water and other materials during the last century (Steffen et al. 2007, 2011), well beyond the boundaries for the resilience and sustainability of human activities on the planet (Rockström et al. 2009). In particular, humans have transformed the global water system (Vörösmarty et al. 2004), by building 45,000 large dams and over 800,000 low dams (Nilsson et al. 2005), in addition to extensive waterways and systems for groundwater abstraction (Acreman et al. 2000). Nowadays, in many regions water consumption is much higher than water availability (Sabater 2008), a situation that can only be maintained by means of water transfers from other basins. Regulation, diversion and abstraction of water are expected to increase in the near future in response to climate change and human population growth (Poff et al. 2003; Palmer et al. 2008; Finer & Jenkins 2012).

Water abstraction reduces flow, modifies hydrological regimes and results in a contraction of river ecosystems (Stanley et al. 1997), especially in dry periods, when most of the discharge is abstracted (James et al. 2008). Ecosystem contraction decreases the surface and quality of lotic habitats, damaging river communities (Anderson et al. 2006; James et al. 2008; Murchie et al. 2008). It also reduces the assimilation capacity of streams (Liu et al. 2005) and affects nutrient availability (von Schiller et al. 2011). Moreover, even when they are small, diversion dams can constitute an important barrier for organisms (Nislow et al. 2011), thus threatening biodiversity within the hydrographic network. There is less information on the effects of water abstraction on stream ecosystem functioning (Dewson et al. 2007b), although impacts are likely since all hydraulics, channel morphology and biodiversity are tightly linked to ecosystem processes (Hall et al. 2002; Gücker & Boëchat 2004; Elosegi et al. 2011; Elosegi & Sabater 2013). Ecosystem functioning is one of the main goals of stream and river management (Boulton 1999) and an essential driver of key ecosystem services (Costanza et al. 1997; Sweeney et al. 2004), and thus, it is crucial to understand how water abstraction affects ecosystem functioning.

Stream ecosystem functioning comprehends a variety of processes including production, retention and decomposition of organic matter, or retention and recycling of nutrients (von Schiller et al. 2008; Young et al. 2008; Elosegi et al. 2010). These processes change at different spatial and temporal scales and respond to environmental changes specifically (Bunn & Davies 2000; Young et al. 2008). Storage and breakdown of coarse organic particulate matter are among the processes susceptible to water abstraction. Dams of all size, from debris dams and beaver dams to large reservoirs, can trap organic matter (Gurnell 1998; Flores et al. 2011; Sanchez-Vidal et al. 2013) and thus, reduce inputs into downstream reaches, whereas reduced discharge can promote the accumulation of organic inputs (Brookshire & Dwire 2003; Dewson et al. 2007b). The overall balance between these two contrasting effects is unknown, and can depend on site particularities. These changes in storage of organic matter, together with other abiotic and biotic factors that are altered by water abstraction (e.g. decreased water velocities, lower oxygen concentrations or changes in macroinvertebrate communities), might reduce breakdown rates of organic matter. All these effects could have important consequences, since both storage (Pozo et al. 1997) and breakdown (Gessner & Chauvet 2002) of organic matter are key processes on which stream ecosystem productivity depends (Vannote et al. 1980; Wallace et al. 1997; Tank et al. 2010). Even if abstraction would not affect storage and breakdown at the patch scale (i.e. measured per square meter of stream bed), as it decreases the surface of stream channels (Stanley et al. 1997), it could still have an effect at the reach scale (i.e. measured per linear meter of channel), which is more meaningful at the global scale.

Therefore, it is important to assess the impact of water abstraction on storage and breakdown of coarse organic matter. In mountain streams there are major difficulties to fulfill this goal since discharge is highly variable, the abstraction points are often in remote places, and the power companies are reluctant to share information on the volume of water diverted. Also, streams can differ in their response to water abstraction depending on basin or reach characteristics, making it important to find streams under similar environmental conditions. We studied the effects of water abstraction on storage and decomposition of coarse particulate organic matter by comparing reaches located upstream and downstream from five low dams. We hypothesized that i) the impacts of water abstraction on hydraulics will affect the storage of benthic organic matter, ii) water abstraction will reduce the breakdown rates of organic matter, and iii) differences will be greater when analyzed at the reach scale than at the patch scale.

Materials and methods

Experiments were performed in five headwater mountain streams in the basins of rivers Oria and Urumea (Navarre, Spain), named here A to E (Table 1; Fig. 1). They range in altitude from 250 to 615 m a.s.l., and drain basins over schist and sandstone ranging from 2.04 to 10.59 km^2, mostly covered by native deciduous forests and rough mountain pastures, with very little or no human settlements. They all have unpolluted, low conductivity water, and human impacts are limited to free-ranging cattle. The climate is temperate humid oceanic, with rainfall over 2000 mm, evenly distributed throughout the year. Each stream is affected by a hydropower scheme, consisting of a low dam (2-5 m height) and a channel that diverts water to a hydropower plant located some km below. All dams are small and mostly filled with cobbles and gravel. Therefore, the volume of stagnant water is very small, and the residence time of water of the order of seconds, few minutes at most. Because they are old concessions, the hydropower companies are not forced to establish environmental flows, so they divert as much water as channels can carry and turbines are able to process, even completely drying the streams during low flows, except for minor filtrations in the dam and water gates.

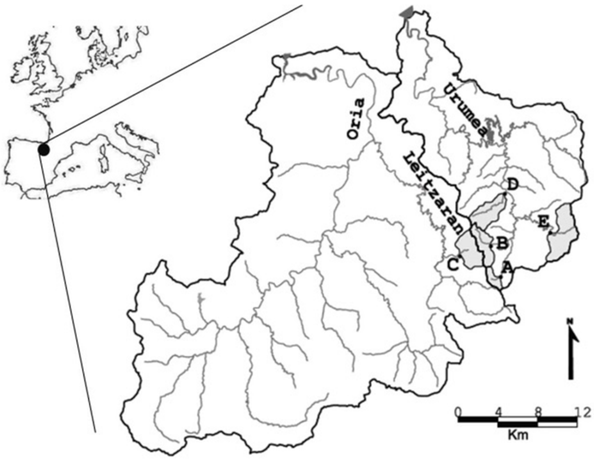

Figure 1. Study area showing the location of the 5 study sites (A to E) and the drainage basins of rivers Oria and Urumea. In gray, areas drained by the streams at the study sites. Note that the Leitzaran Stream is a tributary of the Oria River.

Table 1. Main characteristics of the five streams. Maximum diversion: maximum amount of water diverted by each hydropower; diversion length: length of the reach affected by water abstraction.

Site	Stream	Basin	Drainage area km^2	Altitude m. a.s.l.	Maximum diversion L s^{-1}	Diversion length km
A	Beriñes	Urumea	2.04	600	100	2.7
B	Sarasain	Urumea	5.04	615	500	3.5
C	Franki	Oria	6.60	590	700	1.9
D	Urdiñola	Urumea	6.96	250	800	1.4
E	Asura	Urumea	10.59	460	800	8.1

We selected two 100 m-long reaches per stream: a Control reach not affected by water abstraction immediately upstream from the pool of stagnant water retained by the dam, and an Impact reach immediately downstream from the dam. Two consecutive experiments were performed, one in winter and one in spring, to study how the effect of abstraction depends on the proportion of water diverted, and thus, on stream discharge.

On each occasion (n = 6) we measured temperature, dissolved oxygen concentration (WTW 315i), pH (Hanna Hi 9025) and conductivity (WTW 340i), and took water samples (300 mL, filtered through Whatman GF/F) for nutrient analysis. Water samples were carried to the laboratory in an ice chest and frozen at -20 ºC until analysis. Nitrate, ammonium and soluble reactive phosphorus were determined by spectrophotometry (APHA 1992). To characterize physical habitat, 10 transects were made equidistantly along each reach, where width and depth of the stream channel and water velocity (A.OTT Kempten Z30 current meter) were measured.

The amount of benthic particulate organic matter (BPOM) stored in the wetted channel was measured once per breakdown experiment. 10 Surber samples (30 x 30 cm, 1 mm mesh) were collected randomly within the wetted perimeter of each reach, washed in the field and frozen at -20 ºC until processing. Samples were later thawed, oven-dried (70 ºC, 72 h), weighed, combusted (500 ºC, 8 h) and weighed again to obtain the ash free dry mass (AFDM). Results were analyzed per surface unit (g AFDM m^{-2}) and per length unit (g AFDM m^{-1}), which were estimated multiplying the storage per surface unit with the average width of the wet channel.

To measure litter breakdown, freshly fallen black alder (*Alnus glutinosa* (L.) Gaertner) leaves were collected in autumn, air-dried at room temperature (20 ºC) to constant weight, and enclosed in labeled 5-mm mesh plastic bags (5 ± 0.05 g). Litter bags (12 per reach and experiment) were carried to the field, and tied with fishing line to metal bars or roots in the stream channels on 12th December 2011 for the winter experiment and on 28th March 2012 for the spring experiment. 5 replicates were retrieved from every reach after 2 weeks, processed to forecast the date when the bags remaining in the streams would lose 50% of the leaf mass (T_{50}), and the date of the fastest reach used to retrieve all remaining bags. Leaching was calculated in the laboratory on an additional set of five bags that were kept under water that was continuously renewed at 10 ºC for 24 h. Initial dry mass of material in the bags was corrected for leaching to exclude the effect of this site-independent chemical process. Upon retrieval, bags were stored in individual zip-lock bags and carried to the laboratory on ice. Samples were rinsed with stream water to remove invertebrates and mineral particles. AFDM of the remaining material was determined following the same procedure described above for BPOM. Breakdown rates were calculated according to the negative exponential model (Petersen & Cummins 1974).

At T_{50} invertebrates in litter bags were collected on a 500-µm sieve and preserved in 70% ethanol. Macroinvertebrates were identified to the lowest practical taxonomic level (genus in general), counted, and assigned to functional feeding group according to Merritt & Cummins (1996) and Tachet et al. (2002). The biomass of shredders was determined gravimetrically after drying animals at 70 ºC for 72 h. Results were expressed as number of invertebrates per gram of litter AFDM and mg of shredders per gram of litter AFDM.

BPOM and invertebrate data were log and log+1 transformed respectively to achieve requirements for parametric analyses. Differences in physicochemical characteristics, in physical habitat and in the amount of BPOM stored per surface and linear units were analyzed by a two-way ANOVA (Reach and Stream as fixed factors). Breakdown rates were compared by a two-way ANCOVA (breakdown rate as dependent variable, Reach and Stream as fixed factors, and time as covariable). Density and biomass of invertebrates were tested by means of a two-way ANOVA (Reach and Stream as fixed factors). To search for general differences in macroinvertebrate communities, a non-metric multidimensional scaling (nMDS) was also performed based on the Bray-Curtis dissimilarity matrix, followed by a PERMANOVA (10^6 permutations) to test the differences between reaches and among streams. These analyses were performed with abundance data at the family level. Pearson's correlation coefficients were calculated between decomposition rates and density and biomass of shredders associated to bags.

Results

The five dams diverted almost 100% of the discharge at base flow, the impacted reaches receiving water only through filtrations in the dams and floodgates, whereas the proportion of water diverted decreased as discharge increased (Fig. 2). Therefore, mean discharge ranged from 69.7 to 637 L s^{-1} in Control reaches and from 7.8 to 242 L s^{-1} in Impact reaches. On average, discharge was 2-9 times lower in Impact reaches, but even a 700-fold decrease was measured in stream C. Differences in discharge between Control and Impact reaches were statistically significant (two-way $\text{ANOVA}_{\text{Reach}}$: $F_{1,50} = 15.15$, $p < 0.0001$). Water abstraction did not affect water quality (two-way $\text{ANOVA}_{\text{Reach}}$: $p > 0.05$). Mean water temperature ranged from 9.2 to 10.5 ºC and all reaches were well oxygenated. pH and conductivity were low and did not change between Control and Impact reaches, but differed among streams (two-way $\text{ANOVA}_{\text{Stream}}$: $p < 0.05$), being higher in stream A than in the rest (post hoc Tukey test). These differences were also reflected in the concentration of nitrate, which was higher in stream A (one-way $\text{ANOVA}_{\text{Reach}}$: $F_{4,20} = 39.8$, $p < 0.0001$). Still, the concentration of nutrients was low in all five streams and similar in Control and Impact reaches (Table 2).

The decrease in discharge led to a significant reduction in the wetted perimeter of reaches affected by abstraction (Fig. 2). On average, Impact reaches were 40% narrower (two-way $\text{ANOVA}_{\text{Reach}}$: $F_{1,454} = 167.3$, $p < 0.0001$) and 35% shallower (two-way $\text{ANOVA}_{\text{Reach}}$: $F_{1,453} = 53.99$, $p < 0.0001$), and water velocity was 34% slower (two-way $\text{ANOVA}_{\text{Reach}}$: $F_{1,48} = 9.08$, $p = 0.004$). In extreme cases, reductions of 70%, 75% and 90% were observed, respectively (Table 2).

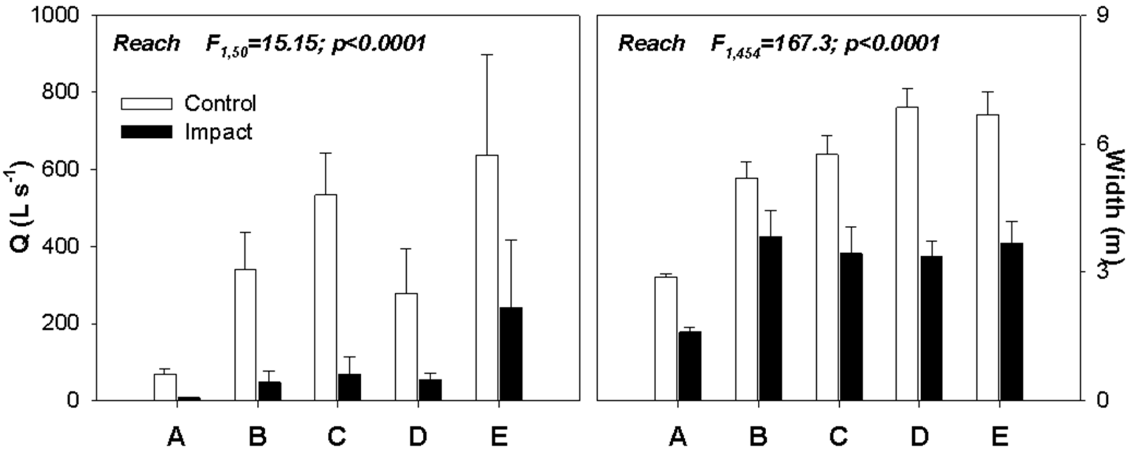

Figure 2. Discharge (left) and width (right) measured in Control and Impact reaches of the five streams during both experiments. Error bars show SE. Results from two-way (Stream x Reach) ANOVA are also shown.

Table 2. Mean ± SE of the physicochemical variables measured in Control (C) and Impact (I) reaches of the five streams during both experiments. (v = velocity; T = temperature; O_2 = dissolved oxygen concentration; Conduc. = conductivity; [NO_3^-] = nitrate concentration; [NH_4^+] = ammonium concentration; [PO_4^{-3}] = phosphate concentration).

STREAM	**A**		**B**		**C**		**D**		**E**	
REACH	**C**	**I**	**C**	**I**	**C**	**I**	**C**	**I**	**C**	**I**
Depth (cm)	10.7 ± 0.6	8.3 ± 1.0	19.6 ± 0.6	10.6 ± 2.6	25.7 ± 2.7	15.8 ± 1.2	23.0 ± 1.9	8.6 ± 1.6	23.2 ± 1.9	23.4 ± 2.0
v (cm s^{-1})	34.0 ± 5.4	29.5 ± 10.6	41.3 ± 6.8	16.7 ± 3.9	47.2 ± 8.0	13.1 ± 3.5	39.1 ± 7.9	30.0 ± 4.4	40.6 ± 6.9	41.0 ± 11.0
T (ºC)	10.3 ± 0.5	10.5 ± 0.4	9.5 ± 1.1	9.3 ± 1.2	9.7 ± 1.3	9.4 ± 1.2	9.7 ± 0.9	9.5 ± 0.9	9.2 ± 0.8	9.3 ± 0.9
O_2 (mg L^{-1})	10.6 ± 1.0	9.3 ± 0.9	10.8 ± 0.9	10.8 ± 0.8	12.2 ± 1.5	10.5 ± 0.7	11.4 ± 0.7	11.6 ± 0.9	11.4 ± 0.4	11.0 ± 0.4
pH	8.1 ± 0.1	7.8 ± 0.2	7.3 ± 0.3	7.2 ± 0.3	7.3 ± 0.1	7.6 ± 0.1	7.2 ± 0.1	7.1 ± 0.2	7.9 ± 0.2	7.1 ± 0.1
Conduc. (μ*S* cm^{-1})	217 ± 14.4	212 ± 18.1	56.2 ± 6.6	58.2 ± 5.5	47.1 ± 4.9	52.2 ± 7.0	52.0 ± 3.0	51.2 ± 3.0	36.9 ± 1.9	54.6 ± 16.2
[NO_3^-] (mg L^{-1})	2.12 ± 0.21		0.55 ± 0.05		0.50 ± 0.13		0.96 ± 0.11		0.56 ± 0.04	
[NH_4^+] (mg L^{-1})	0.20 ± 0.02		0.18 ± 0.05		0.12 ± 0.02		0.29 ± 0.04		0.18 ± 0.04	
PO_4^{-3} (mgP L^{-1})	0.03 ± 0.006		0.02 ± 0.008		0.03 ± 0.008		0.05 ± 0.02		0.03 ± 0.01	

In winter, storage of BPOM ranged from 20 to 153 g per surface unit (m^{-2}), and from 112 to 1073 g per length unit (m^{-1}) in Control reaches, while it ranged from 20 to 117 g m^{-2}, and from 87 to 480 g m^{-1} in Impact reaches (Fig. 3). Water abstraction affected BPOM similarly in the five streams (two-way ANOVA$_{\text{Stream*Reach}}$: $p > 0.05$), reducing storage per surface unit (two-way ANOVA$_{\text{Reach}}$: $F_{1,90} = 4.01$, $p = 0.048$) and, more evidently, per length unit (two-way ANOVA$_{\text{Reach}}$: $F_{1,90} = 15.7$, $p < 0.0001$).

Overall, more BPOM was stored in spring: 23 – 705 g per surface unit (m^{-2}), and 168 − 1989 g per length unit (m^{-1}) in Control reaches; 58 – 1233 g m^{-2}, and 261 – 3772 g m^{-1} in Impact reaches (Fig. 3). Contrasting with the winter experiment, storage of BPOM tended to be higher in Impact reaches except in stream A, but differences were not statistically significant (two-way ANOVA$_{\text{Reach}}$: $p > 0.05$), less so when analyzed per length unit.

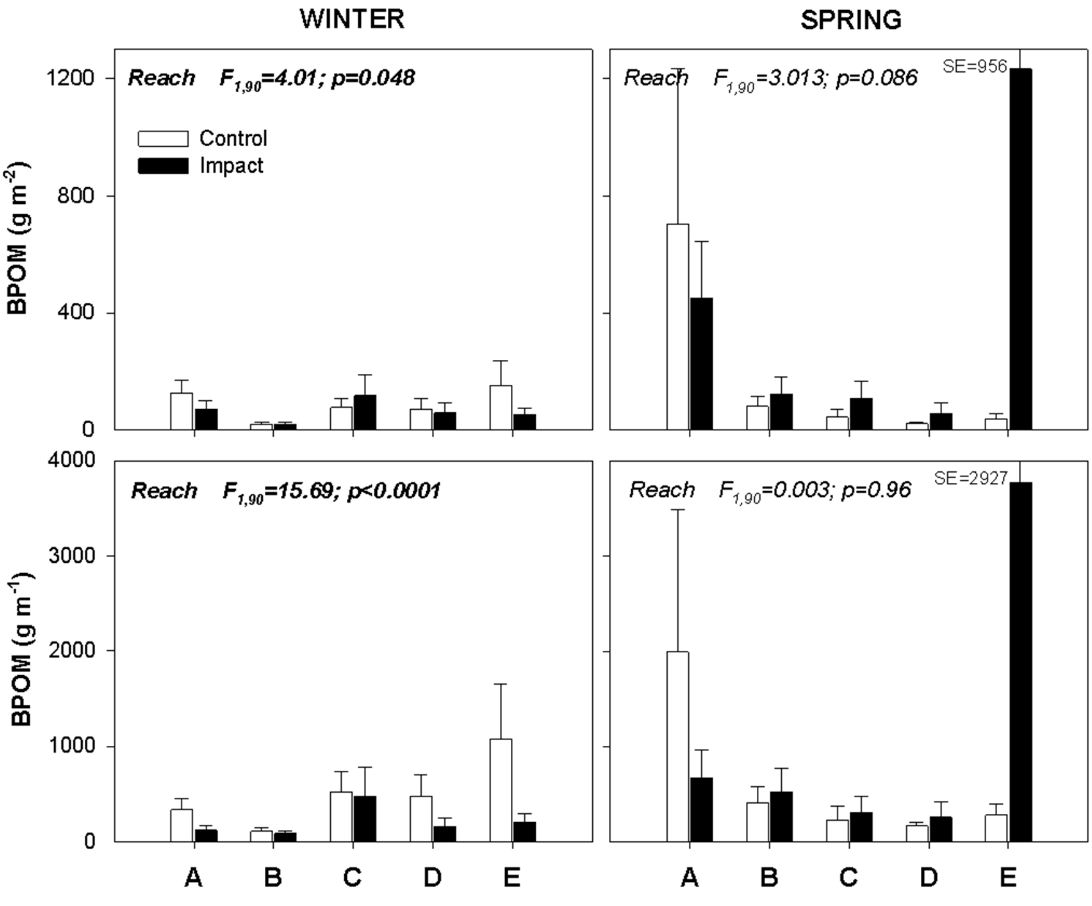

Figure 3. Storage of benthic particulate organic matter (BPOM) measured per surface (up) and length (down) units in Control and Impact reaches of the five streams in winter (left) and in spring (right). Error bars show SE. Results from two-way (Stream x Reach) ANOVA are also shown.

In winter, alder leaf breakdown rates ranged from 0.019 to 0.078 day^{-1} in Control reaches and from 0.010 to 0.042 day^{-1} in Impact reaches (Fig. 4). With the exception of stream B, breakdown rates were 36-60% smaller in Impact reaches, the overall effect of abstraction being statistically significant (two-way ANCOVA$_{\text{Reach}}$: $F_{1,133}$ = 6.94, p = 0.009). In spring, leaf litter broke down faster, at rates ranging from 0.022 to 0.049 day^{-1} in Control reaches and from 0.026 to 0.047 day^{-1} in Impact reaches (Fig. 4). In this second experiment the Impact:Control ratios of breakdown rates were much closer to 1 (0.7 − 1.2) comparing to the ones obtained in winter (0.4− 0.7). Besides, spring results yielded no statistically significant differences in breakdown rates between Control and Impact reaches (two-way ANCOVA$_{\text{Reach}}$: $F_{1,132}$ = 0.20, p = 0.889).

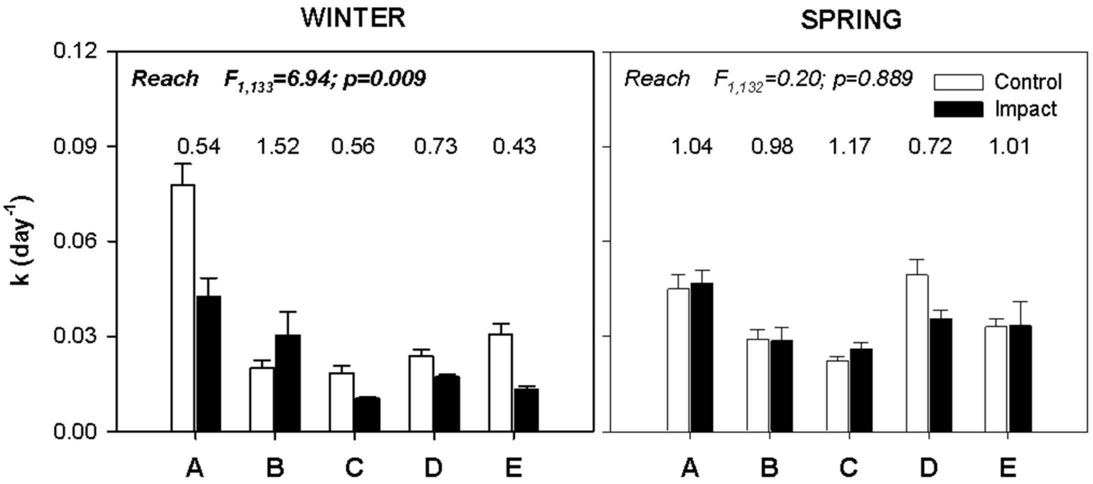

Figure 4. Breakdown rates (day^{-1}) of alder leaves in Control and Impact reaches of the five streams in winter (left) and in spring (right). Error bars show SE. Results from two-way (Stream x Reach) ANCOVA are also shown.

In winter, water abstraction did not affect the total density of macroinvertebrates associated to litter bags (two-way ANOVA$_{\text{Reach}}$: $F_{1,35}$ = 0.66, p = 0.42), which, excluding stream A, did not exceed 100 invertebrates gAFDM^{-1} (Fig. 5). Macroinvertebrates in bags were much more abundant in spring, even exceeding 3000 invertebrates gAFDM^{-1} in the Control reach of stream D (Fig. 5). Excluding stream A, lower densities were measured in Impact reaches. However, these differences were not statistically significant (two-way ANOVA$_{\text{Reach}}$: $F_{1,34}$ = 3.89, p = 0.057) and, overall, showed a pattern similar to the one found in winter.

