Mammalian Biology
https://doi.org/10.1007/s42991-022-00265-z

ORIGINAL ARTICLE

Trophic competition in a guild of insectivorous semi-aquatic vertebrates in a Pyrenean headwater stream: diet specialisation in the endangered *Galemys pyrenaicus*

Alejandro López-de Sancha[1] · Romero Roig[2] · Pere Aymerich[3] · Anna Vila-Gispert[1] · Helena Guasch[4]

Received: 22 December 2021 / Accepted: 20 May 2022

Abstract

Conservation of vulnerable species in headwater streams requires good knowledge of their resource use and how they interact with competitors. In this study, we characterised the macroinvertebrate community of a Pyrenean headwater stream and assessed how it was used as a food resource—above all, in terms of prey electivity and diet overlap—by three semi-aquatic insectivorous vertebrates (*Galemys pyrenaicus*, *Neomys fodiens* and *Cinclus cinclus*). With this information, we examined the diet specialisation of the vulnerable Pyrenean desman (*G. pyrenaicus*) in the stream and analysed its implications for its conservation. There was a clear dietary overlap between these three predators, which resulted in interspecific trophic competition. *G. pyrenaicus* tended to avoid terrestrial prey and focused on abundant and energetically profitable rheophile species, for which it is well adapted. This diet specialisation makes it vulnerable to any decrease in food availability resulting from anthropogenic stressors such as damming, which can reduce habitat quality and prey availability. More research is needed to fully understand prey electivity in *G. pyrenaicus* and so be able to suggest effective conservation measures for this species.

Keywords *Galemys pyrenaicus* · *Neomys fodiens* · *Cinclus cinclus* · Diet · Macroinvertebrates · Conservation ecology

Introduction

Headwater streams are unique habitats characterised by cold oligosaline waters, special hydrological conditions and fast water flow with conspicuous seasonal variability (Milner and Petts 1994; Giller and Malmqvist 1998). These fragile ecosystems are threatened by numerous anthropogenic stressors including habitat destruction, flow regulation and pollution (Bona et al. 2008; Dudgeon 2010), all of which can provoke a shift in the availability of certain basal ecosystem resources, thereby intensifying competitive interactions between the consumers of this type of resources (Biffi et al. 2017a). This is especially relevant in biodiversity conservation, which requires the effective application of good knowledge of the interactions between species and their environment. The ecological niche theory (Hutchinson 1957) states that sympatric species can co-exist by exhibiting a degree of niche differentiation in prey or habitat use due to competitive interactions (Pianka 1974). Macroinvertebrates are one of the key basal food resources for many semi-aquatic vertebrate predators in headwater streams (Allan 1995), which makes them potential competitors (Biffi et al. 2017a). For the effective conservation of these vertebrates, it is thus crucial to analyse their resource use and any potential niche overlaps with their competitors (Dudgeon et al. 2006).

The Pyrenean desman *Galemys pyrenaicus* (E. Geoffroy Saint Hilaire, 1811, Talpidae), endemic to headwater streams in the mountains of the Pyrenees and north of the Iberian Peninsula, is a semi-aquatic vertebrate of great conservation concern. It is listed as Endangered by the IUCN (Quaglietta, 2021) as its populations are rapidly declining (Charbonnel et al. 2016; Aymerich and Gosàlbez 2018). It is known to be a generalist rheophile predator with a trophic preference

Handling editor: Sabine Begall.

✉ Alejandro López-de Sancha
alejandro.lopez@udg.edu

[1] Faculty of Sciences, Institute of Aquatic Ecology, University of Girona, Maria Aurèlia Capmany i Farnés nº 69, 17003 Girona, Spain

[2] Catalan Natural History Institution, Barcelona, Spain

[3] BiBio Research Group, Natural Sciences Museum of Granollers, Granollers, Spain

[4] Continental Ecology Department, Blanes Centre for Advanced Studies, Blanes, Spain

for Trichoptera, Ephemeroptera and Plectoptera found in riffle sections of streams (Bertrand 1994; Santamarina 1993; Castién and Gosàlbez 1999; Esnaola et al. 2018). Whilst some authors indicate that it also consumes a substantial amount of terrestrial prey (Gillet 2015; Biffi et al. 2017a; Esnaola et al. 2021), others suggest that in fact it consumes very little such prey (Santamarina 1993; Bertrand 1994; Castién and Gosálbez 1999; Hawlitschek et al. 2018).

Galemys pyrenaicus shares habitat and prey resources with other semi-aquatic insectivorous vertebrates including the white-throated dipper *Cinclus cinclus* (Linnaeus, 1758) (Santamarina 1993; Bertrand 1994), a bird that consumes a great variety of prey items, with trichopterans and terrestrial prey known to be staples (Santamarina 1990, 1993; Taylor and O'Halloran 2001). *G. pyrenaicus* also shares food resources with a number of species of water shrews depending on the location. In Pyrenean headwater streams, *G. pyrenaicus* co-exists with the Eurasian water shrew *Neomys fodiens* (Pennat, 1771) (Castién and Gosálbez 1999; Biffi et al. 2017a), which is also known to be a generalist predator in this aquatic environment that includes an important amount of terrestrial prey in its diet (Castién and Gosálbez 1999; Churchfield and Rychlik 2006). Hence, available information regarding the diet of these three semi-aquatic vertebrates suggests that they all feed on stream macroinvertebrates, especially Trichoptera, Ephemeroptera and Plecoptera, although each has a preference for certain groups and includes terrestrial prey to some extent in its diet. It is also important to note that these species have different adaptations for capturing their prey. The Pyrenean desman has physiological and morphological features that afford it greater efficiency for capturing aquatic prey than the dipper or the water shrew. It is fully adapted to aquatic prey hunting and it can remain underwater for up to four minutes (Richard and Micheau 1975); by comparison, *N. fodiens* only submerges for up to 24 s (Mendes-Soares and Rychlik 2009) and *C. cinclus* for up to 30 s (Tyler and Ormerod 1988). Thus, the foraging efficiency provided by its diving ability allows *G. pyrenaicus* to specialise on aquatic prey due to the balance between the energetic costs of foraging and the energy provided by prey consumption.