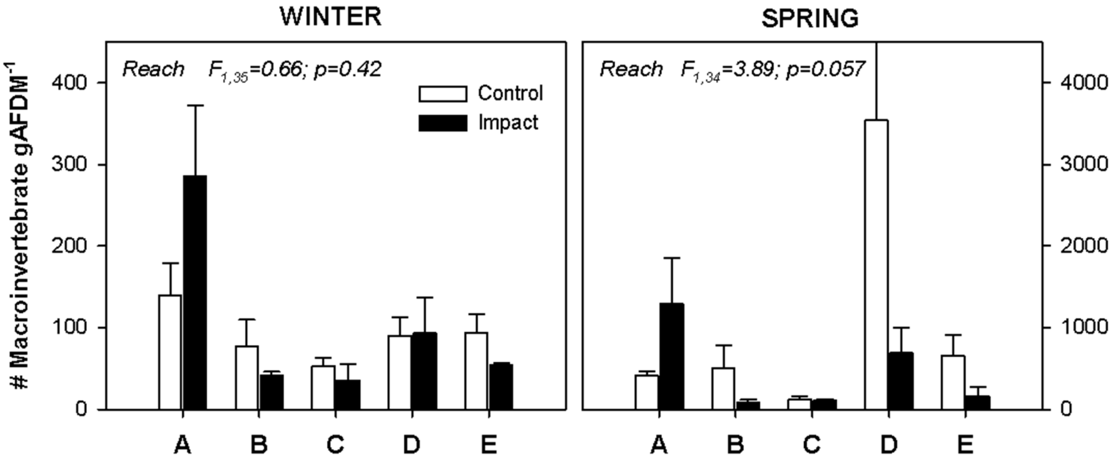

Figure 5. Density (# $gAFDM^{-1}$) of macroinvertebrates associated to litter bags in Control and Impact reaches of the five streams in winter (left) and in spring (right). Error bars show SE. Results from two-way (Stream x Reach) ANOVA are also shown.

Similarly to total density, the structure of macroinvertebrate assemblages associated to litter bags showed no consistent patterns. The nMDS (Fig. 6) and the PERMANOVA analyses showed differences to be non-significant, but slightly higher among streams than between reaches, both in winter (Stream: *PseudoF*4,9 = 1.97, *p* = 0.06; Reach: *PseudoF*1,9 = 1.05, *p* = 0.43) and in spring (Stream: *PseudoF*4,9 = 1.53, *p* = 0.12; Reach: *PseudoF*1,9 = 0.88, *p* = 0.53).

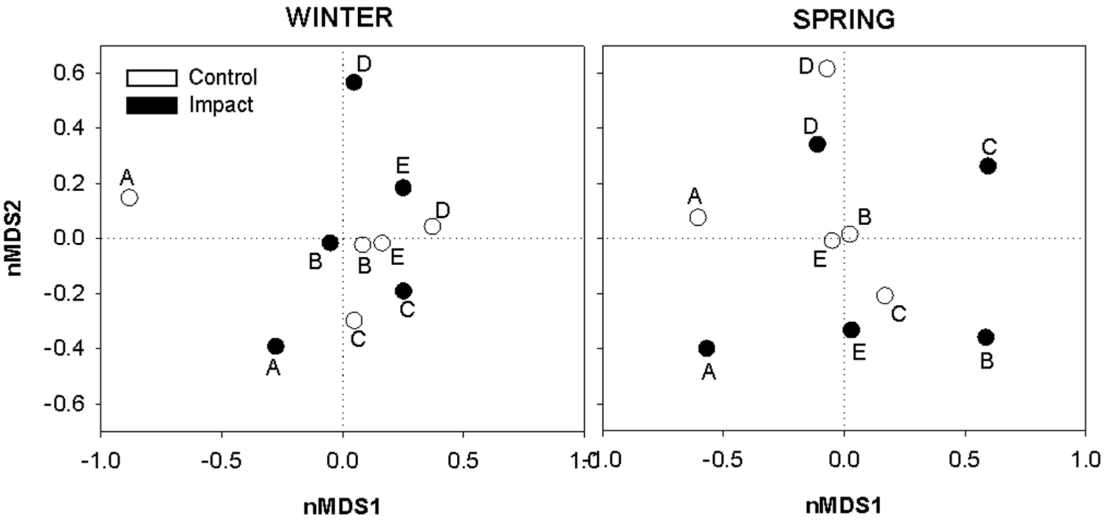

Figure 6. Non-metric multidimensional scaling ordination (nMDS) of macroinvertebrate assemblages associated to litter bags, taking into account the mean density of each family in each reach (n = 5).

In winter, shredders averaged 19% of total macroinvertebrates in Control reaches, and 10% in Impact reaches. Significantly lower densities of shredders were measured in Impact reaches (two-way ANOVA$_{\text{Reach}}$: $F_{1,35} = 5.7$, $p = 0.022$), but biomass did not differ between reaches (two-way ANOVA$_{\text{Reach}}$: $F_{1,35} = 1.03$, $p = 0.32$). Overall, shredders were more abundant in spring, both in terms of density and biomass (Fig. 7). However, they comprised a lower proportion of total macroinvertebrates: 15% in Control reaches and 9% in Impact reaches. The density of shredders displayed a pattern similar to that found in winter, and decreased significantly below dams (two-way ANOVA$_{\text{Reach}}$: $F_{1,34} = 10.4$, $p = 0.003$). On the contrary, the trends in shredder biomass seemed to be reversed, but again, these differences were neither consistent nor statistically significant (two-way ANOVA$_{\text{Reach}}$: $F_{1,34} = 0.64$, $p = 0.43$). Both density and biomass of shredders in litter bags were strongly correlated with decomposition rates in winter (density: $r = 0.92$, $p = 0.002$; biomass: $r = 0.91$, $p = 0.003$), and in spring (density: $r = 0.85$, $p = 0.017$; biomass: $r = 0.95$, $p = 0.0003$).

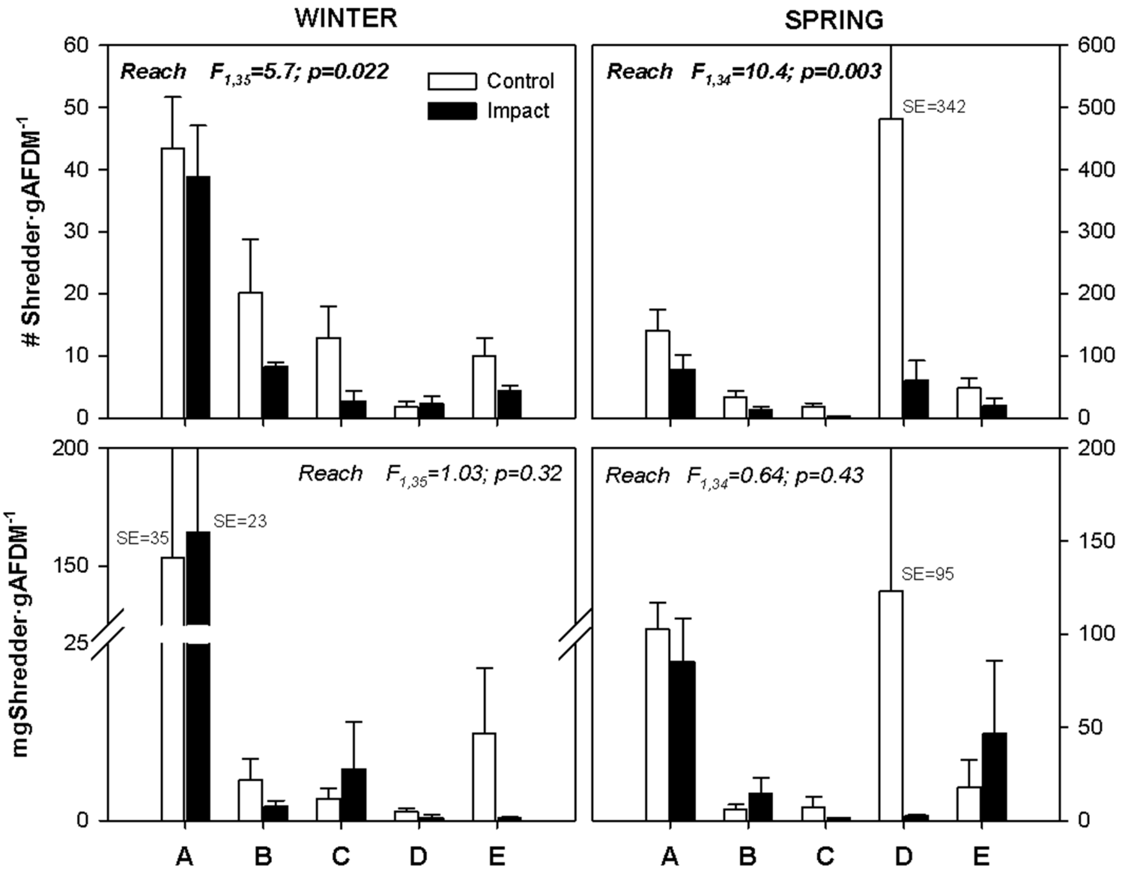

Figure 7. Density (# gAFDM^{-1}) and biomass (mg gAFDM^{-1}) of shredders associated to litter bags in Control and Impact reaches of the five streams in winter (left) and in spring (right). Error bars show SE. Results from two-way (Stream x Reach) ANOVA are also shown.

Discussion

Water abstraction can impact streams by altering the hydrological regime, water physicochemical characteristics, fluvial communities and ecosystem processes. Many studies reported water abstraction to increase water temperature and pH (Rader & Belish 1999; McIntosh et al. 2002), to slow down current velocity (McIntosh et al. 2002; Dewson et al. 2007b), to promote sedimentation (Wright & Berrie 1987; Castella et al. 1995) and to decrease macroinvertebrate abundance and diversity (Petts & Bickertin 1994; Cazaubon & Giudicelli 1999). These studies included diverse rivers (from small mountain streams in the Rockies to large Mediterranean rivers) as well as different water abstraction schemes (from manipulative experiments to water pumping), and thus, their conclusions seem pretty solid. In contrast, water abstraction did not affect water physicochemical characteristics in our streams, as water temperature, dissolved oxygen concentration, pH, conductivity and nutrient concentration did not differ between Control and Impact reaches. The lack of response seems to be a consequence of the strong shade and low nutrient levels in the headwater streams we studied, the small size and the fast renewal of the low dams, and the short distance between Control and Impact reaches.

The most obvious and consistent impacts of water abstraction in our study sites were those related to physical habitat. Water diversion resulted in much narrower wetted perimeter, shallower water column and slower flow velocity. These effects on channel width and depth are what Stanley et al. (1997) called "ecosystem contraction", and can have deep effects on stream communities and ecosystem processes (Murchie et al. 2008; Elosegi et al. 2010; von Schiller et al. 2011). Regarding the processes this study focused on, slower water velocity is a key factor promoting retention of organic inputs (Snaddon et al. 1992), so we could expect a higher storage of organic matter in our Impact reaches. Dewson et al. (2007b) also observed that streams accumulated significantly more organic matter after diverting 86 to 95% of the discharge from three different streams. Our spring results showed similar trends, even though differences between Control and Impact reaches were not statistically significant. On the contrary, in winter less BPOM was stored in Impact reaches, showing that the effects of water abstraction can depend on season, and probably on discharge. In our study sites most organic matter enters the stream in autumn with leaf abscission, and is transported downstream mainly in high flows, thus making the storage of BPOM highly dependent on the relative timing of floods and inputs (Pozo et al. 1997). During base flow the dams we studied diverted almost all of the water, and with it most or all BPOM, thus creating a strong barrier effect on upstream transport, that can override the effects of enhanced retention capacity, especially outside the abscission period. The diverted organic matter is transported through the canals and trapped by a metallic grid just before the tube from the canal to the turbines. These grids are cleaned automatically, and the organic matter is dumped beside the canal, far from the stream channel, and thus, lost from the stream ecosystem. In periods of higher flow the barrier effect is probably related to the proportion of water diverted. The fact that storage of BPOM was higher in spring suggests that lateral and upstream inputs were important during our experiment, indicating there were high flows that overcame low dams and carried organic matter to Impact reaches, where it was easily retained due to reduced discharge and water velocity. Therefore, our results suggest that the overall balance between these two contrasting effects depends not only on site particularities, but also on season and on the timing of floods with respect to leaf abscission.

We expected water abstraction to reduce organic matter breakdown rates, as a consequence of reduced velocity, and perhaps of impacted stream communities. Our results corroborated this hypothesis, but only in winter. Temperature, pH and nutrient concentration strongly influence decomposition of organic matter (Dangles et al. 2004; Greenwood et al. 2007; Benstead et al. 2009; Dang et al. 2009). However, in this study water abstraction did not affect water quality, and thus, physicochemical variables could not explain the observed differences. Moreover, decomposition is an integrative process that includes abrasion, microbial colonization and invertebrate consumption (Graça 2001; Hieber & Gessner 2002). Some studies suggested decomposition was enhanced by abrasion (Chauvet et al. 1993; Heard et al. 1999), whereas others concluded flow-related fragmentation not to be a significant determinant of breakdown rates (Rader et al. 1994; Casas et al. 2000; Ferreira et al. 2006; Dewson et al. 2007b). The reason behind these differences may lay in the levels of discharge tested, as it is evident that strong floods fragment leaves in bags, even scour bags downstream. Our results suggest physical abrasion did not play a decisive role in the decomposition process. In fact, hydraulic differences between Control and Impact reaches were similar in winter and in spring, whereas differences in decomposition rates were limited to winter. Therefore, slower decomposition could be attributed to impaired fungal and/or macroinvertebrate communities, as has been shown elsewhere (Dewson et al. 2007b; Death et al. 2009; Schlief & Mutz 2009).

Water abstraction did not affect the total density of macroinvertebrates and the structure of macroinvertebrate assemblages found in litter bags. However, shredder density was significantly lower in Impact reaches, which could explain the differences observed in breakdown rates in winter (Graça 2001; Martínez et al. 2013a). We can only speculate about the reason behind the lack of effect of abstraction in spring breakdown rates, as water physicochemical characteristics, physical habitat and macroinvertebrate assemblages associated to bags showed very consistent patterns in both winter and in spring. Perhaps the lack of differences between Control and Impact reaches is linked to the overall higher abundance of organic matter in spring.

Overall, although trends we described were fairly consistent, the impact detected seemed not to be very strong, and to be limited to winter. Nevertheless, changes observed in winter could have important consequences for stream ecosystems, especially considering that the life cycles of many macroinvertebrate taxa are synchronized with leaf abscission in fall. Allochthonous organic matter is the main energy source supporting food webs, especially in small forested streams (Fisher & Likens 1973; Webster et al. 1999). Many trophic levels depend on the processing of organic matter by microorganisms and macroinvertebrates (Wallace et al. 1997; Graça 2001). Therefore, the fact that water abstraction led to a decrease in both storage and decomposition of organic matter could affect stream productivity (Vannote et al. 1980) and alter the trophic structure of fluvial ecosystems (Casas et al. 2000).

From a biogeochemical standpoint an interesting question would be how the differences between Control and Impact reaches change with the distance downstream from the dam. The response is hard to predict, and likely case-specific, as it depends at least on the accretion of groundwater, which tends to increase downstream discharge, and in the confluence of tributaries, some of which are also affected by the diversion canals. It could also be more meaningful to present our results in terms of carbon instead of organic matter. However, since we did not measure carbon content of leaves and BPOM, we preferred to express our results as organic matter as a more accurate expression of our results. The carbon content of most leaf species in our streams, including alder, is around 40-50% (Martínez et al. 2013b), similar to BPOM accumulations (calculated from data shown by Flores et al. 2014). These ratios can be used to have a rough estimate of the impacts of water abstraction on the carbon flux.

Finally, our results showed the importance of the scale at which impacts are analyzed. Streams and rivers provide important ecosystem services (Costanza et al. 1997; Thorp et al. 2010), including the retention and consumption of organic matter (Acuña et al. 2013). These services are essential for the future human well-being (Perrings et al. 2010) and thus, when analyzing services and impacts, the reach scale or the global accounting can be much more important than the account per surface unit. In particular, the most evident effect of water abstraction is the contraction of the aquatic ecosystem, and therefore, streams are greatly reduced in extent, being impacts likely to be much stronger at the reach scale. In this study, differences in storage of organic matter between Control and Impact reaches almost doubled when results were analyzed per linear meter, indicating the overall effects of water abstraction were highly underestimated when using surface units, and therefore highlighting the importance of the scale for analyzing results and assessing overall impacts.

Conclusion

The effects of water abstraction on organic matter dynamics were fairly consistent but limited to winter, showing that impacts can depend on season. In winter, water abstraction reduced storage and decomposition of organic matter, which can impact the energetic basis of stream ecosystems. The differences were more evident when results were expressed per linear meter, showing that the global accounting of impacts and services can be misestimated by focusing only on the patch scale.

Acknowledgements

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CHAPTER 3

Changes in discharge preferentially affect surface more than subsurface breakdown of organic matter in a mountain stream

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Abstract

Discharge fluctuations modify water depth and velocity in streams and this can affect leaf litter breakdown, which is an important ecosystem function. Both during droughts, when parts of the surface dry out, and during floods, which scour the benthic surface, macroinvertebrates can seek refuge in the subsurface. Therefore, as an important part of them depend on organic matter, the effects of discharge fluctuations on leaf breakdown might be greater on the surface than in the subsurface of lotic ecosystems. To test this hypothesis, we measured microbial and total breakdown rates of alder (*Alnus glutinosa* (L.) Gaertner) both on the surface and in the subsurface in two areas of a stream: the permanently wet channel and the parafluvial areas. Reduced discharge only dried out the surface of the parafluvial areas, and thus, breakdown rates were only reduced in this habitat. In contrast, breakdown rates were similar in both habitats of the permanently wet channel, but also in the subsurface of the parafluvial area. The subsurface can mitigate the effects of discharge alterations on the breakdown of organic matter in streams, which might be critical for the productivity of these ecosystems under increased drought frequencies in streams.

Keywords: leaf litter bags, wet channel, shredders, flood, drought, microbial breakdown, parafluvial, surface-subsurface

Introduction

Allochthonous organic matter such as leaf litter, is the main food resource for heterotrophs in many streams and rivers (Cummins et al. 1989; Tank et al. 2010), where litter breakdown is a pivotal ecosystem function that drives the productivity of these systems (Wallace et al. 1997). The biota in these systems depends heavily on detritus and environmental stressors. Those stressors, such as droughts, can greatly alter food webs since they affect detritus dynamics, (e.g. Wallace et al. 1997). Droughts are important disturbances in streams and rivers (Lake 2003; Poff et al. 2003), and are predicted to increase globally as a consequence of ongoing climate change and increased water abstraction (Milly et al. 2005; IPCC 2014). Fluctuations in water discharge affect the availability and quality of organic matter (Ylla et al. 2010), leading to changes in the breakdown rates of detritus and alterations to stream food webs (Langhans & Tockner 2006; Leberfinger et al. 2010; Datry et al. 2011). Severe drought reduces the surface of wet habitats and increases the proportion of dry sediments in the active channel (i.e. parafluvial areas – often the marginal area of the stream) and reduces hydrological connectivity (Lake 2003). This is turn, impacts aquatic communities and ecosystem processes (Boulton 2003). In particular, organic matter deposited in dry parafluvial areas breaks down much slower than that in the wet channel (Romaní et al. 2012). In general, cycles of emersion and immersion of detritus result in decreased breakdown rates (Langhans & Tockner 2006; Corti et al.

2011, Foulquier et al. 2014). The wetting and drying cycles appear to affect invertebrate-mediated breakdown more strongly than microbial-mediated detritus decomposition (Martínez et al. 2015), because microbes colonize litter more rapidly than invertebrates (Gessner et al. 1999), and because the residual water in drying leaf packs can allow microbial survival (Sanders & Webster 1978; Sridhar & Bärlocher 1993).

In addition to the organic matter deposited on the surface, substantial amounts of leaf litter can be buried among sediment during storms (Herbst 1980; Naegeli et al. 1995), where it breaks down more slowly than on the surface (Cornut et al. 2010; Marmonier et al. 2010; Flores et al. 2013). Nevertheless, since sediments can retain water during surface drying (Lake 2003), benthic organisms can seek refuge by moving vertically into the subsurface (Stanley et al. 1994; Stubbington 2012), where they concentrate at high densities (Delucchi 1989). Therefore, it is probable that these organisms have a strong effect on organic matter decomposition and that a significant part of the total breakdown occurs in the subsurface layer, especially when breakdown rates are measured over time (capturing dry and wet periods) and at the reach scale. The subsurface might be particularly important in temporary streams, or in rivers with shallow banks or extensive floodplains, where drying and rewetting cycles can be frequent. Nevertheless, to date, little information is available concerning whether the effect of droughts on leaf breakdown differs between the surface and the subsurface.

We addressed this question by incubating leaf litter bags on the benthic surface and in the subsurface layer of a mountain stream; bags spanned a range of water depths and experienced different drying frequencies. Our study aimed to test four hypotheses. Firstly, the abundance, taxonomic richness and diversity of macroinvertebrates is lower in periodically dry bags. Secondly, surface breakdown in periodically dry bags is slower than in permanently submerged bags, due to lower macroinvertebrate densities in periodically dry areas (subsurface and/or adjacent wet surface areas) and the inactivation of microbial activity. Thirdly, surface drying affects macroinvertebrate-mediated breakdown more than microbially-mediated breakdown, because microbes resume their activity more rapidly following submersion. Fourthly, leaf breakdown in the subsurface layer will be more stable than at the surface (because it does not dry out), contributing to breakdown rates more than the surface in parafluvial areas.

Materials and methods

Study site

The study was conducted in a 50-m reach of the Erroiarri Stream, a third-order mountain stream that drains a 2.9-km^2 catchment over granite and schist in the basin of Artikutza (N. Iberian Peninsula; UTM X: 597874; Y: 4785730). The entire basin of Artikutza (3,638 Ha) was bought in 1919 by the municipality of San Sebastian, to ensure the supply of high quality drinking water, and since then, has been managed as a strict reserve (Castro 2009). Consequently, most of the basin is covered with mature beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) forests. The substrate composition in the streambed of the Erroiarri Stream is: bedrock (5.1%), boulder (>256 mm; 8.9%), cobble (64–256 mm; 42.3%), pebble (4–64 mm; 23.4%), gravel (2–4 mm; 15.1%) and sand (<2 mm; 5.2%). The weather station in the basin of Artikutza recorded a mean rainfall of 2,526.7 mm per year and mean annual air temperature of 12.2 °C (http://meteo.navarra.es/).

Experimental procedures

We measured the decomposition of black alder (*Alnus glutinosa* (L.) Gaertner), the most common riparian tree species in the study area, following standard methods described in Graça et al. (2005). Recently fallen leaves were collected, air-dried, weighed, and enclosed in mesh bags. We used coarse bags (5 mm mesh, 5 ± 0.05 g of leaves per bag) to measure total breakdown and fine bags (100 µm mesh, 3 ± 0.05 g of leaves per bag) to assess microbial breakdown. Bags were set in pairs, with each fine bag being enclosed within a coarse bag so that the environmental conditions were as similar as possible within each bag pair. On 5 December 2013, 48 bag pairs were deployed in the field, tied with fishing line to 12 metallic bars along the experimental reach (50 m), and weighed with cobbles to secure them against the bottom. Since we could not predict which areas of the surface were going to be dry or remain submerged during the experiment, metallic bars were placed at different water depths to examine the effects of changes in discharge on surface and subsurface breakdown: four in deep water (>15 cm at the time of deployment), four in shallow water (range: 2–15 cm), and four in dry areas (ca. 5 cm higher than water level). Four pairs of bags were tied to each bar, two of which were placed on the surface and the other two were buried carefully in the subsurface layer, by removing it with a spade and replacing the top 5–10 cm of the sediment.

Half of the bags were retrieved on day 13 to measure breakdown rates (see below) with which the time expected for bags to lose 50% of their initial mass was estimated, which was day 67. Therefore, on day 67, all remaining bags were retrieved and were immediately enclosed within individual zip bags to minimize the loss of macroinvertebrates, and were transported in a portable cooler to the laboratory. The remaining leaf litter was rinsed with stream water, oven-dried (70 ºC, 72 h) and ashed (500 ºC, 5 h), to determine the ash-free dry mass (AFDM) (Graça et al. 2005). During the sampling period, four coarse bags were found open, with the closing fishing lines broken, and these bags were discarded for subsequent analyses; the fine bags within these bags were unharmed and were considered for study.

Weekly, we determined the water temperature, conductivity, pH and dissolved oxygen concentration (WTW Multi 350i SET, Yellow Spring, USA) at the downstream end of the reach. Water velocity (Martin Marten Z30, Current Meter, Barcelona, Spain) and depth were measured at those places where the bags were incubated. Subsurface water samples were not taken, as we expected them to be very similar to those of flowing water, due to the high permeability of the coarse substrate (see substrate composition above) and to the shallow incubation depth of the bags. Daily discharge data were obtained from the regression between weekly discharge measured in the field and data from the continuous gauging station of Añarbe (UTM X: 593514; Y: 4786717), 8 km further downstream. Water samples were taken in polyethylene bottles, filtered through fiberglass filters (Whatman GF/F 0.7 µm, Whatman International Ltd., Maidstone, England) and transported to the laboratory for spectrophotometric analysis of nitrate, ammonium, soluble reactive phosphorus and dissolved organic carbon (DOC) (APHA, 1992).

Macroinvertebrates associated with coarse mesh bags at day 67 were collected via a 500-µm sieve and preserved in 70% ethanol. All the bags were submerged at this sampling time. Using the macroinvertebrate key of Tachet et al. (2002), individuals were counted and identified mainly to the genus level, except Chironomidae, Limoniidae, Psychodidae and Limnephilidae, which were identified to the family level and Oligochaeta, to the order level.

Data analysis

The relationship between water depth and water velocity was tested using log-transformed values to avoid heteroscedascity. As zeroes were present among the data, a constant was added to water depth (+0.5) and water velocity (+0.05) prior to log-transformation.

As we hypothesized that the drying of the bags reduces the abundance, taxonomic richness and diversity of macroinvertebrates (first hypothesis), we calculated taxa richness and the Shannon–Weaver diversity index (Shannon & Weaver 1949) for both the total macroinvertebrate assemblage and for the shredders functional feeding group only (described as such following Merritt & Cummins 1996). Therefore, taxa richness and diversity, together with abundance, were used as macroinvertebrate descriptors. Linear mixed-effects models (LME; Pinheiro & Bates 2000) were used to compare the six descriptors of the community for Habitat (Surface or Subsurface) and Location (Wet channel or Parafluvial area), both as fixed factors, with Bag Group as a random factor. The Habitat × Location interaction was used to show whether, as hypothesized, surface drying affected the surface assemblages more than the subsurface macroinvertebrate assemblages. To test whether water depth was related to macroinvertebrate descriptors, we constructed a LME model with Mesh (Coarse or Fine) and Habitat as fixed factors and Water Depth as a covariate, taking into account only bags from the wet channel. The location of bags that were permanently inundated was considered “wet channel”, whereas bags that were inundated for part of the experiment were considered to be in the “parafluvial” location.

The leaf mass remaining in the bags was expressed as the ratio between the final weight and the estimated initial leaf AFDM. Breakdown rates were calculated using the negative exponential model (Petersen & Cummins 1974):

$$M_t = M_0 \cdot e^{kt}$$

where M_t = mass at time t, M_0 = mass at time 0, and k = breakdown rate and t = time in days.

The effect of the different sources of variation on the breakdown rate was tested using LME models with Sampling Date, Bag Group and Bag Pair as random factors. Mesh Habitat and Location were considered as fixed factors in the analyses. This test enabled us to respond to the second hypothesis (source of variation Location), the third hypothesis (source of variation Mesh) and the fourth hypothesis (Habitat × Location interaction). The effect of water depth on the breakdown rate in the wet channel was also tested using LME models, taking into account three sources of variation (Mesh and Habitat as fixed factors and Water Depth as a covariate). Again, Sampling Date, Bag Group and Bag Pair were used as random factors. The Pearson correlation was used to test the relationship between water depth and velocity.

When testing for the relationship between macroinvertebrate descriptors and breakdown rate, heteroscedascity was corrected by means of log–log linear regression analyses. A constant was added to shredder diversity (+1), to allow log-transformation. When necessary, data where transformed (log (x+1)) to meet the assumptions of the parametric analyses. We used restricted maximum likelihood (REML) to estimate the components of the variance in all mixed-effects models. All statistical analyses were conducted using R statistical software (version 3.1.2; R Development Core Team, 2014; Vienna, Austria).

Results

Discharge and abiotic parameters

The discharge was relatively constant (mean ± SE, 0.36 ± 0.036 $m^3 s^{-1}$) until day 56, when a flood occurred (4.85 $m^3 s^{-1}$), after which the discharge remained above 0.55 $m^3 s^{-1}$ until the end of the experiment, on day 67 (Fig. 1). Therefore, bags initially incubated in dry areas remained dry for most of the first period, and were submerged for most of the last two weeks (from day 56 to 67), whereas all bags that were initially submerged, remained so during the entire experiment (with 12.0 cm of water depth and 0.1 m s^{-1} of mean flow velocity). The water depth and water velocity correlated positively (Pearson: $r = 0.35$, $p < 0.0001$); the highest velocity (0.96 m s^{-1}) was measured at the deepest (28 cm) sampling point and the lowest velocities, near 0 m s^{-1}, in the shallowest parts. The physicochemical characteristics of the water remained relatively constant during the experiment, with low temperatures (7.7 ± 0.28 ºC) and conductivities (60.08 ± 1.58 µS cm^{-1}), neutral pH (7.27 ± 0.16), high oxygen concentrations (12.3 ± 0.27 mg L^{-1}), low nutrient concentrations (PO_4^{3-}-P: 4.0 ± 0.71 µg L^{-1}, NH_4^+-N: 12.0 ± 2.84 µg L^{-1}, NO_3^--N: 529.8 ± 88.04 µg L^{-1}) and a DOC concentration of 1.1 ± 0.13 mg L^{-1}.

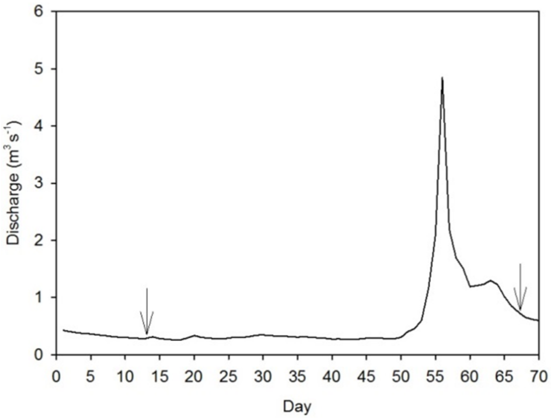

Figure 1. Discharge in the Erroiarri Stream during the experiment. Arrows show the two days when the bags were retrieved from the stream.

Macroinvertebrates

A total of 733 macroinvertebrate individuals were found in the 20 coarse bags sampled at day 67, ranging in density from 9 to 76 individuals per bag (mean ± SE, 31.6 ± 3.5). Shredders contributed to 23.3% and 28.6% of the total invertebrate abundance in the subsurface of the parafluvial and the wet channel, respectively. The abundances were 46.7% and 43.4% for the surface. The most abundant taxa were: Orthocladiinae (Chironomidae:Diptera, 23.6% of the total invertebrate abundance), *Amphinemura* (Nemouridae:Plecoptera, 11.3%), Oligochaeta (10.9%), *Echinogammarus* (Gammaridae:Amphipoda, 9.2%), Tanytarsini (Chironomidae:Diptera, 6.2%) and *Leuctra* (Leuctridae:Plecoptera, 5.9%) from a total of 45 macroinvertebrate taxa. The number of shredder taxa accounted for 35% of all the invertebrate taxa in the subsurface of the wet channel, for 42% in the surface in the parafluvial zone. We did not observe significant differences between the two habitats (Surface *vs*. Subsurface) in total invertebrate abundance (Table 1; LME, Habitat: $p = 0.29$). Focusing on the first hypothesis, although differences in location (Wet channel *vs*. Parafluvial areas) were also non-significant (Table 1; LME, Location: $p = 0.41$), the interaction term between these two factors indicated that incubation in the parafluvial areas significantly reduced total invertebrate abundance in the surface bags subject to drying, but not in the subsurface bags (Fig. 2; Table 1; LME, Habitat × Location: $p = 0.036$). Shredder abundance, total invertebrate and shredder taxa richness and total macroinvertebrate diversity were lower in the subsurface than in the surface sediments (Table 1; LME, Habitat: p = 0.043, p = 0.007, p = 0.08 and p = 0.013, respectively). Nevertheless, no other interaction term between location and habitat was significant for the descriptors of the biota, meaning that for five out of six community descriptors, the bags subjected to dry periods did not show significantly lower values, contrary to our first hypothesis. Similarly, the water depth of permanently submerged bags was not related to any descriptor of the community and showed no significant interaction with habitat.

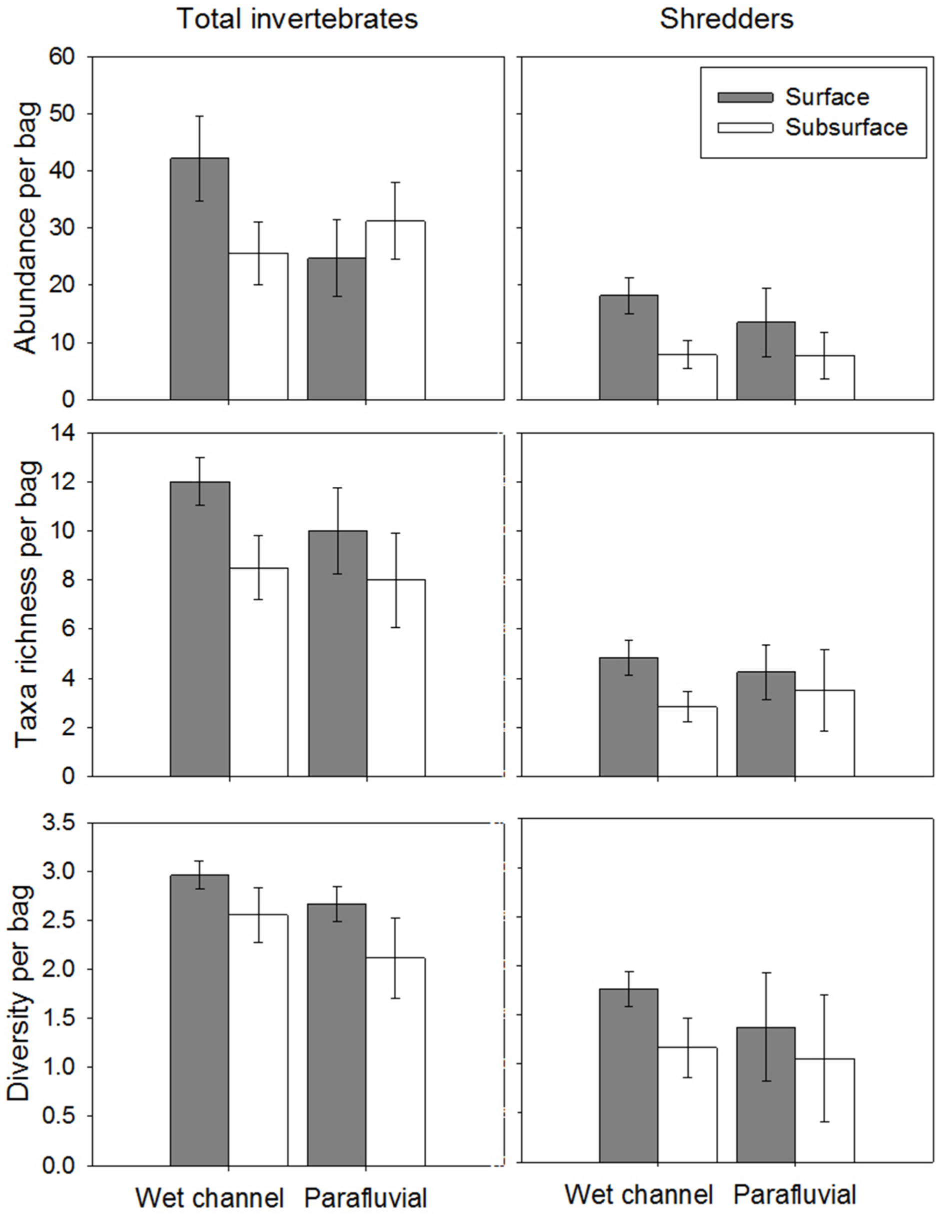

Figure 2. Abundance, taxa richness and diversity of total invertebrates and shredders in the wet channel and in parafluvial areas, at both the surface and in the subsurface layer. Mean values and ± standard errors are shown.

Table 1. Linear mixed-effects model results for the descriptors of total invertebrates and shredders.

		Total invertebrates			Shredders		
Variable	Source of variation	MS	*F*	*p*	MS	*F*	*p*
Abundance	Habitat	0.046	1.44	0.29	0.835	3.66	0.043
	Location	0.018	0.56	0.41	0.304	1.33	0.21
	Habitat × Location	0.141	4.42	0.036	0.025	0.11	0.71
Richness	Habitat	42.05	9.41	0.007	11.250	3.17	0.08
	Location	2.167	0.48	0.44	0.005	0.001	0.97
	Habitat × Location	2.700	0.60	0.39	1.875	0.13	0.42
Diversity	Habitat	1.078	6.92	0.013	1.186	2.07	0.13
	Location	0.191	1.23	0.23	0.179	0.31	0.54
	Habitat × Location	0.025	0.16	0.65	0.094	0.16	0.65

Breakdown rates

Breakdown rates ranged from 0.0064 d^{-1} to 0.0355 d^{-1}. Concerning the second hypothesis, both total and microbial breakdown rates were lower in the surface bags in the parafluvial area compared to in the other treatments (Fig. 3). Statistics supported this interpretation, with the overall surface and subsurface breakdown rates not showing significant differences (Fig. 3; Table 2; LME, Habitat: p = 0.44). Moreover, breakdown rates were significantly lower in the parafluvial area than in the permanently wet channel (Fig. 3; Table 2; LME, Location: p = 0.03), resulting in a statistically significant interaction between location and habitat (Fig. 3; Table 2; LME, Habitat × Location: p = 0.003).

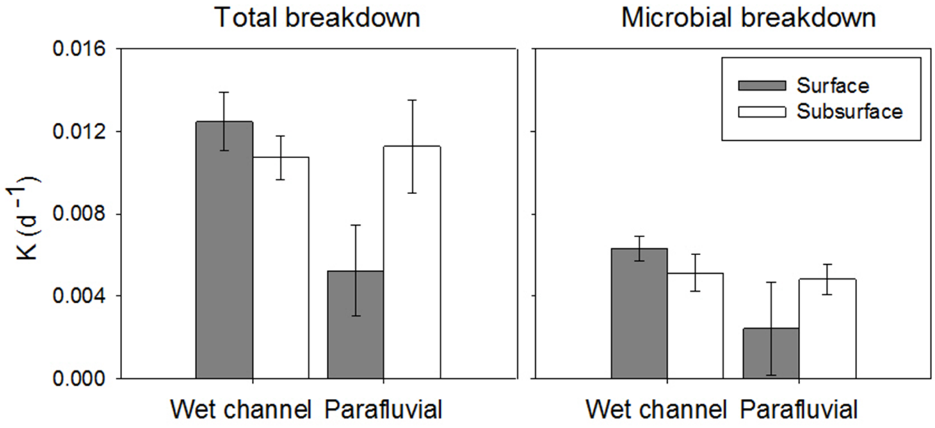

Figure 3. Total and microbial breakdown rates for alder leaves depending on the location (Wet channel and Parafluvial areas) for the surface and subsurface. Mean values and ± standard errors are shown.

Microbial breakdown rates, measured in fine-mesh bags, were significantly lower than total breakdown rates (Table 2; LME, Mesh: $p < 0.001$). Considering the third hypothesis, the mixed-effects model suggested that both types of breakdown responded similarly to the habitat and the bag location (Fig. 3; Table 2; LME, Habitat × Mesh: $p = 0.68$, Location × Mesh: $p = 0.21$, Habitat × Mesh × Location: $p = 0.05$). Regarding the fourth hypothesis, the relative contribution of the subsurface to the breakdown rate was higher in the parafluvial areas, especially in coarse bags, as shown by the ratio of subsurface:surface breakdown rate in both the wet channel (Total = 0.94; Microbial = 1.03) and in parafluvial areas (Total = 1.32; Microbial = 1.15).

For permanently submerged bags, the breakdown rate did not relate to water depth (Table 3; LME, Water Depth: $p = 0.64$), but it increased with water depth for surface bags, and decreased for subsurface bags (Table 3; LME, Habitat × Water Depth: $p = 0.034$). The relative contribution of the subsurface to the breakdown increased from the deeper bags (>12 cm of water column depth), with a subsurface:surface breakdown rate ratio of 0.92, to the shallower bags (<12 cm deep), with a ratio of 1.07.

Table 2. Linear mixed-effects model results for the breakdown rate (d^{-1}) of alder leaves. *p*-values are obtained from likelihood ratio tests. *MS values have been multiplied by $10^{\wedge 6}$ for clarity.

Source of variation	MS*	*F*	*p*
Habitat	9.32	1.11	0.442
Mesh	706.79	84.09	<0.001
Location	43.78	5.21	0.032
Habitat × Mesh	1.69	0.20	0.676
Habitat × Location	75.11	8.94	0.003
Mesh × Location	13.76	1.64	0.205
Habitat × Mesh × Location	30.82	3.67	0.050

Table 3. Linear mixed-effects model results for the breakdown rate (d^{-1}) of alder leaves for the submerged bags in the wet channel. *MS values have been multiplied by $10^{\wedge 3}$ for clarity.

Source of variation	MS*	*F*	*p*
Habitat	12.67	1.35	0.168
Mesh	552.79	58.70	<0.001
Water depth	1.75	0.19	0.643
Habitat × Mesh	4.07	0.43	0.487
Habitat × Water depth	42.36	4.50	0.034
Mesh × Water depth	0.21	0.02	0.877
Habitat × Mesh × Water depth	17.91	1.90	0.145

Significant positive relationships were observed between breakdown rates and all the macroinvertebrate descriptors, except for the total macroinvertebrate abundance (Fig. 4).

Discussion

Because discharge fluctuates in a stream, macroinvertebrates are forced to migrate from drying sections to wet parts of rivers (Delucchi 1989). Not all macroinvertebrate species can migrate horizontally to the wet parts of the surface, or vertically to the subsurface, and thus, discharge fluctuations can act as an environmental filter for the macroinvertebrate community in parafluvial areas (Bunn & Arthington 2002). We therefore hypothesized (first hypothesis), that the macroinvertebrate assemblage in the surface of the parafluvial

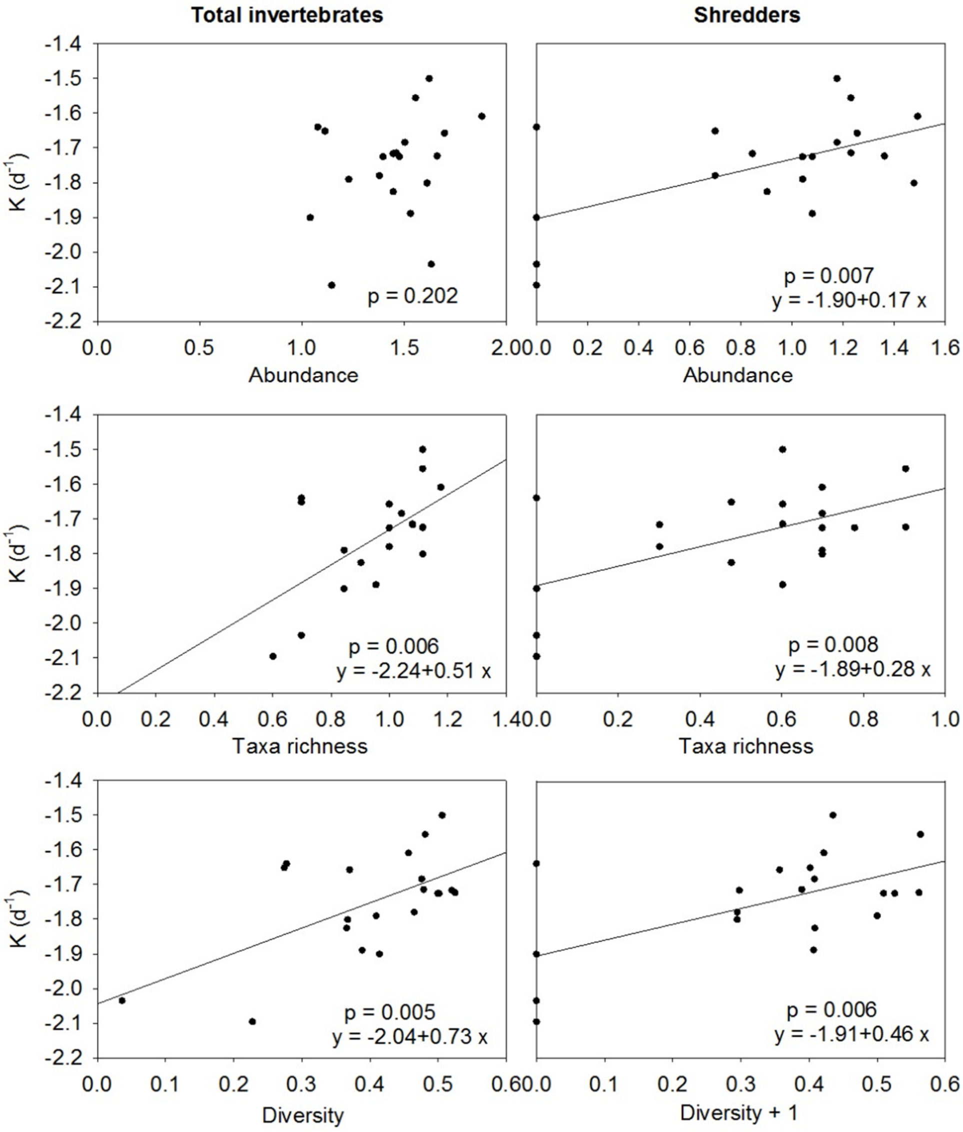

Figure 4. Log-log plots for the descriptors of macroinvertebrates in bags and the breakdown rate of alder leaves. The *p*-values of the relationship and fitted lines are also shown. A constant was added to shredder diversity (+1) to allow log-transformation, as zeroes were present.

area, which is subject to these discharge fluctuations, would show a lower species richness, diversity and abundance. Our study, which only dealt with invertebrates colonizing leaf bags, did not show clear evidence for this environmental filtering. Total macroinvertebrate abundance in surface bags was lower in the parafluvial area compared to the wet channel. Nevertheless, neither taxa richness nor the diversity of the total community and none of the three descriptors for the shredders manifested a significant difference between the parafluvial area and the wet channel. It should be borne in mind that the bags in the wet channel were submerged for the duration of the experiment (67 days), whereas the bags in the parafluvial area were only submerged for the last 17 days. This result demonstrates the ability of macroinvertebrates to rapidly colonize parts of the surface that have been submerged recently and agrees with the findings of other authors that support the high resilience of macroinvertebrate communities that experience droughts (Boulton et al. 2003). Despite the lack of a strong response of the community to the incubation in parafluvial areas, concerning the second hypothesis, the response of leaf decomposition was highly significant. Our results showed surface decomposition to be slower in intermittently dry parafluvial areas than in the permanently wet channel, confirming the findings of other studies that found the duration of drying to be crucial for the decomposition rate (Pinna & Basset 2004; Langhans & Tockner 2006; Corti et al. 2011; Datry et al. 2011). The good fit between the metrics of macroinvertebrates and the breakdown rate, also observed in previous studies (Acuña et al. 2005; Corti et al. 2011), supports the idea that the effect of drying on the breakdown rate was mediated by the detrimental effect on consumers.

According to the literature, drying slows both total and microbial breakdown (Bruder et al. 2011; Corti et al. 2011). Nevertheless, as we hypothesized (third hypothesis), some studies suggest that microbial decomposition activity can resume within one day of flow resumption (Thomas et al. 1990; Langhans & Tockner 2006; Dang et al. 2007), whereas it usually takes longer for invertebrates to recover from drying (Datry et al. 2011; Martínez et al. 2015). The rapid resumption of microbial activity is explained in part because microbes can persist even in moist material (Sanders & Webster 1978; Sridhar & Bärlocher 1993). In contrast, the reactivation of macroinvertebrate-mediated breakdown can be slower, since invertebrates need to migrate to these materials. In the present experiment, breakdown in parafluvial areas was reduced for both coarse and fine mesh bags. We consider that similarities in the microbial and total decomposition might be due to the discharge regime throughout the experiment, in which the surface bags in parafluvial areas spent 50 out of the 67 days of incubation out of the water and were submerged only for the last 17 days. When submerged, the microbial community needed to colonize the material for the first time and both microbial community and invertebrates require more than two weeks to reach their peak biomass on leaf litter (Hieber & Gessner 2002), and consequently, their peak consumption rates. We predict that if the materials in the parafluvial area had been subject to drying–rewetting cycles, the differences between microbial- and invertebrate-driven breakdown would have been higher.

Although some studies found breakdown rates to be similar in surface and subsurface areas (e.g. Rounick & Winterbourn 1983), leaves buried in the subsurface usually break down more slowly compared to the surface (Cornut et al. 2010). The effect of burial on decomposition rates depends on the type of sediment (Flores et al. 2013) and the accessibility of food patches to shredders (Navel et al. 2010). The sediment might constrain access and movement of some taxa, and thus filter the community, taxa with appropriate morphological characteristics (i.e. smaller, narrower and more flexible) being more abundant in the deeper layers (Omesová et al. 2008). In addition, depending on grain size and hydraulic connectivity, oxygen levels can decrease within a few centimeters into the sediment, which reduces macroinvertebrate abundance (Strommer & Smock 1989; Strayer et al. 1997) and the biomass of fungi (Crenshaw et al. 2002), which are very sensitive to hypoxia (Medeiros et al. 2009). In our experiment, the effect of burial was less marked, probably due to the shallow depth (5–10 cm) compared to other studies (e.g. Cornut et al. 2010 incubated at 25–30 cm). Additionally, the characteristics of the streambed in Erroiarri might also favor subsurface activity: because the basin is almost entirely covered with mature forests, the streambed is composed of coarse substrata and fine sediment accumulations are rare, resulting in an overall high vertical connectivity. The disturbance of the substrate to locate the bags in the subsurface can also artificially enhance the vertical connectivity (Marmonier et al. 2010) and become an artefact in this type of study. Nevertheless, the coarseness of the substrata and the shallowness of the incubation within the subsurface should minimize this effect in our study.

The subsurface bags were constantly underwater, and in support of our fourth hypothesis, breakdown rates in the subsurface layer did not differ between the wet channel and parafluvial areas, contrasting with differences in surface breakdown between the two locations. Similarly, the abundance of total macroinvertebrates was lower on the surface of the parafluvial area than in the wet channel, whereas it was very similar in the subsurface layer in both locations. These results demonstrate that the shallow subsurface can retain flow and maintain macroinvertebrates and litter decomposition in streams with dry beds. Moreover, even if the surface does not dry out, previous studies have demonstrated water depth to be an important driver of the community composition (Graça et al. 2004; Beauger et al. 2006), and thus, can potentially affect breakdown rates. Therefore, our study showed that even taking into account only the bags in the wet channel the activity of consumers was gradually transferred from the surface to the subsurface as water depth is reduced, which can be interpreted as a sign of the adaptation of the community to discharge fluctuations.

Freshwater ecosystems are particularly vulnerable to global environmental changes and detritus processing is one of the key ecosystem processes affected (Kominoski & Rosemond 2012). Altered patterns of precipitation will make extreme events (e.g. droughts and floods) more frequent in many regions of the globe and this might have important consequences for detritus processing (Hutchens & Wallace 2002; Tibbets & Molles 2005; Sabo et al. 2008). Overall, our results showed that in certain types of streams, the subsurface can play an important role in maintaining key ecosystem processes (the breakdown of organic matter) when the surface becomes dry, although the magnitude of this role might depend on the local characteristics of the stream section (i.e. substrate, inputs of fine sediments) and seasonal changes. Future scenarios of global environmental change point towards stronger fluctuations in precipitation and more frequent water extraction for human use, which will cause stronger oscillations in water levels. This study suggests that the impact of surface drying on detritus decomposition will partly be mitigated by the activity in the top layer of the subsurface.

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CHAPTER 4

Hydrological contingency: drying history affects aquatic fungal breakdown

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Microbial Ecology submitted

Abstract

Ongoing climate change, and intensification of land use and water abstraction are magnifying the relevance of drying events worldwide, not only affecting the frequency and severity of droughts, but also resulting in totally unnatural hydrological patterns. Longer and more severe droughts have been shown to reduce organic matter breakdown, whereas the effects of drying history, i.e. the specific sequence of different conditions to which organic matter is exposed has seldom been addressed, although it could have important consequences for microbial communities colonizing and decomposing leaf litter in streams, due to their marked temporal dynamics. Therefore, we studied how the degree of drought-related stress affects fungal activity and microbial decomposition, and whether the impacts depend on the timing of stress. In microcosms we recreated areas with flowing water (aerated water), isolated pools with stagnant water (non-aerated water) and dry beds (dry sediments). Combining these conditions and their sequence, we created 9 treatments (10 with the control) that differed in the stress level (low, medium, high) and the timing of peak stress (early, middle, late) and measured fungal biomass, sporulation, microbial respiration and decomposition of alder disks. The effects of drought-related stress levels were not consistent among response variables, which probably reflects that we recreated a small stress range. However, the effects of disturbances were systematically more detrimental in early stages of the decomposition process, and resulted in a lower fungal biomass and activity, and reduced litter decomposition. These results suggest that the effects of stress on breakdown-associated variables depend not only on the intensity and duration of stress, but also on its timing, early stress exerting greater impact than late stress on breakdown.

Keywords: aquatic hyphomycete, microbial community, organic matter decomposition, drought, timing

Introduction

Streams and rivers exhibit highly dynamic hydrologic regimes, which are a key factor structuring these ecosystems (Sabater et al. 1995; Lake 2003; Poff et al. 2003). In intermittent streams, hydrologic dynamics are characterized by alternate drying and rewetting periods (Sabater et al. 2008). In general, stream flow decreases slowly and isolated pools are formed before flow ceases and the stream surface completely dries up, whereas flow is re-established either gradually or abruptly (von Schiller et al. 2011). The effect of drying has been described as ecosystem contraction, flow recovery as ecosystem expansion (Stanley et al. 1997; Ward & Tockner 2001). Therefore, intermittent streams are spatially dynamic ecosystems that undergo cycles of contraction, fragmentation and expansion (Acuña et al. 2005). In Mediterranean streams these patterns are relatively predictable (Gasith & Resh 1999), but in other cases droughts may occur unpredictably, aseasonally, supra-seasonally or hardly ever (Lake 2003; Sabater et al. 2008). However, contraction-fragmentation-expansion cycles are common in most river ecosystems, part of the benthic habitat being alternatively immersed and exposed to air (Tockner et al. 2000; Foulquier et al. 2014).

Drying and rewetting cycles have important consequences for aquatic communities (Boulton 2003) and stream processes such as organic matter breakdown (Corti et al. 2011; Solagaistua et al. 2015). Organic matter breakdown is a major ecosystem-level process in streams running through forested catchments (Webster & Benfield 1986; Abelho 2001) and results from the complex interaction of several abiotic and biotic processes, such as leaching, mechanical abrasion, microbial degradation, and fragmentation by invertebrates (Graça 2001; Hieber & Gessner 2002), which are all modulated by drought and flood cycles. In particular, flow reduction has been shown to slow down organic matter decomposition in the wetted channel (Abril et al. 2015; Arroita et al. 2015). Pool isolation and water stagnation rapidly alter water physico-chemical properties, even resulting in hypoxic conditions, which triggers changes in leaf-associated microbial communities and processes, and reduces macroinvertebrate density (Acuña et al. 2005; Canhoto & Laranjeira 2007; Foulquier et al. 2014), thereby slowing down litter decomposition (Medeiros et al. 2009; Schlief & Mutz 2011; Mora et al. 2015). Organic matter stranded in emerged sediments also breaks down much more slowly than that in the wetted channel (Langhans & Tockner 2006; Romaní et al. 2012). Moreover, drying and hypoxia events produce legacy effects that reduce leaf litter breakdown long after the flow has resumed (Datry et al. 2011; Dieter et al. 2011; Martínez et al. 2015).

Flow dynamics are likely to be seriously altered in the near future, affecting stream communities and processes. The severity, frequency and occurrence of droughts are increasing in many regions due to ongoing climate change, and intensification of land and water uses are magnifying the relevance of these drying events worldwide (Milly et al. 2005; IPCC 2014). In particular, human activities can affect not only the frequency and severity of drying events, but also result in totally unnatural hydrological patterns, such as those produced by hydropeaking, where large portions of stream channels are periodically immersed and emersed (Jones 2014), which can produce severe impacts in communities and ecosystem functioning (Hall et al. 2015). Microbial diversity and activity, macroinvertebrate richness and density, and organic matter breakdown have been shown to depend on the duration (Langhans & Tockner 2006; Larned et al. 2007; Riedl et al. 2013) and severity (Bruder et al. 2011) of drying events, the cumulative duration of emersion being more important than drought frequency (Corti et al. 2011; Foulquier et al. 2015).

Unlike the intensity and frequency of droughts, the drying history, i.e. the specific sequence of different conditions to which organic matter is exposed, has never been addressed by researchers. However, the drying history could have important consequences for microbial communities colonizing and decomposing leaf litter in streams, due to their marked temporal dynamics (Bärlocher 2009). Quickly after impaction and germination of fungal spores on leaves, mycelial biomass increases exponentially until it stabilizes, or even decreases (Gessner & Chauvet 1994; Suberkropp 2001; Artigas et al. 2011). Similarly, fungal sporulation rates peak 2-3 weeks after colonization and decrease afterwards (Bärlocher 2009). The relative importance of different groups or taxa also seems to change along the decomposition process (e.g. Gessner & Chauvet 1994; Duarte et al. 2010; Mora 2015). Therefore, it is likely that the effects of pool isolation, drought and rewetting differ depending on when they occur in the succession of events that lead to complete decomposition of leaf litter (Bruder et al. 2011).

Here we simulated different drying histories manipulating aeration and water level under laboratory conditions to test 1) whether the degree of stress, hypoxia or drought, reduces fungal activity and organic matter decomposition, 2) whether the intensity of effects is affected by the sequence of stress events, and 3) whether these potential differences remain even after flow is resumed. We hypothesized drought to exert a stronger effect than lack of aeration on the microbial community and leaf decomposition. We also expected the drying history to affect microbial activity, early impacts being more detrimental than late ones because the decomposition process would be subject to legacy effects for longer.

Materials and methods

Freshly fallen black alder (*Alnus glutinosa* (L.) Gaertner) leaves were collected in autumn, air-dried to constant mass and stored in dark at room temperature (20 ºC). Leaves were soaked and 2550 disks (12 mm in diameter) were punched out with a cork borer. Disks were arranged in groups of 10, identified, weighed, enclosed in 100 µm-mesh bags and incubated in the headwaters of the Agüera Stream (N. Iberian Peninsula; 43º 12’ 36’’ N, 3º 16’ 12’’ W) for one week (13-21 February 2013) to allow fungal colonization. Previous studies reported the Agüera Stream headwaters to be oligotrophic and rich in aquatic hyphomycetes (Pérez et al. 2012). During field incubation, mean water temperature was 8 °C, pH 7.4, conductivity 70.8 $\mu S \cdot cm^{-1}$ and water was oxygen saturated (for more details about the Agüera Stream see Elosegi et al. 2002, 2006). After that week, bags were carried to the laboratory and all but 5 groups of 10 disks were extracted from bags and arranged in a microcosm consisting of a 300-mL glass beaker filled with 60 cm^3 of coarse siliceous sand (2-4 mm) that was previously ashed (500 °C, overnight) and washed with de-ionized water.

In these microcosms we recreated different conditions that leaves could be subject to in drying watercourses: areas with flowing water, stagnant water and dry beds. Flowing water (F) was simulated with aerated water, stagnant water (S) without aeration and dry bed (D) without water. Combining these conditions and their sequence, we created 10 treatments: one was constantly aerated for 6 weeks, and was considered the non-stress Control (Table 1). The other 9 treatments were arranged in 3 groups of increasing stress and differed in the timing of peak stress. In the low stress level (L) leaves were subject to 2 weeks of non-aeration during the 6-week period (3 treatments, with non-aeration in the initial (L.1, the first two weeks), middle (L.2, weeks 3 and 4) and late (L.3, weeks 5 and 6) phases, respectively). In medium stress level (M) leaves were subject to 2 weeks of drought during the 6-week period (3 treatments, with drought in the initial (M.1), middle (M.2) and late (M.3) phases, respectively). High stress level (H) was the most stressing, as leaves were subject to 2 weeks of drought and 4 weeks of non-aeration (3 treatments, with drought in the initial (H.1), middle (H.2) and late (H.3) phases, respectively). After these 6 weeks, the experiment was extended by 4 recovery weeks (R), during which all microcosms were kept with aerated water, which would simulate flow resumption.

During the 10 weeks microcosms were kept at 6 ºC, with a 12:12 light regime. In beakers with water, temperature and dissolved oxygen concentration were measured twice a week and water was changed every week to avoid the concentration of potentially toxic substances. Water for renewal was brought from the Agüera Stream every week and filtered through 100 µm pore size Nytal mesh to remove organic matter. It must be noted that this mesh size can exclude the largest conidia, but not the most abundant microbial inoculum. Adding new spores to microcosms probably homogenized fungal assemblages and made it difficult to detect the disappearance of sensitive taxa, but we aimed to recreate conditions in streams, where new spores arrive when flow is resumed. Every 2 weeks we sacrificed 5 replicate microcosms per treatment to measure fungal biomass, sporulation rates of fungi, microbial respiration and decomposition of alder leaves (5 microcosms$\cdot$treatment$^{-1}\cdot$date^{-1} x 10 treatments x 5 dates = 250 microcosms). On each sampling date 5 of the disks in each microcosm (containing a total of 10 disks) were used to measure respiration rate and ergosterol content subsequently, and the other 5 to estimate sporulation rates. All disks were used to measure decomposition.

Biomass

Fungal biomass was estimated as ergosterol content in disks, which is the main component of fungal cell membrane as well as one of the best descriptors of metabolically active fungal biomass (Gessner & Schmitt 1996; Charcosset & Chauvet 2001; Abelho 2009). From each microcosm, 5 disks out of 10 were frozen at -80 °C after being used to measure

Table 1. Combinations of experimental treatments. All variables were measured after each 2-week period. F = flowing water (aerated water), S = stagnant water (non-aerated water), D = drought (dry). En = experimental phase, Rn = recovery phase. * indicate peak stress.

Stress level	Timing of peak stress	Treatment	Phase: weeks E2: 1-2	E4: 3-4	E6: 5-6	R2: 7-8	R4: 9-10
		Control	F	F	F	F	F
L (low)	1	L.1	S*	F	F	F	F
	2	L.2	F	S*	F	F	F
	3	L.3	F	F	S*	F	F
M (medium)	1	M.1	D*	F	F	F	F
	2	M.2	F	D*	F	F	F
	3	M.3	F	F	D*	F	F
H (high)	1	H.1	D*	S	S	F	F
	2	H.2	S	D*	S	F	F
	3	H.3	S	S	D*	F	F

respiration (see below). Frozen samples were lyophilized and weighed to obtain dry mass (DM). Lipids were extracted by incubating lyophilized samples with 0.14 M KOH in methanol at 80 ºC for 30 min in a shaking bath. Ergosterol was separated and concentrated by solid-phase extraction (Waters Sep-Pack® Vac RC, 500 mg, tC18; Gessner and Schmitt, 1996) and quantified through high pressure liquid chromatography (HPLC, Waters). HPLC system consisted of one pump, injector, column (Licrospher 100 RP-18, 25cm, Merck), UV detector set at 282 nm and a recording unit. Chromatograms were set as follows: 100% mobile phase (100% methanol), flow rate of 1.4 $mL·min^{-1}$, column temperature at 33 ºC, detection wavelength at 282 nm and injection volume of 10 µL. Ergosterol was quantified based on the comparison with ergosterol standards (1-100 $µg·mL^{-1}$, 98% purity ergosterol, Fluka). Results were expressed as µg of $ergosterol·gDM^{-1}$.

Sporulation

To analyze fungal sporulation (i.e. reproductive activity of fungi), the other 5 disks were incubated in 100-mL Erlenmeyer flasks with 25 mL filtered stream water (0.7 µm pore size glass fiber filters, Whatman GF/F) on an orbital shaker (60 rpm; Multitron II) for 48 h at 10 °C (Bärlocher 2005b). Conidial suspensions were decanted to 50-mL centrifuge tubes and 2 mL of 37% formalin were added to fix conidia. Distilled water was added up to 35 mL. The suspensions were stirred to ensure a uniform distribution, and an aliquot was filtered (5 µm pore size mixed cellulose filters, Millipore SMWP). Filters were stained with Cotton Blue in lactic acid (0.05%) and conidia identified and counted under a bright field Leica microscope (a minimum of 300 conidia counted or 0.09 cm^2 of surface viewed). Disks were lyophilized and weighed, and sporulation rates were expressed as number of conidia released·min^{-1}·gDM^{-1}.

Respiration

Microbial respiration rates were measured using a closed six-channel dissolved oxygen measuring system (Strathkelvin 928 System). Oxygen electrodes were calibrated with a solution of 2% sodium sulfite in 0.01 M sodium borate (0% O_2), and 100% O_2 saturated distilled water. Five disks per microcosms were incubated together in chambers with 3 mL 100% O_2 saturated filtered stream water (10 ºC, 40 min) homogenized with a magnetic stirring bar. Chambers without disks were used as a control for oxygen depletion in the water. Oxygen consumption rates were calculated by subtracting the oxygen consumption in the control chamber over a 20-min interval to the consumption in the chamber with the sample. Results were expressed as $mgO_2 \cdot h^{-1} \cdot gDM^{-1}$.

Decomposition

Decomposition was expressed as the percentage of leaf mass loss during the microcosm experiment. Five out of the 255 10-disk groups incubated in the stream for one week were carried to the laboratory, immediately lyophilized and weighed to correct the leaf mass lost during the colonization period in the stream. Remaining mass in each microcosm was calculated summing DM of the 10 disks after lyophilization and expressed as percentage.

Data treatment

The total amount of ergosterol, the cumulative spore production and the cumulative oxygen consumption were calculated following Gessner & Chauvet (1997). The effect of stress level and timing of peak stress were analyzed using data measured at the end of the experimental phase (E6) and during the recovery phase (R2 and R4) by means of a two-way ANOVA, with both stress level (L, M, H) and timing (1, 2, 3) as fixed factors. Interaction between both factors was not significant in all analyses and, therefore, was removed from all two-way ANOVAs. Because timing of the peak stress could not be defined in the non-stress condition, these analyses excluded the Control treatment. Therefore, differences with respect to the non-stress condition were tested by a one-way ANOVA with treatment (the 10 treatments) as fixed factor. Post-hoc Tukey HSD tests were performed when ANOVAs yielded significant differences. When necessary, data were log-transformed to obtain requirements for parametric analyses. To search for general differences in conidial assemblages, a non-metric multidimensional scaling (nMDS) was also performed based on the Bray-Curtis dissimilarity matrix, followed by a PERMANOVA (10^6 permutations) to test the differences along time and among stress levels, timing and treatments. Linear regressions were used to test the relationship between mean ergosterol concentration during the experiment, the cumulative sporulation, the cumulative respiration, and the remaining mass of alder disks at the end of the experiment. All statistical analyses were conducted using R statistical software (version 3.0.2; R Core Team, 2014; Vienna, Austria).

Results

Lack of aeration caused small but statistically significant ($F_{1,449}$ = 159.9, $p < 0.0001$) reduction in oxygen concentration: the minimum saturation measured in non-aerated microcosms was 85%, but the mean saturation during the whole experiment was around 95% in all treatments. Similarly, temperature of water without aeration was higher ($F_{1,426}$ = 50.95, $p < 0.0001$) and the mean temperature during the experiment was slightly higher in treatments within the H stress level (6.26 ºC) than in the rest of the treatments (5.95 ºC).

Biomass

Ergosterol concentration in the Control treatment ranged between 87 and 340 µg·gDM^{-1}, whereas the lowest (1 µg·gDM^{-1}) and highest (531 µg·gDM^{-1}) values of ergosterol concentration were measured in the H stress level, in E2 phase of H.1 treatment and R2 phase of H.3 treatment, respectively (Fig. 1). Although ergosterol concentration measured at the end of the experimental phase (E6) was highest in Control microcosms, these differences were only marginally significant if treatments were considered independently ($F_{9,40}$ = 2.04, p = 0.060). There were significant differences among stress levels ($F_{2,40}$ = 3.44, p = 0.042), but they did not follow the stress gradient: ergosterol content was lowest in disks that were only subject to two weeks of drought (M stress level), highest in leaves subject to a combination of drought and non-aeration (H stress level) and intermediate in leaves subject only to non-aeration (L stress level). The timing of peak stress did not affect ergosterol concentration measured in the E6 phase ($F_{2,40}$ = 0.84, p = 0.441). Subjecting all treatments to aerated water for two weeks stimulated fungal growth in treatments combining drought periods with non-aeration (Fig. 1). Therefore, ergosterol content measured in the R2 phase showed similar patterns but greater differences among stress levels ($F_{2,40}$ = 9.35, $p < 0.001$), ergosterol content in treatments within H stress level being even higher than in the Control treatment ($F_{9,40}$ = 7.61, $p < 0.0001$). Flow resumption also revealed significant differences among timings and, as hypothesized, treatments impacting the late phase showed a higher ergosterol concentration than the ones impacting earlier stages ($F_{2,40}$ = 8.10, p = 0.001). Differences among timings remained in the R4 phase ($F_{2,40}$ = 6.33, p = 0.004), whereas the ones among stress levels disappeared ($F_{2,40}$ = 1.88, p = 0.166). The peak of the total amount of ergosterol was highest in the H stress level (20.4 - 23.9 µg; Table 3) and was measured after subjecting disks to aerated water (R2 phase), whereas in the Control treatment and in the L stress level it only reached 15.6 µg and occurred at the beginning of the experiment (E2 phase). The peak of the total amount of ergosterol, as well as the phase when it occurred, was more variable in the M stress level (Table 3).

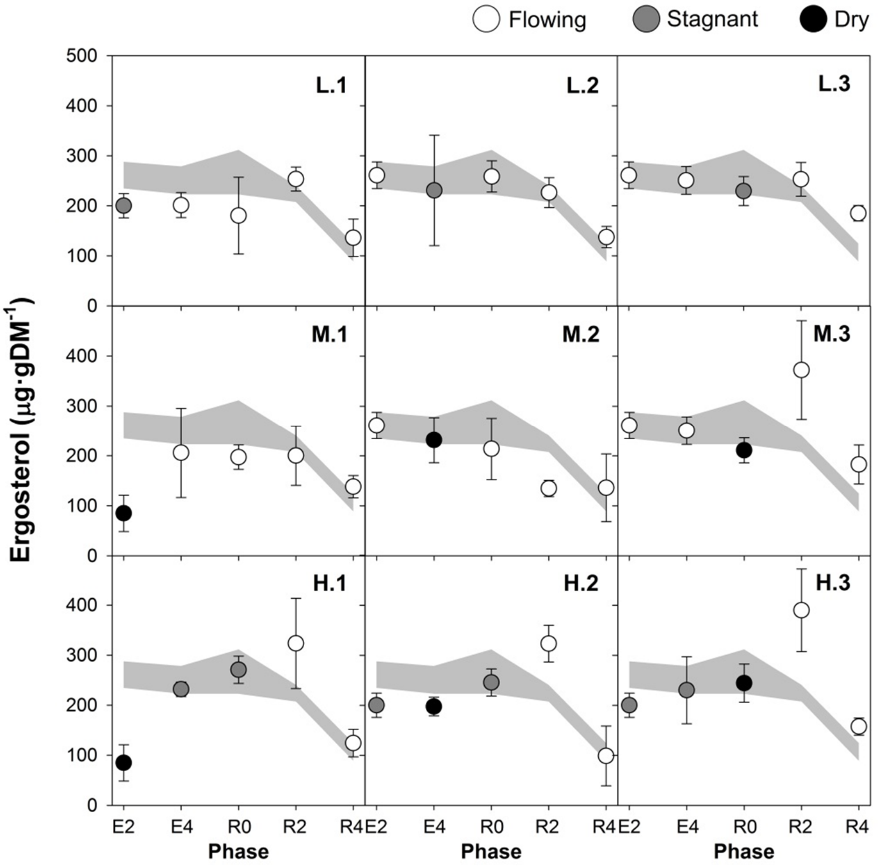

Figure 1. Ergosterol concentration in the low (L), medium (M) and high (H) stress levels with peak stress in the initial (1), middle (2) and late (3) phases. The light grey area indicates 95% confidence interval (CI) of the Control treatment. Color of points indicates the condition in microcosm during the preceding two weeks to measurements. Error bars show 95% CI.

Sporulation

In total, 20 hyphomycete taxa were identified, but only 6 appeared in all treatments and sampling dates, accounting for more than 95% of the conidia in every sample: *Alatospora acuminata, Anguillospora filiformis, Anguillospora* sp, *Articulospora tetracladia, Crucella subtilis* and *Flagellospora curvula*. Although the conidial assemblage changed significantly along time (PERMANOVA: $pseudoF_{3,80} = 0.14$, $p < 0.0001$), these changes were not consistent among stress levels, as shown by statistically significant interaction between stress level and time (PERMANOVA: $pseudoF_{9,104} = 0.13$, $p < 0.0001$), and were mainly driven by the appearance of rare taxa in isolated samples. Changes in assemblages during non-aeration of dry periods were minor, and no taxa proliferated nor disappeared in these conditions. Mean sporulation rates in the Control treatment decreased from 512 spores·min^{-1}·gDM^{-1} on the first sampling date to 68 spores·min^{-1}·gDM^{-1} on the last one (Fig. 2). Sporulation also showed a decreasing trend in the L stress level, falling down to 37 spores·min^{-1}·gDM^{-1} in L.1 microcosms, whereas rates were more variable in M and H stress levels and showed minimum and maximum values at different stages. Therefore, even if sporulation rates differed significantly among stress levels, these differences were not consistent at different phases and did not confirm our hypotheses: sporulation in the H stress level was highest in the E6 phase, while it was lowest in the R2 phase (Table 2).

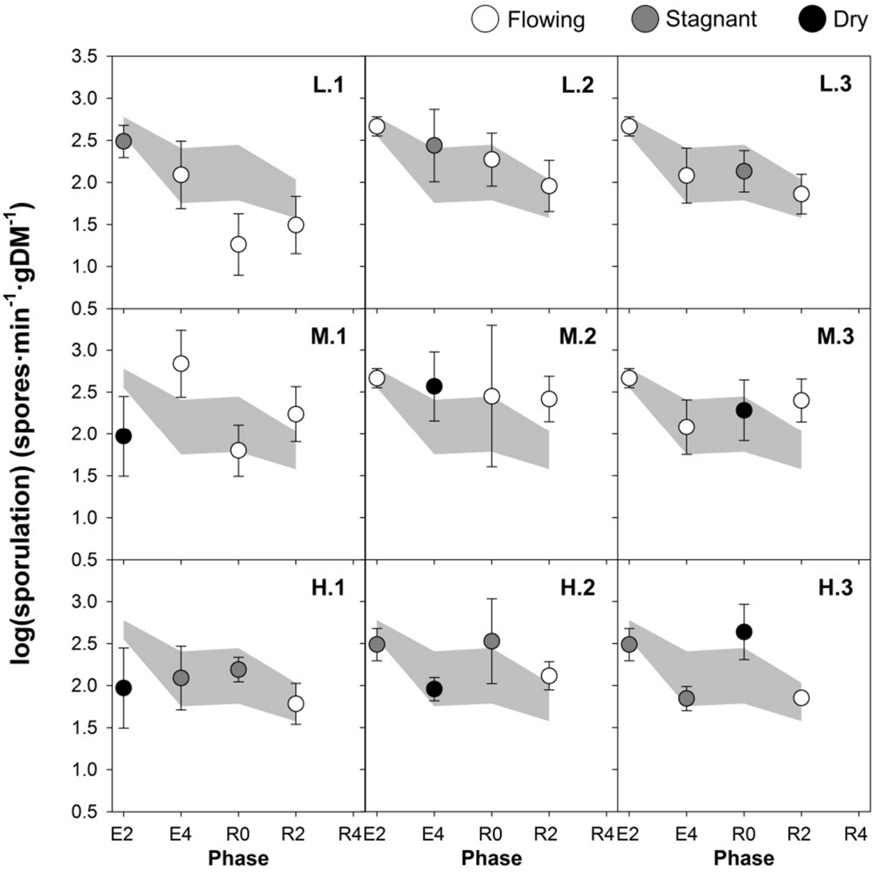

Figure 2. Sporulation rates in the low (L), medium (M) and high (H) stress levels with peak stress in the initial (1), middle (2) and late (3) phases. The light grey area indicates 95% confidence interval (CI) of the Control treatment. Color of points indicates the condition in microcosm during the preceding two weeks to measurements. Error bars show 95% CI. Note that values are log-transformed.

Table 2. Statistical results. Post hoc Tukey HSD tests were only performed when the two-way ANOVA yielded significant differences. Letters are ordered from highest (a) to lowest values.

VARIABLE	PHASE	STRESS LEVEL				TIMING OF PEAK STRESS			
		DF	*F*	*p*	Tukey HSD	DF	*F*	*p*	Tukey HSD
Ergosterol (μg.gDM^{-1})	E6	2,40	3.44	0.042	H^a L^{ab} M^b	2,40	0.84	0.441	
(non-transformed)	R2	2,40	9.35	< 0.001	H^a L^b M^b	2,40	8.10	0.001	3^a 2^b 1^b
	R4	2,40	1.88	0.166		2,40	6.33	0.004	3^a 2^b 1^b
Sporulation	E6	2,22	5.41	0.012	H^a M^{ab} L^b	2,22	9.11	0.001	3^a 2^a 1^b
(log-transformed)	R2	2,22	17.13	< 0.0001	M^a L^b H^b	2,22	5.02	0.016	2^a 3^{ab} 1^b
	R4	-	-	-	-	-	-	-	-
Cumulative sporulation	E6	2,4	4.17	0.105		2,4	1.66	0.299	
(non-transformed)	R2	2,4	4.82	0.086		2,4	4.15	0.106	
	R4	-	-	-	-	-	-	-	-
Respiration	E6	2,40	3.31	0.047	M^a H^{ab} L^b	2,40	4.30	0.020	3^a 2^{ab} 1^b
(non-transformed)	R2	2,40	0.20	0.823		2,40	2.85	0.069	
	R4	2,40	1.04	0.363		2,40	0.31	0.733	
Cumulative respiration	E6	2,4	2.51	0.197		2,4	4.72	0.088	
(non-transformed)	R2	2,4	1.48	0.330		2,4	6.17	0.060	
	R4	2,4	0.48	0.649		2,4	7.00	0.049	3^a 2^{ab} 1^b
Remaining mass	E6	2,40	3.73	0.033	L^a M^{ab} H^b	2,40	2.58	0.088	
(non-transformed)	R2	2,40	23.68	< 0.0001	M^a L^b H^c	2,40	3.02	0.060	
	R4	2,40	5.55	0.007	L^a M^a H^b	2,40	3.84	0.030	2^a 3^{ab} 1^b

The total production of spores was not affected by the stress level ($F_{2,4}$ = 4.82, p = 0.086), even though fungi in the M stress level produced 50% more conidia than the ones in the L and H stress levels (Table 3). On the contrary, the timing of peak stress significantly influenced sporulation rates and, as hypothesized, treatments subject to stress in the initial phase showed lower rates in the E6 phase ($F_{2,22}$ = 9.11, p = 0.001), differences being similar after flow resumption ($F_{2,22}$ = 5.02, p < 0.016; Table 2). Accordingly, treatments impacting the first two weeks produced, on average, 35% less conidia than those impacting the middle of the experimental phase and 20% less than those impacting the late experimental phase (Table 3), although differences were not statistically significant ($F_{2,4}$ = 4.15, p = 0.106; Table 2).

Table 3. The peak of the total amount of ergosterol and the phase when it was measured for each treatment. Mean oxygen consumption and spore production at the end of the experimental (E6) and recovery (R4, R2 in the case of cumulative sporulation) phases.

Treatment	Peak ergosterol		Cumulative respiration (mgO_2)		Cumulative sporulation (spores x10^6)	
	Phase	µg	E6	R4	E6	R2
Control	E2	15.55	11.85	18.88	0.89	1.00
L.1	E2	14.83	11.43	17.75	0.71	0.74
L.2	E2	15.55	11.35	19.25	1.08	1.25
L.3	E2	15.55	11.93	19.05	0.89	1.01
M.1	E4	14.36	10.09	16.79	1.34	1.47
M.2	E2	15.55	12.65	19.45	1.42	1.86
M.3	R2	18.19	12.83	21.34	0.95	1.20
H.1	R2	20.41	9.46	17.47	0.53	0.67
H.2	R2	20.46	10.74	18.42	0.92	1.31
H.3	R2	23.91	11.56	19.65	0.9	1.24

Respiration

Mean respiration rates in the Control treatment decreased from 0.275 $mgO_2 \cdot h^{-1} \cdot gDM^{-1}$ on the first sampling date to 0.183 $mgO_2 \cdot h^{-1} \cdot gDM^{-1}$ on the last date. Only respiration rates measured in the E2 phase after being without aeration or dry were completely out of the 95% CI of the Control treatment (Fig. 3). However, respiration rates measured at the end of the experimental phase significantly differed among stress levels ($F_{2,40}$ = 3.31, p = 0.047) and timing of peak stress ($F_{2,40}$ = 4.30, p = 0.020; Table 2). Differences among stress levels followed neither the severity gradient, nor the pattern observed for ergosterol concentration and sporulation, rates being fastest in the M stress level (on average, 0.26 $mgO_2{\cdot}h^{-1}{\cdot}gDM^{-1}$) and slowest in the L stress level (on average, 0.20 $mgO_2{\cdot}h^{-1}{\cdot}gDM^{-1}$). Like fungal biomass and sporulation, microbial respiration rates were highest in treatments impacted in the late experimental phase (on average, 0.25 $mgO_2{\cdot}h^{-1}{\cdot}gDM^{-1}$) and lowest in the ones impacted in the initial phase (on average, 0.19 $mgO_2{\cdot}h^{-1}{\cdot}gDM^{-1}$). Nevertheless, subjecting all treatments to aerated water resulted in similar respiration rates during the recovery phase ($p > 0.05$; Table 2). Stress level did not affect the total amount of oxygen consumed either by the end of the experimental phase ($F_{2,4} = 2.51$, $p = 0.197$) or by the end of the recovery phase ($F_{2,4} = 0.48$, $p = 0.649$), even though the patterns were similar, consumption being highest in the M stress level and lowest in the H stress level (Table 3). Similarly, differences among timing of peak stress remained constant and fungi perturbed in the late and initial experimental phases consumed, respectively, the highest and lowest amount of oxygen, with these differences being statistically significant by the end of the experiment ($F_{2,4} = 7.00$; $p = 0.049$; Table 3).

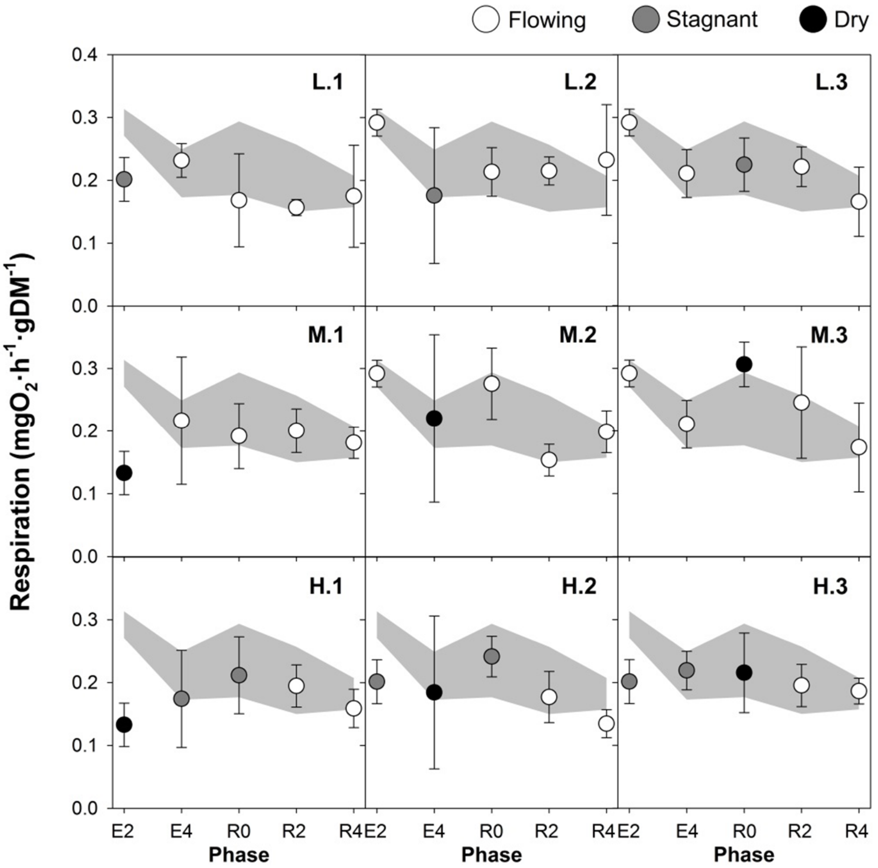

Figure 3. Respiration rates in the low (L), medium (M) and high (H) stress levels with peak stress in the initial (1), middle (2) and late (3) phases. The light grey area indicates 95% confidence interval (CI) of the Control treatment. Color of points indicates the condition in microcosm during the preceding two weeks to measurements. Error bars show 95% CI.

Decomposition

Alder disks in the Control treatment lost, on average, 25% of their initial DM, with decomposition mainly occurring during the first 6 weeks (Fig. 4). Decomposition in treatments within L stress level was similar to that in the Control treatment, i.e. being significantly higher than in M and H stress levels ($F_{2,40} = 3.73$, $p = 0.033$; Table 2). Although decomposition in L.3 and L.2 tended to be higher than in L.1 (Fig. 4), overall, they were not statistically different ($F_{2,40} = 2.58$, $p = 0.088$). Flow resumption accelerated decomposition in the M stress level and by the end of the experiment leaf disks within L and M stress levels lost, on average, around 25% of their initial DM, like in Control microcosms. Subjecting treatments within H stress level to aerated water did not counterbalance the reduction of decomposition due to the first 6-week period, and disks only lost 10-15% of the initial DM ($F_{2,40} = 5.14$, $p = 0.010$). Flow resumption also revealed differences among timings, decomposition being lowest in treatments perturbed in the initial phase and highest in the ones perturbed in the medium phase ($F_{2,40} = 3.50$, $p = 0.040$).

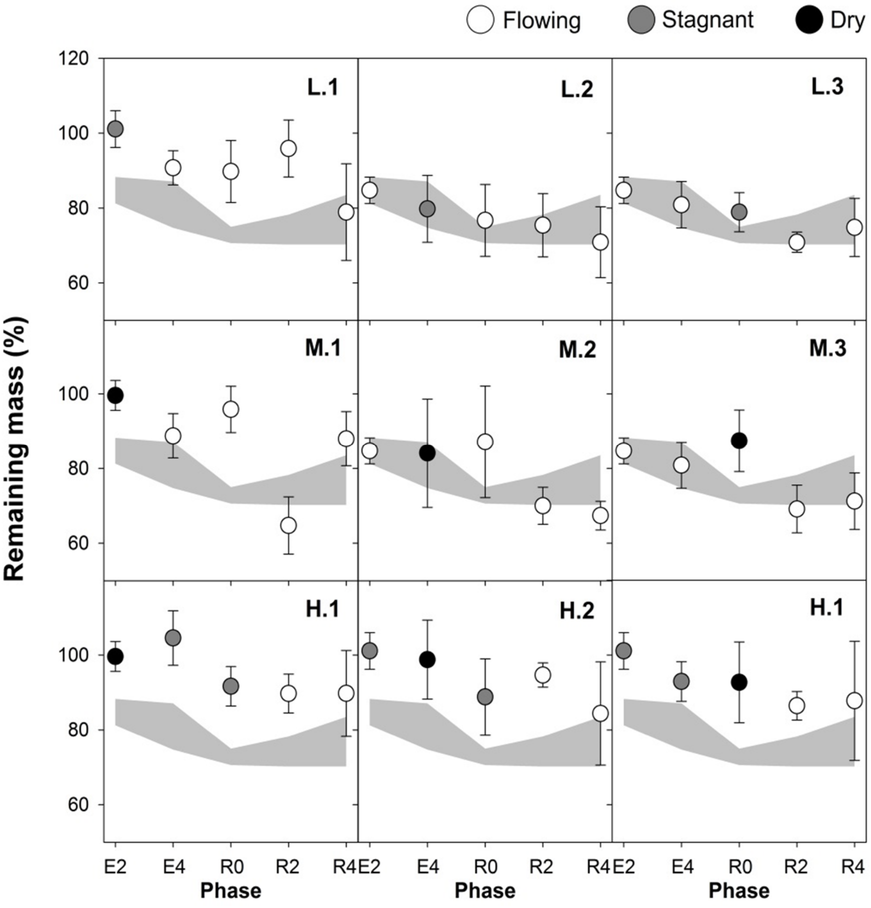

Figure 4. Remaining mass of alder disks in the low (L), medium (M) and high (H) stress levels with peak stress in the initial (1), middle (2) and late (3), phases. The light grey area indicates 95% confidence interval (CI) of the Control treatment. Color of points indicates the condition in microcosm during the preceding two weeks to measurements. Error bars show 95% CI.

The remaining mass of alder disks at the end of the experiment was significantly related only to the cumulative respiration ($r^2 = 0.40$, $p = 0.048$): the higher the oxygen consumption, the lower the remaining mass. Among all the other possible regressions, only the one between mean ergosterol concentration and cumulative respiration was statistically significant ($r^2 = 0.56$, $p = 0.012$).

Discussion

Differences among stress levels in our experiment had no consistent effects on most measured response variables, probably reflecting that we recreated a small stress range. Our experimental conditions had little effect on aquatic hyphomycete assemblages and seemed neither to benefit nor to lead to extinction of any taxa, six taxa always accounting for more than 95% of the conidia. In addition, although microbial variables, both structural (biomass and structure of fungal assemblages) and functional (rates of fungal sporulation and microbial respiration), showed significant differences at the end of the experimental phase, they did not rank following the stress gradient, neither did the different variables show a common ranking among stress levels. However, despite the small differences and the lack of consistent patterns in the variables so far mentioned, decomposition of alder disks was significantly reduced in the H stress level, thus showing a pronounced effect of lack of aeration and drought. On the other hand, early impacts tended to be more detrimental than impacts at a later stage, resulting, in general, in a lower fungal biomass and activity, and reduced litter decomposition.

Pool isolation and water stagnation are known to alter water physico-chemical properties, enhancing the accumulation of organic matter, concentrating nutrients and potentially toxic leachates, increasing water temperature and often resulting in hypoxic conditions (Lake 2003; Canhoto & Laranjeira 2007), which strongly affects microbial communities and processes (Foulquier et al. 2014). The conditions in our experimental treatments were less harsh, as a consequence of weekly water renewal and the experiment being performed in closed systems at constant temperature, contrasting with the higher temperature commonly observed in isolated pools (Boulton 2003; Muñoz 2003). The effect of non-aeration in our microcosms was biologically irrelevant even on oxygen concentration, although it can be extremely strong in the field (Acuña et al. 2005) and severely impair aquatic fungi (Medeiros et al. 2009). Other effects of aeration might remain important in our experiment, namely turbulence, which increases the probability of a spore to colonize leaf litter, promotes nutrient renewal and decreases the concentration of potentially toxic exudates close to the microbial community (Schlief & Mutz 2007; Canhoto et al. 2013). Still, results obtained in non-aerated treatments were very similar to those in Control microcosms, especially in treatments impacting middle (L.2) and late (L.3) phases. It is likely that the effects of non-aeration would be stronger if they had resulted in stronger anoxia, as has often been reported for drying streams (Acuña et al. 2005).

Drying alters the structure and activity of microbial assemblages, and slows down the decomposition of organic matter stranded in emerged sediments (Romaní et al. 2012; Mora 2015). Nevertheless, most studies are focused on summer droughts characterized by high temperatures and very dry air conditions (Ylla et al. 2010; Vázquez et al. 2011), whereas temperature in our chamber was cold and atmosphere very humid. These conditions could lead to underestimation of the effects of natural summer droughts, but could also reflect better human-induced droughts in humid regions (e.g. caused by water abstraction). As a result, alder disks did not completely dry up and, because aquatic fungi are able to persist in moist substrata (Sanders & Webster 1978; Sridhar & Bärlocher 1993; Chauvet et al. 2015), fungal activity in our microcosms recovered quickly after rewetting, as has been described elsewhere (Langhans & Tockner 2006). Indeed, at the end of the experiment, mass loss in the M stress level was similar to that in Control and L microcosms. Our results agree with those from Bruder et al. (2011) that showed severe drying (oven dried) to have long-term consequences on fungal biomass, whereas the effects of less severe desiccation, more similar to natural conditions in streams, were not significant. It is also likely that our experiment underestimated the effects of pool isolation and drought, as other factors such as abrasion and fragmentation by macroinvertebrates, which are important in decomposition (Graça 2001; Hieber & Gessner 2002), are strongly affected by flow reduction (Acuña et al. 2005; Arroita et al. 2015).

Overall, conclusions concerning stress level changed depending on the variable, because variables differ in their sensitivity to stress. In our study, decomposition rate was more sensitive than fungal biomass, sporulation or respiration to differences among stress levels, likely because it integrated all processes occurring during the whole experiment, whereas the rest of the variables relied on punctual determinations informing about the status of microbial assemblages at definite times and, thus, could be more inherent to noise. The significant relationship between total oxygen consumption and alder decomposition suggests cumulative microbial respiration could be an appropriate surrogate, but statistical power was lost when calculating the cumulative oxygen consumption. Although previous studies reported that fungi contributed to more than 98% to the microbial biomass and emphasized the greater role of fungi than bacteria in organic matter decomposition (Baldy et al. 1995; Gulis & Suberkropp 2003; Pascoal et al. 2005), in our study, alder leaf mass loss was not related to mean ergosterol concentration. Some studies also found a strong relationship between sporulation and fungal biomass and/or leaf litter decomposition (Pascoal & Cássio 2004), whereas others reported sporulation not to be related to these variables (Lecerf & Chauvet 2008; Martínez et al. 2014), as in our case. Taxa from several fungal phyla as well as bacteria and archeobacteria are able to colonize leaf litter (Nikolcheva & Bärlocher 2004; Manerkar et al. 2008), all of which do not produce conidia. Moreover, species with high reproductive activity are not always the ones producing more biomass (Duarte et al. 2006) and fungal involvement in leaf decomposition is reflected by the active mycelia, not the conidia.

Finally, the consistency of our results indicating early impacts to be more detrimental than impacts in later stages shows that the legacy effects of stress affect the assemblages even after they return to more benign conditions. Therefore, the impacts of stress on leaf breakdown-associated variables depend not only on the duration of stress, but also on that of post-stress periods. In particular, the effects of droughts on leaf litter decomposition can start as early as in the preconditioning phase (Dieter et al. 2011, 2013) and endure during the whole process (Datry et al. 2011; Martínez et al. 2015). These results could also apply to other ecological processes showing a clear succession of steps in which the last outcome integrates the processes occurring in the entire sequence. For instance, the biomass produced by an ecosystem would be more affected by disturbances occurring early than late in the year. Therefore, the timing of an impact can be as relevant as its intensity or frequency, emphasizing the weight of contingency.

Acknowledgements

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CHAPTER 5

Shrinking out: channel contraction drives the global impact of water abstraction on stream ecosystem functioning

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Abstract

Water abstraction is rapidly increasing worldwide in order to respond to the escalating demand for water, food and energy. Abstraction alters the hydrological regime of streams and rivers, reduces instream habitats, can degrade water quality and affects fluvial communities, and thus, can impair ecosystem functioning, although this aspect has been seldom assessed. We experimentally abstracted water from a headwater mountain stream by putting in operation a long-unused diversion scheme following a Before-After/Control-Impact design. We present a case study of the impacts of abstraction on water quality, biofilm biomass and activity, and on ecosystem processes (nutrient retention, metabolism, organic matter retention and breakdown), at the patch and at the reach scales. Although abstraction did not affect water quality, at the patch scale it reduced the biomass and the alkaline phosphatase activity of biofilm, and the uptake of nutrients, but did not affect either metabolism or litter breakdown. At the reach level all variables except benthic chlorophyll-*a* and leaf retention were significantly reduced by abstraction, as a consequence of the reduced surface of the wetted channel. Our results suggest that water abstraction has a strong impact on stream ecosystem functioning. Despite being derived from a single case study, they show the main impacts to be associated with decreased wetted perimeter, which is a universal consequence of water abstraction. Therefore, they suggest that as water abstraction becomes more prevalent the services we obtain from the functioning of these ecosystems will fade as streams and rivers shrink out.

Keywords: water diversion, biofilm, nutrient retention, metabolism, organic matter, breakdown, ecosystem services, hydropower, low dam

Introduction

Diversion and abstraction of water are prevalent impacts in streams and rivers (Nilsson et al. 2005), likely to increase even more in the near future (Poff et al. 2003; Finer & Jenkins 2012), driven by the escalating demand, especially for irrigation, hydropower and drinking water (Palmer et al. 2008). Worldwide, the surface of irrigated lands has doubled during the last 5 decades (Gleick 2003; FAO 2009) and future projections claim for further expansion (DeFries et al. 2004; Scanlon et al. 2007), in order to counterbalance rising temperatures (Gibelin & Déqué 2003), altered seasonality (Sánchez et al. 2004) and enhanced torrentiality (Räisänen et al. 2004). Concurrently, the energy demand keeps increasing as more than 1.4 billion people still lack access to electricity and the per capita demand of the rest is rising (UNEP 2012b), what makes securing the future energy demand an essential goal for the society (Crousillat et al. 2010; UN-Energy 2010). As the Kyoto protocol enforces nations to reduce their use of fossil fuels (UNEP 2012b), renewable energy sources are gaining importance, hydropower contributing 80% to the total share of renewables (The World Bank 2014a, b). Supply of drinking water is also forcing governments to increasingly build large water abstraction schemes, especially around big towns in dry regions (Dahm et al. 2013). Therefore, water abstraction is increasing rapidly worldwide up to the point that the global water system has been transformed (Vörösmarty et al. 2004) with dams (Nilsson et al. 2005) and extensive waterways and systems for groundwater abstraction (Acreman et al. 2000). The environmental consequences of these changes acquire global dimensions and include the contraction of large lake systems (Beeton 2002), greening of drylands for agriculture (Helldén & Tottrup 2008), or increase in urban sprawl (Deacon et al. 2007). Less is known on the consequences on the donor streams and rivers.

Water can be abstracted from streams and rivers in various ways, but often a weir or dam is used to stop and divert water. There is an extensive body of research on the downstream impacts of large dams, which include changes in hydrology (Poff & Allan 1995), sediment transport (Tena et al. 2011), channel morphology (Lobera et al. 2015), water temperature (Olden & Naiman 2010) and chemistry (Friedl & Wüest 2002), which could have severe effects on riverine communities (Haxton & Findlay 2008). Less is known on the effects of water abstraction by low weirs, likely because they are perceived as less dramatic. Nevertheless, water abstraction in this type of scheme is extremely frequent in the world (Zarfl et al. 2015), and has been reported to reduce discharge, up to the point that it can convert perennial streams into intermittent, which strongly reduces their longitudinal connectivity (Malmqvist & Rundle 2002). Even when it is not so dramatic, reduction in discharge results in a contraction of river ecosystems, decreasing the surface and quality of instream habitats (Stanley et al. 1997). Abstraction by low weirs can also have strong effects on water temperature (Meier et al. 2003; Bae et al. 2015), and greatly reduce biofilm (Mosisch 2001). When water is diverted from the stream channel, many benthic invertebrates move to the remaining pools, where they can accumulate in large densities (Dewson et al. 2007a; Verdonschot et al. 2015), or alternatively, they can abandon the reach through drift (James et al. 2008). Fish communities are also strongly affected (Xenopoulos et al. 2005; Benejam et al. 2010, 2014). Abstraction schemes include other impacts, such as barriers to dispersal (Nislow et al. 2011) or drowning in diversion canals (Benstead et al. 1999; Roberts & Rahel 2008), thus threatening biodiversity within the hydrographic network.

These changes are likely to have detrimental consequences on the functioning of fluvial ecosystems, since all hydraulics, channel morphology and biodiversity are tightly linked to ecosystem processes (Gücker & Boëchat 2004; Elosegi et al. 2011; Elosegi & Sabater 2013). Stream ecosystem functioning comprehends a variety of processes including production, retention and decomposition of organic matter, or retention and recycling of nutrients (von Schiller et al. 2008; Young et al. 2008; Elosegi et al. 2010), and is considered one of the main goals of stream management (Boulton 1999), as it drives key ecosystem services (Costanza et al. 1997; Sweeney et al. 2004). However, to the best of our knowledge, the literature about the impacts of water abstraction on the functioning of stream ecosystems comprises only a few studies, mostly limited to comparisons between reaches upstream and downstream from dams (Arroita et al. 2015). Unfortunately, manipulative experiments on water abstraction are very difficult to perform and have been seldom attempted (e.g. Dewson et al. 2007b). Therefore, it is crucial to gain a better understanding of the impacts of such a prevalent human activity, and to do so by means of more powerful designs.

An important point is the scale at which the impacts of water abstraction are analyzed. The most evident effect of abstraction is the reduction of the surface covered by water ("ecosystem contraction" sensu Stanley et al. 1997). Therefore, even if water abstraction would not affect a variable at the patch scale (i.e. measured per square meter of stream bed), it could have significant effects at the reach scale (i.e. measured per linear km of channel length), as shown by Sweeney et al. (2004) in streams narrowed due to forest clearing. Moreover, from the point of view of global change, as well as from the perspective of ecosystem services, the reach scale is more meaningful than the patch scale (Battin et al. 2009).

We assessed the impact of water abstraction on stream ecosystem functioning at both the patch and the reach scales by means of a manipulative experiment. We measured a range of variables important for stream ecosystem functioning, from biofilm biomass and activity to retention and processing of nutrients and organic matter, in the most comprehensive study so far published as far as we know. We hypothesized water abstraction to deteriorate environmental conditions for organisms. Sessile organisms (biofilm) would respond with decreased biomass, deteriorated physiological status and reduced biological activity, whereas for mobile organisms (invertebrates) we hypothesized an initial concentration as animals move towards the center of the channel in seek for favorable conditions, what would accelerate the consumption of organic matter, followed by a decrease as the animals abandon the reach or die. At the reach scale, we hypothesized the impacts of water abstraction to be accentuated by the reduction of wetter perimeter (ecosystem contraction).

Materials and methods

Study site and experimental design

The study was conducted in Urdallue (43º 12’ 46” N, 1º 48’ 15” W), a headwater mountain stream in the basin of Artikutza (Navarre). It drains a basin of 700 Ha over granite and schist, with an average rainfall over 2,500 mm per year and a mean annual air temperature of 12.2 ºC (http://meteo.navarra.es/). The entire basin of Artikutza (3,638 Ha) was bought in 1919 by the municipality of San Sebastian and managed as a strict reserve to guarantee high quality drinking water, which resulted in an extensive deciduous forest cover (Castro 2009). A number of hydraulic infrastructures (dams, weirs, diversion canals) remain as legacies from past activities, but have been unused during the last decades with the exception of the present experiment.

We experimentally abstracted water by putting in operation one diversion scheme in Urdallue Stream, which consists of a low dam (2 m height) and an underground diversion canal. Because the diversion scheme had not been operating for decades, the dam was filled with gravel- to boulder-sized sediments and did not disrupt bed-load during floods. Therefore, from the point of view of channel form and water quality the impact of the dam seemed negligible. The abstraction experiment thus followed a Before-After/Control-Impact (BACI) design, which is one of the most powerful designs to monitor ecological impacts in rivers (Downes et al. 2002): we set a Control (C) reach upstream from the low dam and an Impact (I) reach immediately below, both 100-m-long; variables were measured in both reaches Before (B) and After (A) opening the lock-gate of the diversion canal, on July 1st 2014. Both reaches were sampled four times within each period (B, A) with a separation of at least seven days between consecutive samples. The lock-gate was regulated to mimic the operation of hydropower schemes in the region, which are allowed to divert up to 90% of the average discharge, but we took additional care not to disrupt longitudinal connectivity, i.e. not to allow the stream to become intermittent.

Hydraulics

Hydraulic parameters were estimated from the time-conductivity curves obtained with pulse additions of a hydrological tracer (Cl^- as NaCl, see below). Discharge and water velocity were calculated based on a mass-balance approach, using electrical conductivity (EC) data as a surrogate of the chloride concentration (Martí & Sabater 2009). Additionally, we placed a levelogger (Solinst Levelogger 3001) in each reach and a barologger (Solinst Barologger 3001) on the ground, which registered data every 10 min from April 30th to September 2nd. Absolute pressure (measured by the leveloggers) was corrected for atmospheric pressure (measured by the barologger) and calibrated with the discharge calculated from time-conductivity curves in order to obtain continuous discharge data.

On each sampling date we measured water temperature, dissolved oxygen concentration (YSI ProODO), pH (Hanna Hi 9025) and EC (WTW 340i), and characterized physical habitat measuring width of the wet channel and water depth in equidistant transects (11 in Control and 9 in Impact; every 50 cm along the transects).

Biofilm

Biofilm was characterized by its biomass, chlorophyll-*a* concentration (Chl-*a*) and exoenzyme activity. In each reach, biofilm was sampled from six cobbles randomly selected in the wet channel, after they were used to measure metabolism (see below). Before diversion, we scraped three samples of an area of 19.60 cm^2 from the surface of each cobble, and used each sample to measure one of the variables mentioned above. Because biofilm abundance and activity decreased considerably during the experiment due to tree canopy development, after diversion we sampled the whole surface of the cobbles. The slurry so obtained per cobble was split in three subsamples, one for each determination. Surface areas were measured using aluminum foil of known density. In these surfaces all the epilithic material was scraped using scalpels, toothbrushes and Pasteur pipettes. Samples were stored with filtered stream water (0.22 μm pore size glass fiber filters, Whatman GSWP) in plastic containers, and carried to the laboratory in an ice box. Samples for biomass and Chl-*a* were frozen (-20 ºC) until analysis. They were later thawed, homogenized and filtered (1.2 μm pore size glass fiber filters, Whatman GF/C). Filters to determine biofilm biomass were dried (70 ºC, 72 h), weighed, ashed (500 ºC, 5 h) and weighed again to obtain ash-free dry mass (AFDM), which was expressed as $g \cdot m^{-2}$. Chl-*a* was extracted from the filters with 90% v/v acetone overnight at 4 ºC and quantified spectrophotometrically (Shimadzu UV1603) after centrifuging (2000 rpm, 10 min; P-Selecta Mixtasel) the extract (Sartory & Grobelaar 1984). Results were expressed as $mg \cdot m^{-2}$. We also calculated the biofilm autotrophic index, which indicates the ratio of biofilm biomass to Chl-*a* (Steinman et al. 2006).

Exoenzyme activity was determined following Saiya-Cork et al. (2002). Biofilm samples were blend with acetate buffer (50 mM, pH 5). The potential activities of alkaline phosphatase (AP) and β-Glucosidase (BG) were assayed fluorometrically (365 nm excitation, 450 nm emissions) using 4-Methylumbelliferyl phosphate and 4-Methylumbelliferyl β-D-glucopyranoside, respectively. Assays were conducted in 96-well microplates, and fluorescence was read with a Tecan GENios microplate reader. Appropriate blanks and controls were used to account for autofluorescence and quenching. Results were expressed as $\mu mol \cdot h^{-1} \cdot m^{-2}$.

Nutrient retention

Retention of NH_4^+-N and PO_4^{3-}-P was measured using the pulse addition technique (Martí & Sabater 2009). After performing addition assays in the entire or part of the Control and Impact reaches, we selected 60-m-long reaches that excluded big pools. NH_4Cl and $Na(H_2PO_4) \cdot H_2O$ were dissolved in 30 L, together with a hydrological tracer (Cl^- as NaCl; Bencala et al. 1987). The amount of reagents was set in order to increase fivefold the background concentration of nutrients. The solution was added to the stream in a single pulse in a point of high turbulence where fast mixing with stream water was ensured. We recorded EC (WTW 340i) at the end of the selected reaches until conductivity returned to pre-addition values. Water samples were collected in 250-mL, acid-washed polyethylene bottles across the breakthrough curve (n = 25 – 40). Water samples were filtered (0.7 µm pore size glass fiber filters, Whatman GF/F) in situ and transported in the same day to the laboratory refrigerated in dark. The concentration of NH_4^+-N was analyzed by colorimetry following a modified Berthelot reaction using salicytate and dichloroisocyanurate (Spectrophotometer Jasco V-630; Krom 1980). The concentration of PO_4^{3-}-P was analyzed colorimetrically following the ascorbic acid method (APHA 1992). We used two methods to calculate nutrient uptake: the Tracer Additions for Spiralling Curve Characterization (TASCC) approach described by Covino et al. (2010) and the classic mass-balance approach using conductivity data as a surrogate of chloride concentration (Martí & Sabater 2009). The latter gave more consistent results, and so, was the method finally used to calculate nutrient travel distance (m), uptake velocity ($m \cdot s^{-1}$) and areal uptake ($\mu g \cdot min^{-1} \cdot m^{-2}$).

Metabolism

Metabolism was measured in closed chambers, as the fact that oxygen concentration was constantly around saturation prevented us from using the open-channel methods. On each occasion, six randomly selected cobbles per reach were enclosed for two hours in 20 x 30 x 15 cm perspex chambers where water was kept recirculating by mean of aquarium pumps (Maxi Jet 750) (Bott et al. 1978). Chambers were submerged in water and three of them were covered with black, opaque plastic. Water temperature and oxygen concentration were measured at the onset and at the end of the experiment (YSI ProODO). Photosynthetically active radiation (PAR) reaching the water surface was recorded every 15 min during the incubations (LI-COR LI-240SA). The volume and the surface of each cobble were measured using a bucket, a beaker and aluminum foil of known density. Changes in oxygen concentration in dark chambers were used to calculate community respiration (CR), those in light chambers to calculate net metabolism (NM), and the sum of both to calculate gross primary production (GPP), which were all expressed as $mgO_2 \cdot h^{-1} \cdot m^{-2}$ (Fellows et al. 2001).

Organic matter retention

Organic matter retention was measured following the multiple-point collection method (Elosegi 2005). Freshly fallen *Ginkgo biloba* L. leaves were collected the previous autumn, air-dried at room temperature (20 ºC) and stored in the dark. Prior to the measurements, leaves were soaked overnight in tap water to ensure neutral buoyancy. The downstream end of each reach was blocked with nets, and 100 leaves were released in the upstream end of the reach. After 30 minutes, we measured the distance travelled by each leaf to the nearest meter. Retention rate (m^{-1}) and average travel distance (m) were calculated following the negative exponential decay model (Newbold et al. 1981; Young et al. 1978). Areal organic matter retention was calculated following the equations used for areal nutrient uptake (Martí & Sabater 2009), assuming a basal concentration of 1 $leaf \cdot m^{-3}$ and results were expressed as $\#leaves \cdot h^{-1} \cdot m^{-2}$. Our assumption of basal concentration was done just to compute the effect of water abstraction on areal retention, but the exact number is irrelevant, as it would affect equally Control and Impact reaches, as far as the diversion does not affect the concentration of leaves in transport.

Organic matter breakdown

Organic matter breakdown was estimated in three consecutive experiments: one before diversion (E1: late June), one immediately after diversion to assess immediate effects (E2: early July), and one after 6 weeks to assess mid-term effects (E3: mid-August). Freshly fallen black alder (*Alnus glutinosa* (L.) Gaertner) leaves were collected the previous autumn, air-dried at room temperature (20 ºC) to constant mass, and enclosed in labeled plastic bags (5 ± 0.05 g in each bag). Fine (1 mm) and coarse (5 mm) mesh bags were used to compare the response of consumers of different size, as we assumed there could be differences in their mobility. Prior to each experiment, litter bags (n = 15 per mesh size, reach and experiment) were enclosed in 100-µm-mesh duffles that exclude invertebrates and pre-conditioned in the stream for two weeks to allow for microbial colonization. Leaching and mass loss during the pre-conditioning time was calculated on an additional set of five bags and used to correct the initial mass in the rest of the bags. After pre-conditioning, bags were tied with nylon line to metal bars or roots in the stream channel at different water depths: in each reach, five bags of each mesh size were placed in shallow areas (< 5 cm), five in medium areas (5 – 15 cm) and five in deep areas (> 15 cm). These areas were chosen the day bags for E1 were deployed, and bags for E2 and E3 were placed exactly in the same spots. Incubation lasted two weeks in each experiment. Upon retrieval, bags were stored in individual zip-lock bags and carried refrigerated to the laboratory. Samples were rinsed with distilled water to remove invertebrates and mineral particles, oven-dried (70 ºC, 72 h), weighed, combusted (500 ºC, 5 h) and weighed again to obtain the AFDM. Breakdown rates were calculated according to the negative exponential model (Petersen & Cummins 1974).

Data treatment

All variables were analyzed at both the patch and the reach scales. Results obtained per surface unit were multiplied by the mean width of the wet channel to calculate variables per unit length. For organic matter breakdown, only bags that were immersed during the whole experiment were used to determine breakdown in the wetted channel (considered the patch scale), whereas all bags, including the ones that got dry, were considered to determine breakdown at the reach scale. Exoenzyme activity, nutrient uptake and metabolic parameters were also analyzed per gram of biofilm to get information on the physiological performance of biofilm.

The effect size of water abstraction was calculated at both scales by dividing average I/C ratios after diversion by ratios before diversion, and expressed as percentage. Values below 100% indicate that water abstraction reduced the value of the variable, and values above 100% that it increased them.

Linear mixed-effect models (Pinheiro & Bates 2000) were performed using period (B, A) and reach (C, I) as fixed factors and sampling date as random factor. Because there was a significant linear relationship between PAR and GPP, PAR was added as a covariable in GPP models. The effect of water abstraction on the variables was given by the interaction between period and reach (BA:CI). To test the impacts on organic matter breakdown, the fixed factor experiment (E1, E2, E3) was used instead of period, and the random factor spot where bags were incubated instead of sampling date. Therefore, the interaction between experiment and reach was analyzed in this case, and Tukey HSD tests were carried out for post hoc pairwise comparisons. When necessary, data were log-transformed to obtain requirements for parametric analyses. We used restricted maximum likelihood (REML) to estimate the components of the variance in all mixed-effects models. All statistical analyses were conducted using R statistical software (version 3.0.2; R Core Team, 2014; Vienna, Austria).

Results

Hydraulics

Discharge in the Control reach ranged from 65 to 1690 $L \cdot s^{-1}$ during the experiment. In general, it showed a decreasing trend through time, typical in the transition from spring to summer, with some peaks during storms, especially on July 3rd, 2 days after opening the lock-gate (Fig. 1). In the Impact reach the dynamics before diversion were exactly the same, but after diversion discharge was reduced to 35% on average (Table 1), except during floods, when the effect of abstraction was barely discernible. Our minimum discharge of 10 $L \cdot s^{-1}$ was very close to the discharge in which the stream became reduced to isolated pools, thus loosing hydrological connectivity. Since we were not allowed to cross this

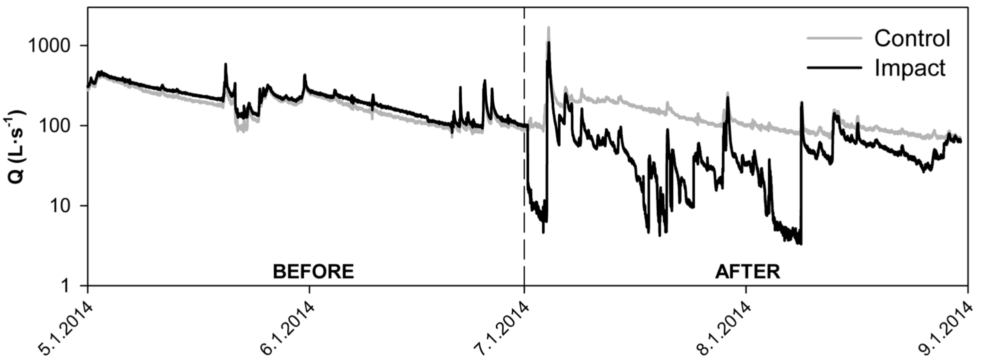

Figure 1. Water discharge in the Control and Impact reaches. The dashed line marks the beginning of diversion. Notice that the y axes is in log scale.

threshold, discharge in the Impact reach was kept always over this value.

Water temperature ranged from 11 to 16 ºC in Control and Impact reaches, it was well oxygenated (saturation = 98 ± 4%), pH kept circumneutral (6.5 ± 0.3) and EC low (47.5 ± 2.6 $\mu S \cdot cm^{-1}$). Water abstraction did not affect water quality (BA:CI: $p > 0.05$), but led to a statistically significant reduction in the wetted perimeter (Table 1). In the Control reach channel width remained between 4.73-5.83 m during the whole experiment, water depth between 9.25-13.09 cm, and water velocity between 0.27-0.47 $m \cdot s^{-1}$, whereas in the Impact reach channel width decreased, on average, from 4.80 to 2.21 m as a consequence of abstraction (F = 138.44, $p < 0.0001$), depth from 9.50 to 5.06 cm (F = 5.98, p = 0.011) and water velocity from 0.44 to 0.18 $m \cdot s^{-1}$ (F = 31.08, $p <$ 0.001).

Biofilm

Biofilm biomass in the Control reach decreased from 10 $g \cdot m^{-2}$ on the first sampling day to 4.20 $g \cdot m^{-2}$ by the second sampling day, and remained between 3 and 5 $g \cdot m^{-2}$ during the rest of the experiment (Fig. 2a). Biomass in the Impact reach showed similar values before water diversion, but abstraction reduced it a further 47%, which was statistically significant (F = 5.18, p = 0.023; Table 1). Biomass at the reach scale displayed the same pattern before diversion and halved in both reaches, but water abstraction reduced biomass in the Impact reach by 74% (F = 26.09, $p <$ 0.0001; Table 1; Fig. 2b).

Chl-*a* concentration at both scales was also highest on the first sampling day and decreased afterwards (Fig. 2c, d). The impact of abstraction on Chl-*a* was not statistically significant either at the patch (F = 0.01, p = 0.928) or at the reach scale (F = 2.57, p = 0.107), despite a reduction, on average, down to 42% in the Impact reach (Table 1). Water abstraction changed the biofilm autotrophic index significantly (F = 3.81, p = 0.047): on average, it increased from 283 to 444 in the Control reach,

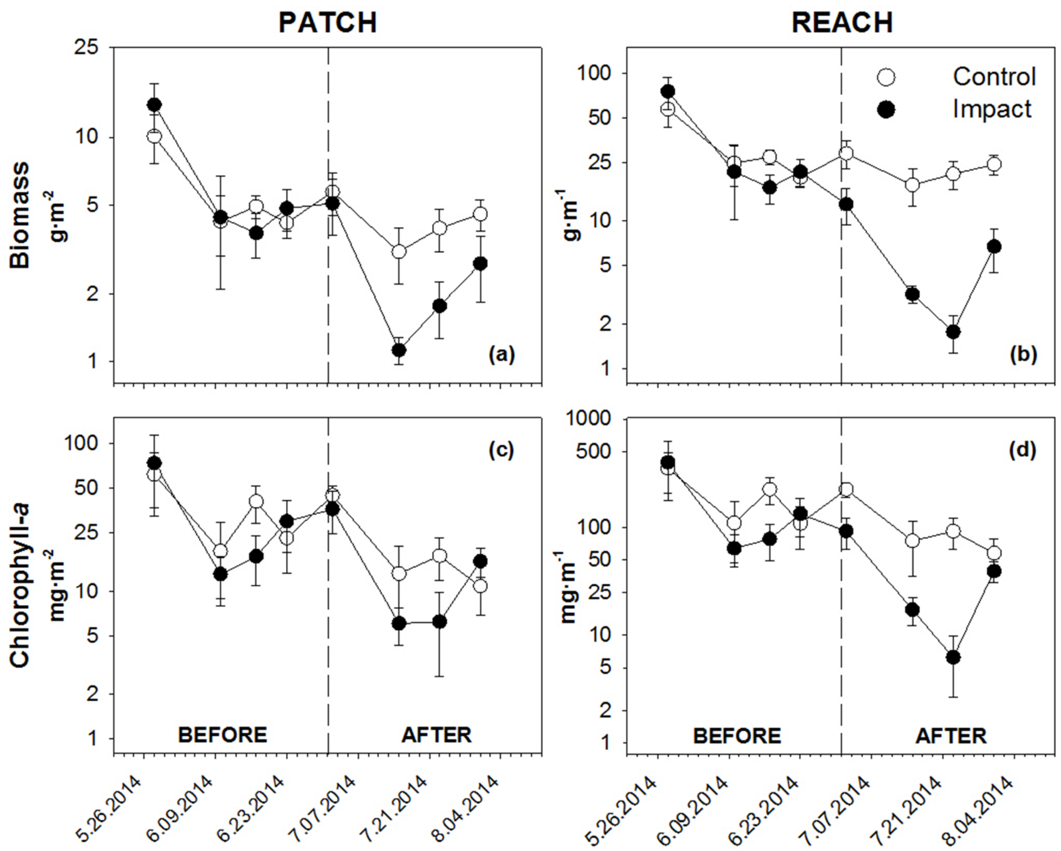

Figure 2. Biofilm biomass (a, b) and Chl-*a* concentration (c, d) at the patch (a, c) and the reach (b, d) scales in the Control and Impact reaches. The dashed line marks the beginning of diversion. Error bars show SE. Notice that the y axes are in log scale.

whereas it decreased from 430 to 263 below the dam (see Appendix 1).

In the Control reach, exoenzyme activities showed an exponential decay at both scales: AP decreased down to 10% and BG to 1% by mid-late June (Fig. 3). In the Impact reach, AP values were similar before diversion, but water abstraction significantly reduced AP activity (Table 1; Fig. 3a, b), differences being higher at the reach scale (patch: $F = 7.71$, $p = 0.006$; reach: $F = 21.13$, $p < 0.0001$). BG activity per square meter did not differ between reaches during the whole experiment ($F = 0.38$, $p = 0.531$; Fig. 3c), but abstraction led to a significant decrease of 55% in BG activity per unit channel length ($F = 7.31$, $p = 0.007$; Table 1; Fig. 3d). Before diversion, AP activity per gram was higher in the Impact reach, but abstraction significantly reduced it to 46% and equalized AP values in both reaches during the After period ($F = 4.19$, $p = 0.037$; see Appendix 1). On the contrary, although differences were not statistically significant ($F = 0.39$, $p = 0.530$; see Appendix 1), BG activity per gram was lower below the dam before diversion and was enhanced by water abstraction, effect size being 233%.

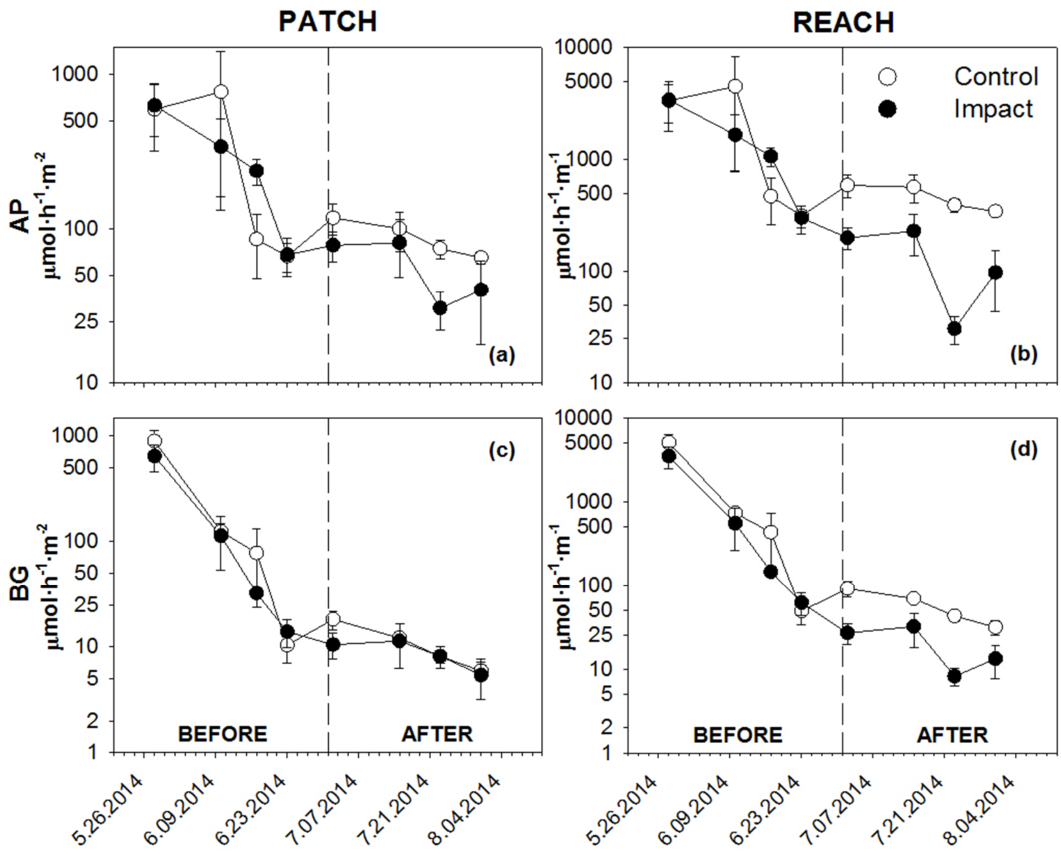

Figure 3. Alkaline phosphatase (AP; a, b) and β-Glucosidase (BG; c, d) activities at the patch (a, c) and the reach (b, d) scales in the Control and Impact reaches. The dashed line marks the beginning of diversion. Error bars show SE. Notice that the y axes are in log scale.

Nutrient retention

Nutrient travel distance was highly variable (NH_4^+: 267 - 3019 m; PO_4^{-3}: 427 - 2454 m) and showed neither a clear temporal pattern nor a significant impact of water abstraction ($p > 0.05$; see Appendix 1). However, abstraction greatly reduced the velocity at which nutrients moved from the water column to the sediment (see Appendix 1). In the Control reach, the uptake velocity of NH_4^+-N ranged between 0.86 and 6.78 mm·s^{-1}, whereas, on average, in the Impact reach abstraction reduced it from 3.19 to 0.17 mm·s^{-1} ($F = 12.18$, $p = 0.002$). Similarly, the uptake velocity of PO_4^{-3}-P ranged between 0.64 and 5.70 mm·s^{-1} upstream from the dam, while it decreased from 3.51 to 0.35 mm·s^{-1} below the dam ($F = 5.07$, $p = 0.017$). The uptake rate of both nutrients per square and linear meter showed very similar trends to that of velocity (Fig. 4) and was significantly reduced by water abstraction ($p = 0.051$ for NH_4^+-N uptake at the patch scale, $p < 0.05$ for the rest; Table 1). On the contrary, results did not reveal any significant effect of abstraction when analyzed per gram of biofilm (NH_4^+-N: $F = 0.91$, $p = 0.3$; PO_4^{-3}-P: $F = 1.61$, $p = 0.155$).

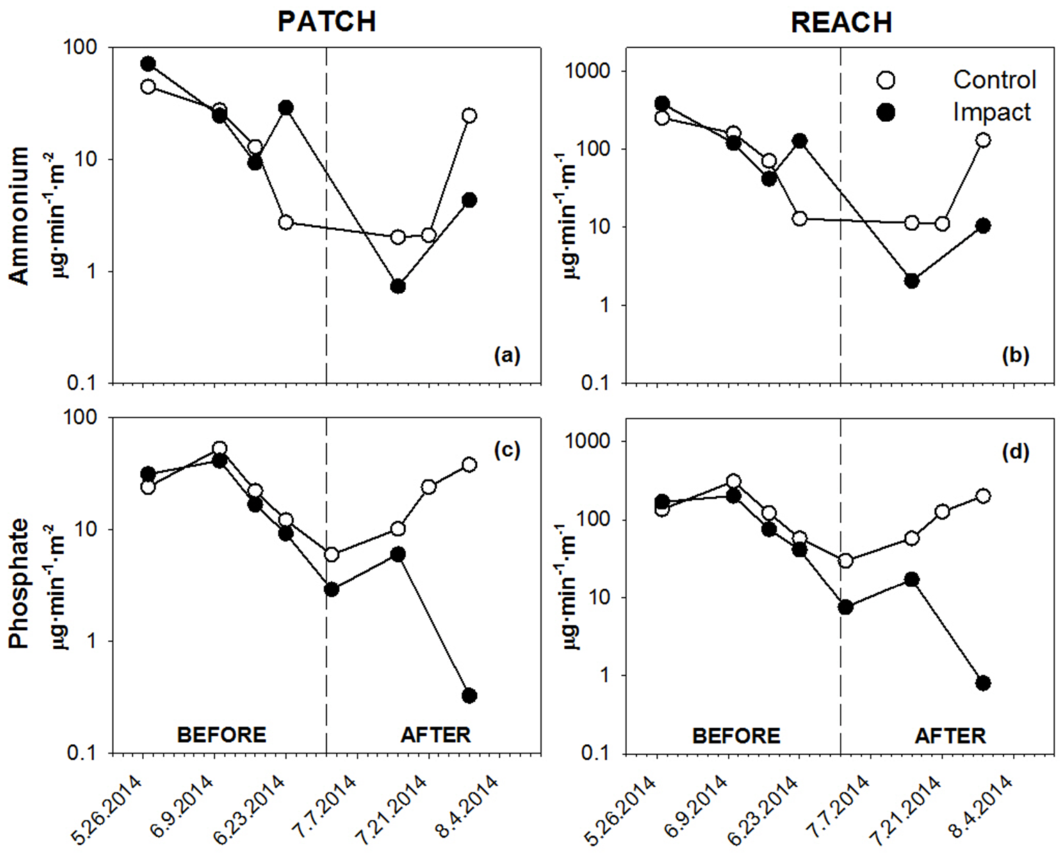

Figure 4. Ammonium (NH_4^+-N; a, b) and phosphate (PO_4^{-3}-P; c, d) uptake rates at the patch (a, c) and the reach (b, d) scales in the Control and Impact reaches. The dashed line marks the beginning of diversion. Notice that the y axes are in log scale.

Metabolism

GPP measured in chambers was higher than CR during the whole study period. In the Control reach, mean GPP ranged from 22 to 68 $mgO_2 \cdot h^{-1} \cdot m^{-2}$ and CR from -11 to -36 $mgO_2 \cdot h^{-1} \cdot m^{-2}$, variability being higher in the Impact reach (Fig. 5). At the patch scale, the effect of diversion on GPP was not statistically significant (F = 0.02, p = 0.85), whereas at the reach scale GPP significantly decreased from 397 to 136 $mgO_2 \cdot h^{-1} \cdot m^{-1}$ as a consequence of ecosystem contraction (F = 32.04, p < 0.001; Table 1). Similarly, water abstraction did not affect CR per square meter (F = 0.82, p = 0.286), but reduced it down to 14% per unit channel length (F = 9.40, p = 0.022). Neither the ratio GPP/Chl-*a* (F = 1.20, p = 0.178), nor CR/AFDM (F = 0.29, p = 0.520) were significantly affected by abstraction (see Appendix 1). Metabolism was not related with exoenzyme activities (r^2 < 0.15, p > 0.05) and nutrient uptake rates (r^2 < 0.30, p > 0.05).

Organic matter retention

Leaf travel distance varied between 55 and 157 m in the Control reach during the whole experiment, whereas in the Impact reach, water abstraction shortened travel distance, on average, from 119 m before diversion to 13 m after (*F* = 17.64, *p* = 0.001; see Appendix 1). Therefore, the proportion of leaves retained per square meter and per unit channel length significantly increased below the dam during diversion (*p* < 0.001). However, because, as far as we know, abstraction seemed not to affect the concentration of leaf litter, these changes were compensated by the decrease in discharge, and thus, overall, abstraction did not alter the amount of leaves retained, either at the patch (*F* = 3.11, *p* = 0.075) or at the reach (*F* = 0.58, *p* = 0.383) scales (Table 1; Fig. 6).

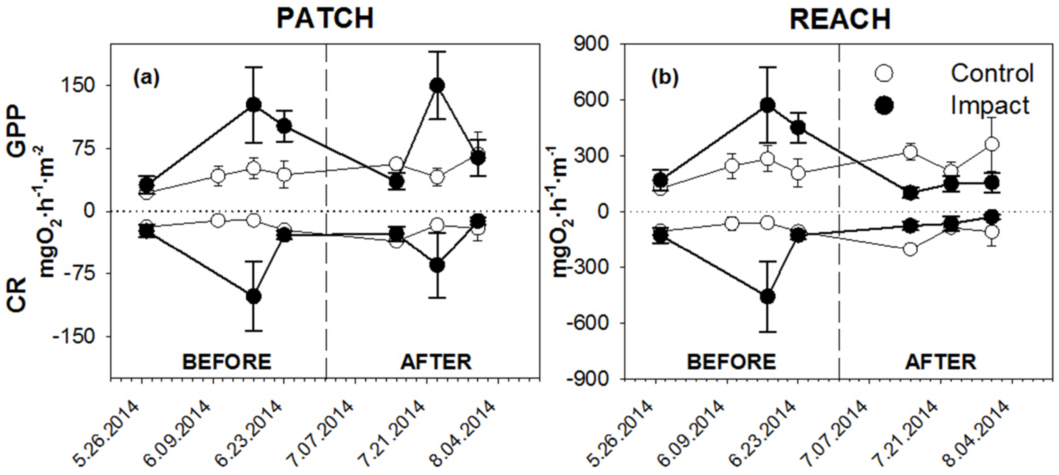

Figure 5. Gross primary production (GPP) and community respiration (CR) at the patch (a) and the reach (b) scales in the Control and Impact reaches. The dashed line marks the beginning of diversion. Error bars show SE.

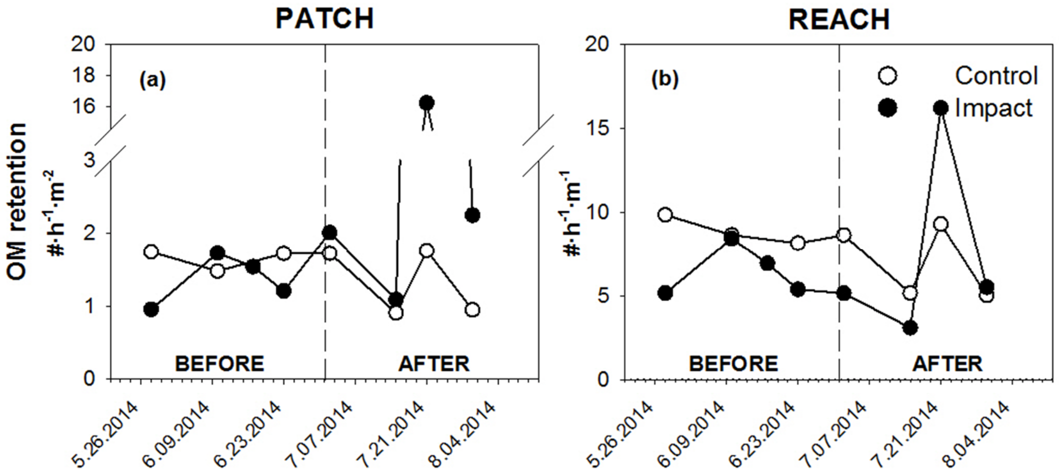

Figure 6. Organic matter (OM) retention rates at the patch (a) and the reach (b) scales in the Control and Impact reaches. The dashed line marks the beginning of diversion.

Organic matter breakdown

26 out of 180 bags got dry, all in the Impact reach after diversion: 14 in E2 and 12 in E3. In the Control reach, average breakdown rate in 5-mm mesh bags halved from 0.035 to 0.017 day^{-1} with abstraction. Analyses of bags permanently immersed (patch scale) did not reveal any statistically significant effect of water abstraction (F = 2.05, p = 0.118; Table 1; Fig. 7a). However, when considering all the bags (reach scale), water abstraction reduced breakdown rates, on average, to 89% compared to breakdown in the Control reach (F = 3.18, p = 0.039; Table 1; Fig. 7b). Breakdown in fine mesh bags showed no temporal trend. At the patch scale, differences between both reaches remained relatively constant during the whole experiment (F = 0.79, p = 0.436), breakdown being higher in the Impact reach (Fig. 7c). On the contrary, differences reversed when including all the bags: breakdown in the Impact reach was higher before diversion and lower after (F = 3.45, p = 0.030; Fig. 7d).

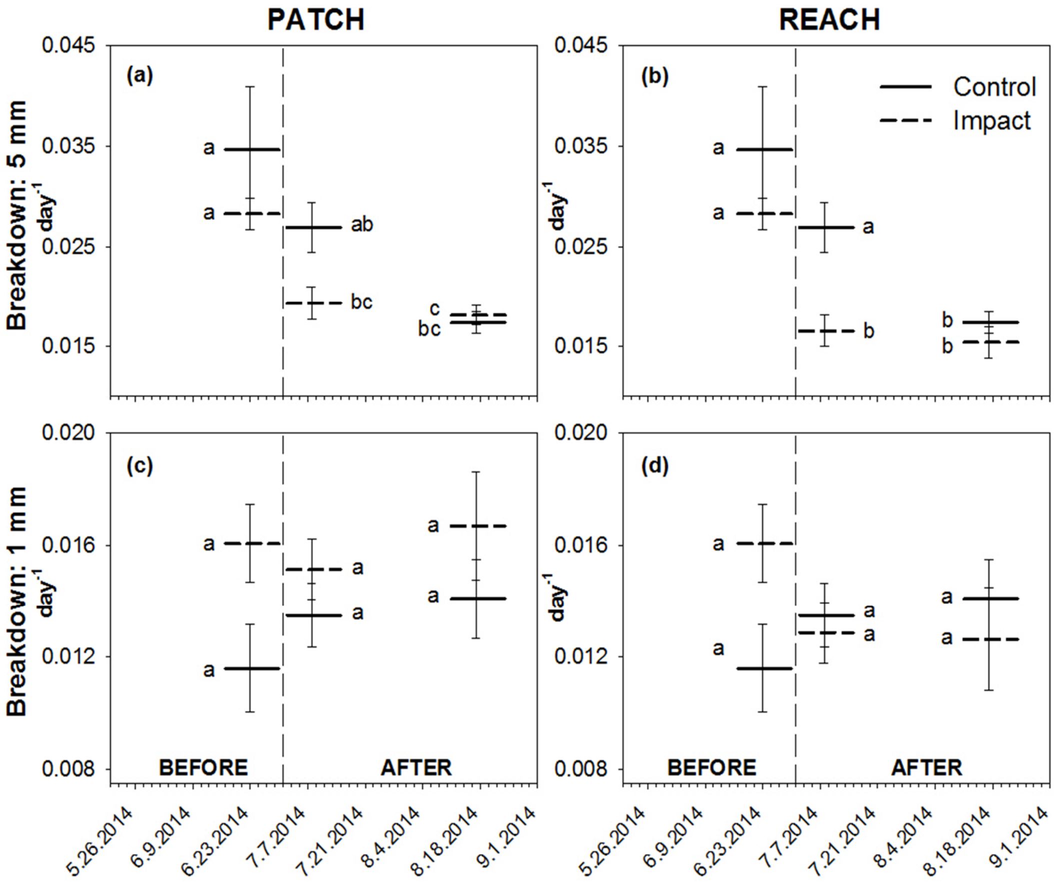

Figure 7. Leaf litter breakdown rates in coarse (5 mm; a, b) and fine (1 mm; c, d) mesh bags at the patch (a, c) and the reach (b, d) scales in the Control and Impact reaches. The vertical dashed line marks the beginning of diversion, horizontal lines the duration of each breakdown experiment. Error bars show SE. Results from post hoc HSD Tukey test are also shown as a-c letters.

Table 1. The effect size and the interaction between period and reach (BA:CI) obtained from linear mixed-effects model for all the variables at the patch and the reach scales. *p* values were obtained by means of likelihood ratio tests.

	Patch scale			Reach scale		
Variable	Effect size (%)	F_{BACI}	*p*	Effect size (%)	F_{BACI}	*p*
Discharge	---	---	---	35.34	302.75	<0.0001
Wetted width	---	---	---	46.81	138.44	<0.0001
Water depth	---	---	---	58.68	5.98	0.011
Water velocity	---	---	---	43.94	31.08	<0.001
Biomass	52.99	5.18	0.023	25.57	26.09	<0.0001
Chlorophyll *a*	85.67	0.01	n.s.	42.20	2.57	n.s.
Phosphatase	47.25	7.71	0.006	24.01	21.13	<0.0001
Glucosidase	101.56	0.38	n.s.	45.17	7.31	0.007
Ammonium uptake	7.82	3.91	0.051	4.11	6.30	0.021
Phosphate uptake	40.41	4.51	0.023	22.72	6.73	0.007
Gross Primary Productivity	84.20	0.02	n.s.	25.91	32.04	<0.001
Biofilm respiration	44.26	0.82	n.s.	13.77	9.40	0.022
Leaf retention	432.78	3.11	n.s.	140.26	0.58	n.s.
Litter breakdown Macroinv.	107.88	2.05	n.s.	88.72	3.18	0.039
Microinv.	83.24	0.79	n.s.	66.83	3.45	0.030

Discussion

Water abstraction reduced discharge in the Impact reach to 35% on average, which led to a decrease in the perimeter of the wetted channel, in biofilm biomass as well as in the rates of diverse processes of stream ecosystem functioning at both the patch and the reach scales. Differences were greater when results were analyzed per linear meter of channel, indicating that the global accounting of the impacts was underestimated when focusing only on the patch scale.

Contrary to other studies that reported water abstraction to increase water temperature and pH (Rader & Belish 1999; McIntosh et al. 2002) and decrease dissolved oxygen concentration (James et al. 2008), our experiment did not affect water quality, as was also reported in a previous study in the region (Arroita et al. 2015). The lack of response probably reflects the strong shade and low nutrient concentration in the stream we studied, the small size of the diversion weir, the fast renewal of the water retained, and the short distance between both reaches. The impact is likely to be stronger further away from the dam or when it creates larger pools upstream (Doyle et al. 2003). Contrasting with the lack of effect on water quality, abstraction strongly affected hydromorphology, resulting in a much narrower wetted channel, shallower water column and slower flow velocity. An important aspect to emphasize is that at some moments our diversion scheme was close to disrupting the superficial flow and shrinking the channel into a series of unconnected pools, which would have strong effects on communities (Acuña et al. 2005) and ecosystem processes (von Schiller et al. 2011). This result casts doubts on the adequacy of environmental flows in the region, which are set close to these thresholds (URA 2014; Arroita et al. 2015).

Hydromorphological changes such as those caused by water abstraction can have large effects on benthic communities. On the one hand, biofilm biomass and activity are highly dependent on water flow, and tend to decrease either at velocities over 1.5 $m \cdot s^{-1}$, which slough biofilm (Francoeur & Biggs 2006), or at very low ones, which increase the thickness of the boundary layer, restricting the advective transport (Bishop et al. 1997) and the diffusion of molecules (de Beer et al. 1996), thereby limiting the renewal of nutrients and other substances within the biofilm. On the other hand, as the stream shrinks benthic invertebrates tend to concentrate in the remaining water in response to the contraction of the wetted channel (Acuña et al. 2005; Dewson et al. 2007a), thus increasing their pressure on biofilm (Hillebrand 2009). In our case, hydromorphological alterations in the Impact reach significantly reduced biofilm biomass, increased the relative abundance of photoautotrophs and decreased AP activity as well as the ratio AP activity:biomass. However, results showed no significant impact on BG activity, nutrient uptake and metabolic parameters per gram of biofilm. Altogether, these results suggest that at the patch scale, water abstraction affected more the biomass than the physiological performance of biofilm per unit biomass.

Nutrient uptake in streams is mainly driven by hydrology, hydraulics and biological activity (Battin et al. 2008), and thus, the changes produced in our experiment after diversion could have a strong impact on nutrient cycling (Argerich et al. 2011). Low flow decreases water depth and increases residence time, thereby increasing its contact with the sediments (Argerich et al. 2008), and resulting in a shorter uptake length (Wollheim et al. 2001; Hall et al. 2002). Contrasting with our hypotheses, water abstraction in our stream did not affect the average distance traveled by N and P, although it reduced both uptake velocity and areal uptake rate, probably as a consequence of reduced biofilm biomass. Our results, thus, confirm nutrient uptake to be ultimately determined by the biotic demand by the biofilm (Hall & Tank 2003). On the other hand, for a total accounting of the impact of abstraction on nutrient dynamics, one should take into account the fate of nutrients in the diversion canal, where nutrient retention can be important (Izagirre et al. 2013). Nevertheless, in our case, the diversion canal was an underground concrete structure where very few biofilm could develop, and thus, it is safe to assume nutrient retention to be negligible there. Therefore, our experiment seemed to reduce strongly the overall amount of nutrients retained in the basin, and this result will likely apply to many other schemes.

Despite a significant decrease in biofilm biomass, AP activity and nutrient uptake, we detected no significant effects of water abstraction on patch-scale metabolism. Although biofilm biomass has been reported to be a good predictor of GPP (Aristegi et al. 2010), often there is no significant relation between both variables (Uehlinger & Naegeli 1998; Fellows et al. 2006), among others, because biofilm communities can differ widely in their health status (Izagirre et al. 2008). Additionally, metabolism chambers are affected by the large patchiness in biofilm (Palmer & Poff 1997), and thus, have relatively low sensitivity to detect subtle changes in metabolism. In our case, the fact that the study reaches were short (100 m) and turbulent precluded us from using the alternative open-channel methods to estimate metabolism. Yet, because both nutrient uptake and metabolism are tightly linked (Hall & Tank 2003), it is reasonable to think water abstraction could reduce whole stream metabolism.

Reduced discharge results in narrower depth and width, and smaller hydraulic power, thereby increasing retentiveness of coarse particulate organic matter (Ehrman & Lamberti 1992; Larrañaga et al. 2003). Therefore, as expected, water abstraction greatly shortened leaf travel distance. However, because the mass of water circulating was greatly reduced, the areal retention of leaves seemed not to be affected by abstraction. This result depends on our assumption that the concentration of particulate organic matter in the water column was not affected by abstraction, what can be case-specific. In our case, there was no pool upstream from the dam and almost all of the water in the Impact reach flowed over the dam, where no leaf accumulation was detected. Therefore, our assumption seems reasonable. In abstraction schemes where a large pool forms above the dam, or where the water circulates through narrow slots, the concentration of leaves could decrease and affect downstream retention.

Regarding decomposition of leaf-litter, most bags remained immersed during the whole experiment despite the strong ecosystem contraction of the Impact reach. We hypothesized that, in an early stage, leaf litter in these permanently immersed bags would break down more quickly because invertebrates would concentrate in remaining wetted areas, whereas, on the mid-term, we expected invertebrates to abandon the reach, thereby decreasing breakdown. Nevertheless, as previous studies reported (Dewson et al. 2007b; Arroita et al. 2015), our results did not reveal significant differences between breakdown in Control and Impact reaches, suggesting little impact on the detrital pathway as long as leaf litter remains wet. The fact that breakdown rates in coarse mesh bags decreased in both reaches could be related to the emergence of large invertebrates (Leberfinger et al. 2010; Dossena et al. 2012).

The impacts of abstraction were significantly more evident at the reach than at the patch scale. A direct effect of water abstraction was the contraction of the aquatic ecosystem, and therefore, the Impact reach was greatly reduced in extent. As a consequence, the impact of abstraction was highly accentuated when the effect of contraction was included in the analysis. The effect size of all variables halved and statistical significance increased considerably, benthic Chl-*a* and leaf retention being the only variables that did not show a significant BA:CI interaction at the reach scale. These results show the main impacts to be associated to the decreased wetted perimeter, which is a universal consequence of water abstraction. Although this observation seems quite evident, most studies only consider the surface unit, highly underestimating the total accounting of the impacts. Two points to discuss when extrapolating the present results are the limited spatial and temporal extent of our experiment. Regarding the spatial extent, the impacts of water abstraction will likely decrease downstream as a result of the inputs of groundwater and tributaries. Nevertheless, diversion schemes often cut totally most of the tributaries, resulting in very significant reduction of flow in their entire length (Izagirre et al. 2013), and thus, it is likely that they exert strong impacts on ecosystem functioning. Concerning the temporal extent, unlike large reservoirs, small diversion schemes have little effect on the hydrological regime, as they are unable to significantly reduce the frequency and magnitude of floods. In by-passed reaches we would not expect to find large increases in biofilm biomass, such as those found below large reservoirs (Ponsatí et al. 2014), which greatly increase river metabolism, compensating for ecosystem contraction (Aristi et al. 2014). Therefore, we expect the general patterns found in the present experiment to hold across broader spatial and temporal scales.

Stream ecosystem functioning is the basis of important ecosystem services (Costanza et al. 1997; Thorp et al. 2010), which should be measured at the reach scale for a global accounting. The changes caused by abstraction will likely reduce the services of maintenance of biodiversity (Dudgeon 2010), of water purification (Perrings et al. 2010), of provisioning of fish (Benejam et al. 2014), as well as of opportunities for recreation. Therefore, as water abstraction becomes more prevalent the services we obtain from the functioning of streams and rivers will fade as these ecosystems shrink out, with detrimental effects for the societal welfare (Arthington et al. 2009).

Acknowledgements

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Appendix 1. Linear mixed-effects model results for all the variables. *p* values were obtained by means of likelihood ratio tests.

VARIABLE	FACTOR	Mean Sq	*F*	*p*
Width (m)	BA	8.33	24.73	<0.001
	CI	2.56	6.27	0.015
	BA:CI	55.69	138.4	<0.0001
Depth (cm)	BA	0.002	10.55	0.012
	CI	0.004	17.17	0.002
	BA:CI	0.001	5.98	0.011
Velocity ($m\cdot s^{-1}$)	BA	0.0081	7.00	0.026
	CI	0.003	3.95	0.438
	BA:CI	0.050	31.08	<0.001
Biofilm ($g\cdot m^{-2}$)	BA	0.238	3.03	0.071
	CI	0.602	7.50	0.008
	BA:CI	0.408	5.18	0.023
Biofilm ($g\cdot m^{-1}$)	BA	0.637	7.29	0.012
	CI	3.69	41.34	<0.0001
	BA:CI	2.29	26.09	<0.0001
Chl-*a* ($mg\cdot m^{-2}$)	BA	0.231	1.55	0.176
	CI	0.292	1.95	0.157
	BA:CI	0.001	0.008	0.928
Chl-*a* ($mg\cdot m^{-1}$)	BA	0.754	4.06	0.042
	CI	2.11	11.29	0.001
	BA:CI	0.479	2.57	0.107
AI	BA	0.043	0.325	0.569
	CI	0.044	0.332	0.564
	BA:CI	0.503	3.81	0.047
AP ($\mu mol\cdot h^{-1}\cdot m^{-2}$)	BA	0.822	4.15	0.043
	CI	0.151	0.710	0.398
	BA:CI	1.53	7.71	0.006
AP ($\mu mol\cdot h^{-1}\cdot m^{-1}$)	BA	1.32	6.52	0.0172
	CI	2.23	10.41	0.004
	BA:CI	4.38	21.13	<0.0001
AP ($\mu mol\cdot h^{-1}\cdot g^{-1}$)	BA	0.194	0.976	0.264
	CI	0.306	2.15	0.167
	BA:CI	0.671	4.19	0.037
BG ($\mu mol\cdot h^{-1}\cdot m^{-2}$)	BA	0.970	5.60	0.022
	CI	0.688	3.89	0.047
	BA:CI	0.066	0.383	0.531

BG **(µmol·h^{-1}·m^{-1})**	BA	1.27	7.35	0.012
	CI	3.92	21.87	<0.0001
	BA:CI	1.26	7.31	0.007
BG **(µmol·h^{-1}·g^{-1})**	BA	0.937	4.35	0.037
	CI	0.001	0.002	0.935
	BA:CI	0.085	0.393	0.530
Sw_N **(m)**	BA	0.108	2.46	0.175
	CI	0.084	1.88	0.156
	BA:CI	0.021	0.386	0.508
Vf_N **(mm·min^{-1})**	BA	0.138	6.00	0.043
	CI	0.365	17.03	0.042
	BA:CI	0.436	12.18	0.002
U_N **(µg·min^{-1}·m^{-2})**	BA	0.584	6.25	0.020
	CI	<0.001	0.442	0.981
	BA:CI	0.429	3.91	0.051
U_N **(µg·min^{-1}·m^{-1})**	BA	0.758	7.87	0.013
	CI	0.078	2.29	0.565
	BA:CI	0.763	6.30	0.021
U_N **(µg·min^{-1}·g^{-1})**	BA	0.454	4.32	0.035
	CI	0.031	0.062	0.543
	BA:CI	0.099	0.906	0.300
Sw_P **(m)**	BA	0.249	1.66	0.166
	CI	0.060	0.405	0.501
	BA:CI	0.065	0.382	0.474
Vf_P **(mm·min^{-1})**	BA	1.30	9.79	0.012
	CI	0.623	4.52	0.073
	BA:CI	0.824	5.07	0.017
U_P **(µg·min^{-1}·m^{-2})**	BA	1.21	9.54	0.011
	CI	0.792	5.79	0.040
	BA:CI	0.705	4.51	0.023
U_P **(µg·min^{-1}·m^{-1})**	BA	1.74	12.57	0.007
	CI	1.49	9.64	0.015
	BA:CI	1.18	6.73	0.007
U_P **(µg·min^{-1}·g^{-1})**	BA	0.434	2.57	0.120
	CI	0.508	2.61	0.114
	BA:CI	0.354	1.61	0.155
GPP **(mgO_2·h^{-1}·m^{-2})**	BA	276.5	1.27	0.170
	CI	4661	0.164	0.620
	PAR	7997	12.00	<0.001
	BA:CI	14.20	0.022	0.850

GPP (mgO$_2$·h^{-1}·m^{-1})	BA	3240	1.47	0.411
	CI	877.0	5.44	0.072
	PAR	56996	12.70	0.005
	BA:CI	63520	32.04	<0.001
GPP (mgO$_2$·h^{-1}·mgChl-*a*$^{-1}$)	BA	93.83	4.02	0.038
	CI	65.01	0.046	0.691
	PAR	38.16	1.91	0.183
	BA:CI	33.91	1.20	0.178
CR (mgO$_2$·h^{-1}·m^{-2})	BA	9.46	0.092	0.780
	CI	1809	2.65	0.068
	BA:CI	519.6	0.823	0.286
CR (mgO$_2$·h^{-1}·m^{-1})	BA	0.479	2.47	0.298
	CI	0.012	<0.001	0.408
	BA:CI	2.44	9.40	0.022
CR (mgO$_2$·h^{-1}·g^{-1})	BA	179.7	1.42	0.192
	CI	425.1	4.15	0.031
	BA:CI	30.80	0.292	0.520
Leaf TD (m)	BA	2552	2.81	0.043
	CI	4979	4.14	0.119
	BA:CI	13749	17.64	0.001
OM retention (#·h^{-1}·m^{-2})	BA	<0.001	<0.001	0.980
	CI	0.006	0.076	0.813
	BA:CI	0.240	3.11	0.075
OM retention (#·h^{-1}·m^{-1})	BA	0.023	0.382	0.516
	CI	0.156	1.81	0.183
	BA:CI	0.056	0.584	0.383
K 5 mm PATCH (day^{-1})	E	0.594	16.06	<0.0001
	CI	0.015	1.14	0.335
	E:CI	0.071	2.05	0.118
K 5 mm REACH (day^{-1})	E	1.05	21.51	<0.0001
	CI	0.139	5.62	0.019
	E:CI	0.156	3.18	0.039
K 1 mm PATCH (day-1)	E	0.047	1.01	0.272
	CI	0.162	4.69	0.018
	E:CI	0.045	0.79	0.436
K 1 mm REACH (day^{-1})	E	0.030	0.518	0.578
	CI	<0.0001	0.001	0.999
	E:CI	0.175	3.45	0.030

CHAPTER 6

General discussion

Overview of main results

This dissertation studied the effects of water abstraction on stream ecosystem functioning, combining observational and manipulative, field and laboratory experiments. Our comparison of reaches upstream and downstream from diversion schemes (Chapter 2) showed water abstraction to reduce the storage and breakdown of coarse organic matter, but suggested that impacts could be season-dependent. Our experiment of breakdown at different microsites (Chapter 3) also showed that the hyporheos could be an important refuge for aquatic organisms, as reported by previous studies (e.g. Stanley et al. 1994; Stubbington 2012), and also a place where ecosystem processes such as organic matter breakdown can proceed when most of the stream channel has dried out, which could mitigate the overall impacts of water abstraction when a large proportion of the discharge is diverted. In addition, results from the laboratory experiment (Chapter 4) showed the effects of drought-related disturbances on breakdown-associated variables to be more detrimental if they occurred in early stages of the decomposition process, indicating the overall effects to depend not only on the duration of the stress, but also on their timing. In the context of water abstraction and organic matter breakdown, these findings could indicate that the impacts of abstraction might be more detrimental during leaf fall, as it would affect litter preconditioning, thereby influencing the whole breakdown process. Indeed, Dieter et al. (2011) reported that accumulation of leaves in anoxic residual pools or dry sediments during the physicochemical preconditioning reduced substrate quality, depressing the activity of decomposers and restricting the efficiency of organic matter processing in streams. Although the latter study was performed in temporary streams, we could expect similar results in streams and rivers affected by water abstraction, since both droughts and abstraction reduce the surface of the wetted channel, to the extent of disrupting the superficial flow leaving many lateral unconnected pools, as observed in Chapters 2 and 5. Finally, the field manipulative experiment (Chapter 5) revealed water abstraction to reduce most stream ecosystem functions, especially biofilm activity and nutrient retention. Furthermore, we also showed the main impacts to be associated to decreased wetted perimeter, which is a universal consequence of water abstraction, indicating that the global accounting of the effects of water abstraction can be highly underestimated when focusing only on the patch scale, as has been done traditionally.

Effects beyond the studied reaches

Organic matter breakdown

Given the prevalence of water abstraction worldwide (Nilsson et al. 2005), as well as the further increase expected in the near future (Poff et al. 2003; Finer & Jenkins 2012; Chapter 1), the global accounting of the impacts of this type of water exploitation could be considerable. Allochthonous organic matter is the main energy source supporting food webs and many ecosystems depend on the processing of organic matter by microorganisms and invertebrates, especially in forested streams where primary production is light-limited by the riparian cover (Wallace et al. 1997; Webster et al. 1999). Most of our results (with the exception of the spring experiment in Chapter 2) showed significant decreases in litter breakdown as a consequence of flow reduction. Therefore, intensive water abstraction could reduce the energy transfer to higher trophic levels, ultimately affecting stream productivity (Vannote et al. 1980) and altering the trophic structure of river ecosystems (Casas et al. 2000). This problem could be intensified by the fact that, at least in most diversion schemes in our region, large amounts of organic matter are usually diverted together with water, which are transported through the diversion canals and trapped by metallic grids just before the tubes from the canals to the turbines. These grids are cleaned automatically, and the organic matter is dumped beside the canals, far from the stream channel, and thus, lost from stream and river ecosystems.

Our results from Chapter 3 suggested that the activity occurring in subsurface layers can significantly contribute to total breakdown, especially when most of the stream channel has dried out. Indeed, although many studies reported organic matter breakdown to be slower in the hyporheos (Cornut et al. 2010; Marmonier et al. 2010; Flores et al. 2013), in our study, both microbial and total breakdown rates in litter bags buried in the wet channel as well as in parafluvial areas were very similar to the ones in the surface of the wet channel. Therefore, the overall decrease in organic matter breakdown due to water abstraction could be overestimated if assessments were limited to the superficial layer. On the other hand, it must be taken into account that we studied natural flow fluctuations in a single stream located in a region with a mean rainfall of 2,500 mm per year (http://meteo.navarra.es/). In fact, it rained in 45 days out of 67 days of the experiment. Therefore, it is likely that the mitigation would be less important in drier areas where the subsurface sediments could also dry out. Flow reduction in stream reaches affected by water abstraction (e.g. Chapter 2 and 5) is generally greater than the flow fluctuation registered in this study, thus being more likely to affect subsurface hydrology too. Besides, the fact that it rained almost every day prevented sediments exposed to air from drying completely, which enables organisms to survive and maintain their decomposing activity (Sridhar & Bärlocher 1993; Langhans & Tockner 2006). Other important factors that should be considered are the type of sediment and the hydraulic connectivity of the stream, since they control the accessibility for organisms (Omesová et al. 2008; Cornut et al. 2010) as well as the oxygen level (Wagenhoff & Olsen 2014) and, thus, the abundance of microorganisms and invertebrates in subsurface layers (Strayer et al. 1997; Crenshaw et al. 2002). Overall, the contribution of subsurface layers would, thus, depend on the effect of water abstraction on subsurface hydrology, on climatic conditions and on the vertical connectivity of the stream.

Biofilm and nutrient retention

The decline in biofilm and nutrient retention caused by water abstraction (Chapter 5) could also have relevant consequences, as it could further intensify the reduction in food and energy sources described earlier. Together with allochthonous organic matter, biofilms also occupy a key position at the base of food webs (Peterson et al. 2001; Rowe & Richardson 2001). Moreover, retention of nutrients is the basis of the self-purification capacity of streams and rivers, one of the most important services provided by these ecosystems (Costanza et al. 2007). Nutrients entering streams from the basin are processed by biofilms through a combination of assimilatory and dissimilatory, microbially-mediated processes, which subsequently regulate their downstream export (Peterson et al. 2001; Bernhardt et al. 2003). Therefore, the reduction in the biomass and activity of biofilm as well as in nutrient uptake observed in this study could increase nutrient delivery to sensitive receiving waters (e.g. lakes, reservoirs, coastal ecosystems), where they can result in eutrophication and hypoxia (Baker & Richards 2002; Smith 2003; Dodds 2006; Alexander et al. 2008).

Open questions

The present research combined descriptive and manipulative, field and laboratory experiments, but was necessarily limited in extent, including only one type of stream, in a small geographic area, and looked at impacts immediately below the weirs. This approach leaves some obvious open questions that must be considered before going beyond our results and speculating about the global magnitude of the impacts of water abstraction, among which the following stand out.

Do impacts decrease downstream?

In this dissertation, the field studies directly assessing the impact of water abstraction on ecosystem functioning (Chapters 2 and 5) were limited to 100-m-long stream reaches located immediately below weirs. Therefore, an essential question to be addressed to estimate the overall impact of water abstraction is how far the effects of reduced discharge extend. Although these effects are likely to decrease downstream due to the inputs of groundwater and tributaries, diversion schemes often totally cut most of the tributaries, resulting in very significant flow reduction along their entire length (Izagirre et al. 2013). In an attempt to gain insight into how flow recovers in a stream affected by water abstraction, we measured discharge in five reaches below the Ameraun diversion scheme, in the Leitzaran Stream (Fig. 1; data provided by Olatz Pereda, UPV/EHU). The Leitzaran stream, close to our study areas, is severely affected by multiple hydropower schemes, to the point that 70% of stream reaches are by-passed (see Table 1 in Chapter 1; PGG 2006). We measured discharge with pulse additions of a hydrological tracer (Cl^- as NaCl; Martí & Sabater 2009) and the expected discharge was estimated as the specific discharge, based on the area drained at each reach. The Ameraun weir diverted almost 95% of the discharge, and discharge remained below 10% of the expected discharge in the first 2 kilometers (Table 1). Further downstream, discharge started to recover, but very slowly, and did not reach 40% of the expected discharge even in the last reach, almost 6 kilometers downstream from the diversion scheme. Besides, out of the 15 kilometers by-passed by the Ameraun, the last 5 kilometers are further affected by another hydropower plant (Fig. 1). Therefore, although flow recovery might greatly differ among streams, at least in some cases it can be slow, suggesting the impacts of water abstraction measured in this dissertation to extend far downstream. An open question is whether communities and processes recover as fast as the discharge, or if impacts on these variables extend even farther.

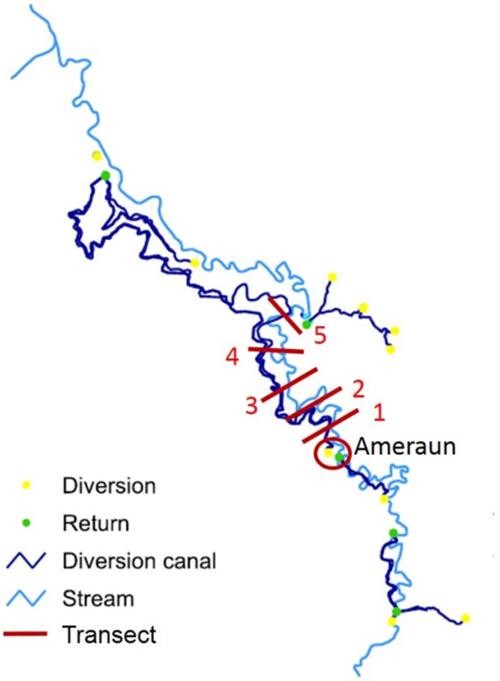

Figure 1. Diversion schemes in the Leitzaran stream and reaches where discharge was measured to estimate how long the effects of water abstraction extend downstream.

Which is the role of dry channels and diversion canals?

Another important constraint of our study is that it was mainly limited to the wetted channel (except breakdown measurements in dry sediments in Chapters 3 and 5). However, diversion schemes not only cause by-passed stream channels to shrink, but also increase the surface of parafluvial areas, as well as creating long diversion canals that are by no means biogeochemically inert (Izagirre et al. 2013). In some cases, the reservoir created by the diversion weir can also play a significant role in ecosystem functioning. Nevertheless, in our region diversion schemes usually

Table 1. Expected (based on the drainage basin size) and measured (data provided by Olatz Pereda, UPV/EHU) discharge along the stream reach affected by the Ameraun diversion scheme in the Leitzaran stream.

Reach	Distance (m)	$Q_{expected}$ ($L \cdot s^{-1}$)	$Q_{measured}$ ($L \cdot s^{-1}$)	Q (%)
1	687	1077.2	93.7	8.7
2	1867	1098.2	93.7	8.5
3	3417	1152.4	151.3	13.1
4	4367	1197.6	198.0	16.5
5	5567	1203.7	475.6	39.5

provide little or no water storage, the residence time of water in pools being of the order of seconds to minutes. By-passed stream sections are characterized by lower discharge, slower water velocity and narrower surface than natural ones (Chapters 2 and 5), whereas diversion canals are hydraulically simple concrete canals, where water column is usually deeper, water moves fast and there is no hyporheos. Dry sediments are habitats in their own right and usually limit the survival and activity of aquatic organisms (Bêche et al. 2009; Romaní et al. 2012), but also differ from other terrestrial habitats in substrate, topography, microclimate, vegetation, inundation frequency and biota (Steward et al. 2012). These changes can have deep effects on water physico-chemical characteristics, biotic communities and ecosystem processes, and the overall impact of water abstraction would depend on the sum of all these effects, both compensations and synergies being possible. For instance, Izagirre et al. (2013) observed that nutrient retention in diversion canals was as high as retention in the control stream channel, what could counterbalance, to a certain extent, the reduced uptake in by-passed channels (Chapter 5). In contrast, retention could be assumed to be negligible in the light-limited underground canal in Chapter 5, further intensifying the decline in nutrient retention. Concerning dry riverbeds, there is little information on their biogeochemical role and they have frequently been neglected, despite being potentially active. Indeed, dry sediments have been shown to maintain some extracellular enzyme activities and carbon processing through sediment biofilms (Zoppini & Marxsen 2011; Pohlon et al. 2013; Timoner et al. 2014). Similarly, results from Chapters 3, 4 and 5 revealed that, despite being significantly slower, organic matter in dry sediments can make an important contribution to total breakdown, and recent studies reported dry riverbeds to be hotspots for carbon emission (Gallo et al. 2014; von Schiller et al. 2014; Gómez-Gener et al. 2015). Therefore, all the compartments as well as their spatial extent should be considered to upscale results and obtain a more realistic picture of the global impact of water abstraction.

Do impacts depend on stream type?

Another point to consider is the fact that the streams we studied were Atlantic mountain streams under minimal human impacts, with high dissolved oxygen concentration, low nutrient concentration and high vertical connectivity. Other types of stream might respond differently. Indeed, there are very diverse freshwater ecosystems affected by water abstraction worldwide, where other factors could interact with abstraction and influence its overall impact on communities and processes. For instance, although abstraction can be very severe in many semiarid regions (Seibert et al. 2006), it might be that their impact is proportionally smaller than the one we detected, because communities in semiarid climates are drought-adapted (Bonada et al. 2007; Daufresne et al. 2009); alternatively, the consequences could be more detrimental because communities might already be under great stress and thus, more vulnerable (Filipe et al. 2013). Water abstraction is also prevalent in large rivers (Zarfl et al. 2015). These ecosystems are characterized by open canopy, although depth and turbidity combine to limit the amount of light reaching the bottom, thus favoring organisms in the water column over those on the benthos (Fig. 2). Therefore, processes that occur in the benthos of headwater streams may also occur in the water column of larger rivers (Reisinger et al. 2015). Since water abstraction significantly decreases not only the surface of the wet channel, but also the depth of the water column, it can promote the growth of benthic organisms and limit water column biota, thereby shifting water column-dominated large rivers to benthic-dominated smaller ecosystems (Fig. 2). It is likely that water abstraction is affecting the equilibrium between alternative stable states, promoting the growth of macrophytes at the expenses of plankton.

How does abstraction interact with other stressors?

Other pressures acting upon streams and rivers can further modulate the impact of water abstraction. Indeed, streams and rivers are subject to multiple pressures, including pollution, modification of riparian areas, flow regulation and invasive exotic species (Sabater 2008; Ricart et al. 2010), which often operate in concert (Fausch et al. 2010; Ormerod et al. 2010). A relevant characteristic of freshwater ecosystems affected by water abstraction that could lead to detrimental synergies with other stressors is the reduced dilution capacity (Menció & Mas-Pla 2008). Urban and agricultural inputs, as well as wastewater treatment plant effluents carry a complex mixture of nutrients and pollutants such as fungicides, insecticides, heavy metals and pharmaceuticals (Kolpin et al. 2004; Merseburger et al. 2009; Aristi et al. 2015), which would dilute less if released in by-

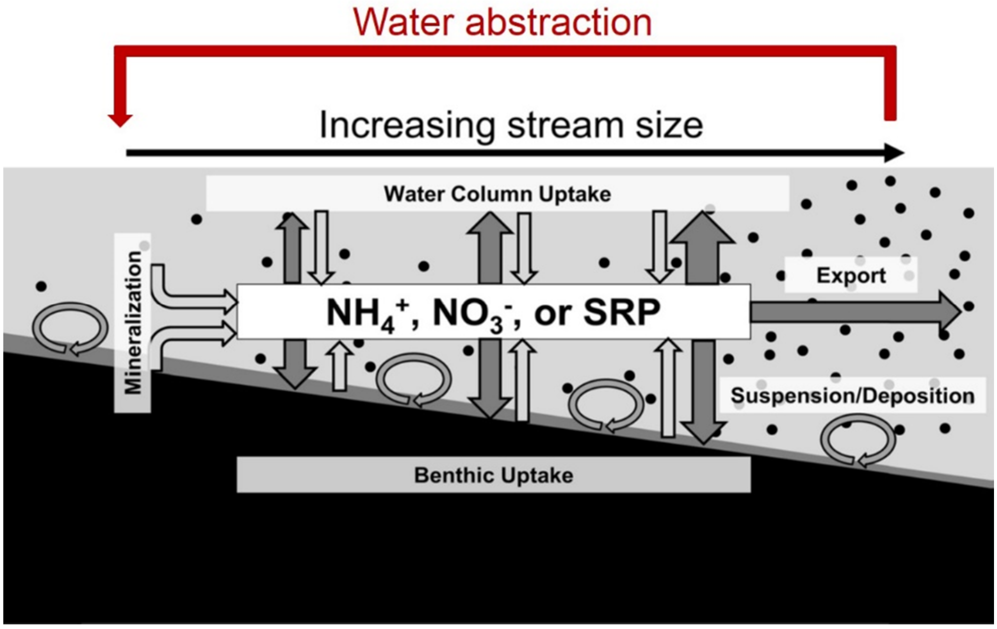

Figure 2. Water column nutrient uptake incorporated into a conceptual model of nutrient uptake along a longitudinal continuum from headwaters to large rivers. The longitudinal transition from headwaters to rivers is accompanied by an increase in depth, represented by the increasing thickness of the water column (light gray). This increase in depth may result in a greater concentration of water column organisms (solid circles) and a decrease in benthic organisms (dark gray line) overlying the stream bed (black). Dissolved nutrients can be taken up by either benthic or water column biota (dark arrows), with a portion of these nutrients being mineralized (light arrows). Modified from Reisinger et al. 2015.

passed stream reaches. Some of these are assimilable substances (e.g. nutrients, organic matter) that subsidize biological activity and enhance ecosystem processes (Merseburger et al. 2005; Greenwood et al. 2007), which could counterbalance the reduction in organic matter breakdown, biofilm and nutrient retention measured in this dissertation (Chapters 2 and 5). However, the same substances can become toxic beyond a threshold. For instance, high nitrogen concentration can saturate biotic uptake, decreasing the efficiency of nitrate removal (Martí et al. 2004; Mulholland et al. 2008; Hall et al. 2009) and increasing nutrient uptake lengths (Dodds et al. 2002; Earl et al. 2006; O'Brien et al. 2007). Similarly, Woodward et al. (2012) showed excessive nutrient loading to inhibit organic matter breakdown. Moreover, toxic pollutants have negative effects on biotic communities (Wilson et al. 2003; de Castro-Catala et al. 2014) as well as on ecosystem processes (Moreirinha et al. 2011; Rosi-Marshall et al. 2013). Therefore, the effects of water abstraction on ecosystem functioning measured in this dissertation could be intensified in streams and rivers receiving high inputs of nutrients and pollutants.

The impact of water abstraction could also act synergistically with erosion and the consequent inputs of fine sediments, which are greatly promoted by agricultural practices, intensive forestry, mineral extraction and urban development (Wood & Armitage 1997). Reduced discharge and water velocity derived from water abstraction enhance deposition of these sediments (Matthaei et al. 2010), which has been shown to alter the structure of biofilm (Wagenhoff et al. 2013; Piggot et al. 2012, 2015a) and invertebrate communities (Niyogi et al. 2007; Townsend et al. 2008; Piggot et al. 2015b), and affect ecosystem processes such as organic matter breakdown and stream metabolism (Niyogi et al. 2003; Young et al. 2008.). Indeed, Matthaei et al. (2010) reported that abstracting water from a stream already subjected to high fine sediment inputs had far worse effects on invertebrates than abstraction from a similar stream with lower sediment levels. Furthermore, fine sediment deposits clog top sediment layers, reducing hydraulic conductivity and associated water flow, which leads to a sharp decrease in oxygen and nutrient concentrations with depth in sediments (Navel et al. 2011). These changes are detrimental for the activity and abundance of leaf-associated microorganisms, decreasing the breakdown of buried organic matter (Omesová et al. 2008; Cornut et al. 2010), which would drastically reduce the mitigation role of subsurface layer described earlier (Chapter 3).

Temporal constraints

Concerning temporal constraints, we studied the effects of water abstraction on stream ecosystem functioning either immediately after a diversion scheme was put in operation (Chapter 5) or long after the diversion schemes were implemented (Chapter 2). Nevertheless, the only measurement shared by these studies was organic matter breakdown. In the scheme we put in operation, water abstraction did not affect breakdown in the wetted channel (Chapter 5). In schemes operating for a long time, water abstraction significantly reduced breakdown in winter, whereas breakdown was unaffected in spring (Chapter 2). We can only speculate whether the impacts of abstraction on biofilm biomass and activity as well as on nutrient retention at the onset of diversion (Chapter 5) would remain constant, would further intensify or, in contrast, biofilms would adapt and, therefore, impacts would mitigate. Unlike large dams, small diversion schemes have little effect on the hydrological regime, as they are unable to significantly reduce the frequency and magnitude of floods (Chapters 2, 3 and 5), during which shear forces and abrasion by transported bed sediments severely damage or eliminate organisms living in the benthos and in the top layers of sediment (McMullen & Lytle 2012). As a consequence, aquatic communities are reset very often also in by-passed reaches. Besides, organisms can easily overcome weirs and low dams, overall, preventing big differentiations in community composition. Therefore, we expect the general patterns found in Chapter 5 to hold across broader temporal scales.

Another time-related aspect is that we found the timing of an impact can be as relevant as its intensity or frequency (Chapter 3), mainly due to strong legacy effects (Datry et al. 2011). Based on these results, together with the ones reported by Dieter et al. (2011), we speculated that the impacts of abstraction might be more detrimental during leaf fall, because it would affect preconditioning of leaf litter, thereby influencing the whole breakdown process. Contrasting with other ecological processes commonly measured in streams, litter breakdown is both sequential and cumulative, as there is a clear sequence of steps (leaching, conditioning, and so), and the last effect is an outcome of the entire sequence. In this context, it really matters whether an impact such as drying occurs early or late in the process, as it really matters whether you suffer a cramp in the initial or in the late phases of a race. From a practical point of view, this information could be used to assess when the impacts are least detrimental and regulate abstraction practices. Nevertheless, it must be emphasized that all these conclusions are derived only from breakdown-associated variables and, although most biological communities and ecosystem processes show temporal dynamics, not all dynamics overlap. For instance, in our latitudes, most organic matter enters the stream in autumn with leaf fall and the life cycles of most decomposers are synchronized with it (Haapala & Muotka 1998), organic matter breakdown peaking in spring coinciding with higher water temperature (Ferreira et al. 2013). In contrast, primary producers and processes related to them are mainly driven by light and nutrient concentration (Romaní & Sabater 1999). Therefore, even though impacts may vary throughout the year, it is hard to predict from our results when the effects of water abstraction on stream functioning would be least detrimental.

Future perspectives

Despite all these spatial and temporal constraints to estimate the global magnitude of the impacts, we showed diversion schemes in the Basque Country to be close to disrupting the superficial flow and shrinking the channel into a series of unconnected pools, which significantly reduced the rates of diverse key processes of stream ecosystem functioning. Therefore, our results cast doubt on the adequacy of the environmental flows, at least in our region, which are set as the 10% of the historical monthly mean (URA 2014). Because the main impacts seem to be associated with the ecosystem contraction, which is a universal consequence of water abstraction, it is likely that the Physical Habitat Simulation System (PHABSIM; Milhous & Waddle 2012) might be more appropriate. However, the present dissertation left many questions unanswered, which constitute important topics for future research and must be addressed to opt for environmental flows and minimize the impacts of water abstraction practices. Firstly, we need to assess the magnitude of the impact in a comprehensive way, for which we require broad studies that measure the amount of water and essential elements circulating from stream channels, the amount circulating from diversion canals, the increase in the surface of dry sediments due to contraction and the contribution of each habitat to ecosystem processes, as well as the potential recovery of discharge and processes downstream. Furthermore, functional variables should be measured at different abstraction intensities to determine whether the magnitude of the impact increases linearly with the proportion of discharge diverted, or, in contrast, there are significant thresholds and non-linearities. Another important aspect related to the magnitude of the impact is how the effects of water abstraction go beyond the studied stream reaches: how much can organic matter breakdown and biofilm biomass decrease before affecting the trophic structure of streams and rivers? how much can nutrient retention decrease before resulting in significant eutrophication problems in sensitive receiving waters? It is necessary to assess how much ecosystem processes can be deviated from natural values without having detrimental cascade effects in order to set thresholds we should not exceed. These thresholds, together with the relationship between abstraction intensity and ecosystem processes, are crucial to establish appropriate environmental flows. Studies should also cover a broad temporal scale that would allow for identifying potentially critical time windows.

In addition, it is indispensable to adapt the management of diversion practices to each stream type, for which it is essential to study the interactions of water abstraction with other elements, identify risk factors and set priorities for each stream type. For instance, in forested streams such as the ones studied in this dissertation, allochthonous organic matter is the main energy source supporting food webs and the productivity of streams greatly depend on organic matter processing. Therefore, managers should consider organic matter dynamics when setting monthly environmental flows in these ecosystems. In contrast, in streams rich in nutrients flowing to a reservoir, minimizing the impacts on nutrient retention might be prioritized, to keep the self-purification capacity of streams. In streams and rivers hosting key species such as brown trout, salmon or Pyrenean desman, their biology and seasonal habitat requirements should be taken into account. Finally, in some cases, such as in stream ecosystems subject to significant pressure, or in those few in an especially good conservation status, water abstraction should be avoided or cease.

Wrapping up, human societies depend on water provided by freshwater ecosystems, which leads to increasing abstraction. Although less dramatic than reservoirs, diversion schemes also have detrimental effects on stream ecosystem functioning, which drives services essential for the societal welfare. It is crucial to identify these impacts as well as their global magnitude in order to develop and improve water abstraction practices that will effectively integrate human and ecosystem water needs in a timely and comprehensive manner. Therefore, there is still much to investigate to determine which schemes should cease, where new schemes should or should not be built, and when and how existing schemes could optimize their functioning to minimize ecological impacts.

CHAPTER 7

General conclusions

1. Water abstraction did not affect water physicochemical characteristics in our streams, but resulted in much narrower wetted perimeters, shallower water columns and slower flow velocities, significantly decreasing the surface and quality of instream habitats.

2. Water abstraction significantly reduced storage and decomposition of organic matter, which can impact the energetic basis of stream ecosystems. However, the effects of water abstraction on organic matter dynamics were limited to winter, showing that impacts can depend on season. Although abstraction affected neither the total density nor the structure of macroinvertebrate assemblages found in litter bags, lower breakdown rates seemed to be related with a reduction in the density of shredders.

3. Among the six descriptors studied, only total macroinvertebrate abundance differed significantly between bags incubated in the surface of the permanently submerged channel and the ones in the parafluvial area only submerged for the last two weeks, demonstrating the ability of macroinvertebrates to rapidly colonize recently submerged areas. In contrast, organic matter breakdown did not recover, both microbial and total breakdown being lower in the surface of parafluvial areas.

4. The richness and diversity of total invertebrates, as well as the abundance and richness of shredders were significantly lower in subsurface layers. In contrast, both microbial and total breakdown rates in litter bags buried in the wet channel and in parafluvial areas were very similar to the ones in the surface of the wet channel, showing that subsurface layers keep breakdown activity even when the surface of benthos has dried out, a common feature of reaches impacted by abstraction. Breakdown in these layers would depend on the effect of water abstraction on subsurface hydrology, on climatic conditions and on the vertical connectivity of the stream.

5. The effects of drought-related stress levels were not consistent among response variables measured in the microcosm experiment, which probably reflects that we recreated a small stress range. Organic matter breakdown was the most sensitive variable to stress levels likely because it integrated all processes occurring during the whole experiment, whereas fungal biomass, sporulation rates and respiration rates were punctual measurements informing about the status of microbial assemblages at that precise moment and thus, could be more subject to noise.

6. The effects of drought-related disturbances on breakdown-associated variables were more detrimental in early stages of the decomposition process, and resulted in a lower fungal biomass and activity, and reduced litter decomposition. These results suggest that the effects of stress on breakdown-associated variables depend not only on the intensity and duration of stress, but also on its timing, early stress exerting greater impact than late stress on breakdown.

7. Water abstraction also decreased biofilm biomass and exoenzyme activity, as well as the uptake of ammonium and phosphate at the patch scale. However, the impacts of water abstraction were highly accentuated when the effect of contraction was included in the analyses, not only on biofilm biomass, exoenzyme activity and nutrient uptake, but also on benthic metabolism and organic matter breakdown. These results showed the main impacts of abstraction to be associated with decreased wetted perimeter, which is a universal consequence of water abstraction, indicating that the global accounting of the effects of water abstraction can be highly underestimated when focusing only on the patch scale, as has been done traditionally.

8. Overall, this dissertation combined descriptive and manipulative, field and laboratory experiments, and showed diversion schemes in the Basque Country to significantly reduce the rates of diverse key processes of stream ecosystem functioning. Therefore, our results cast doubt on the adequacy of the environmental flows, at least in our region.

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