Multiple studies have analysed the diet of the Pyrenean desman and are usually based either on the morphological or genetic identification of the macroinvertebrates found in its faeces; nevertheless, only a few studies have ever compared the interspecific trophic competition between *G. pyrenaicus* and other predators in the same habitat. Although some information on the diet overlap of this species with *N. fodiens* exists (Santamarina 1993; Biffi et al. 2017a), no studies have ever included *C. cinclus* in the comparison, despite its significant use of similar stream macroinvertebrates as a food resource (Santamarina 1990, 1993). Considering that these three predators share a preference for similar macroinvertebrate groups, diet overlap and its consequent interspecific competition is to be expected. However, the physiological and morphological adaptations of *G. pyrenaicus* should make it more efficient at capturing aquatic prey and so diet specialisation on energetically profitable aquatic prey, as well as an avoidance of terrestrial prey, is likely to occur in this species. The aim of this study was thus to characterise the macroinvertebrate community of a Pyrenean headwater stream, describe the diets of the *G. pyrenaicus*, *N. fodiens* and *C. cinclus* individuals that live there, and assess their prey electivity and diet overlap. This information will enable us to improve our understanding of the trophic ecology of *G. pyrenaicus* and its diet specialisation, which, in turn, will help assess how anthropogenic stressors may impair access to key food resources and habitats for this species. We hypothesised that interspecific trophic competition will occur in these three semi-aquatic predators, which will result in diet specialisation in *G. pyrenaicus* on aquatic energetically profitable prey.

Materials and methods

Study area

The study area was a Pyrenean headwater stream named Ribera del Catllar (from now on referred to as Catllar stream), a tributary of the river Ter (Vilallonga del Ter, Catalonia, NE Iberian Peninsula), located at 1200–1600 m a.s.l. We selected four, equally spaced sampling points (Upst. 1, Upst. 2, Down. 1 and Down. 2) (Fig. 1) that are representative of the altitudinal zonation of this stream. A small hydroelectric dam located between the Upst. 2 and Down. 1 sampling points divides the stream into two sectors; this dam diverts most of the upstream water to a hydroelectric station and so downstream of the dam most of the stream's water is derived from a tributary entering from the west. Information about the characteristics of the water on either side of the dam, obtained from a previous characterisation of the stream (López-de Sancha et al. 2022), is given in Table 1.

Macroinvertebrate abundance samplings

The macroinvertebrate abundance samplings were performed at each of the four sampling points once per season over a period of two years (spring 2018 to winter 2020; eight samplings per point), and followed the methodology of the quantitative macroinvertebrate sampling protocols used by the Catalan Water Agency (ACA 2006) and the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA 2013). At each sampling point, the percentage coverage of each type of microhabitat substrate was estimated. Ten 0.125 m^2 sampling units were established at each

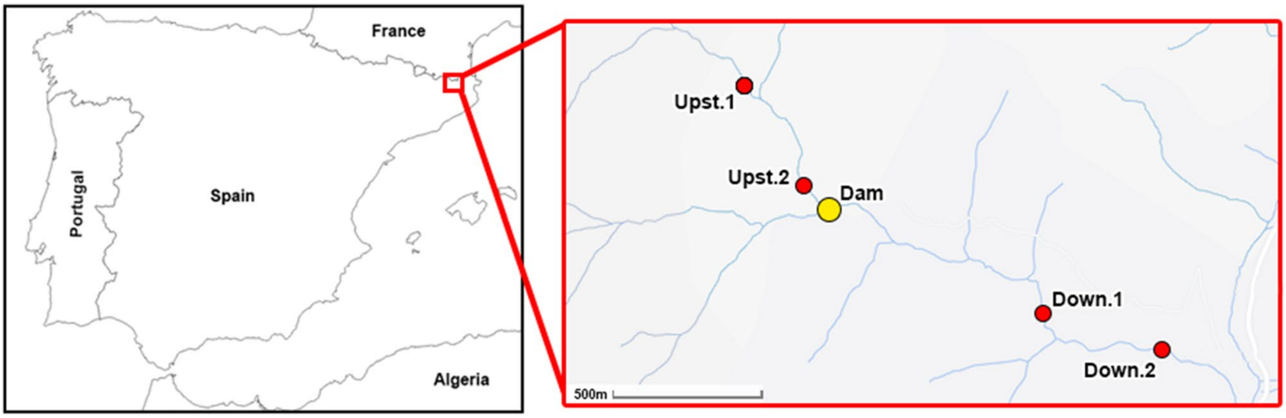

Fig. 1 The basin of the Catllar stream with its main tributaries. The four macroinvertebrate sampling points are indicated with red dots (Upst 1, Upst 2, Down 1, and Down 2) and the dam with a yellow dot. Catllar stream is a tributary of the river Ter located in Catalonia, NE Iberian Peninsula (red square)

Table 1 Average and standard deviation of the water temperature, conductivity, oxygen concentration, pH and flow grouped according to their position in relation to the dam

Parameter	Position		ANOVA analysis	
	Upstream	Downstream	χ^2	*P*
Temperature (°C)	5.2 ± 1.6	6.6 ± 1.6	3.524	0.060
Conductivity (µS/cm)	128 ± 14.2	186 ± 18.2	386.786	< 0.001
Oxygen (mg/L)	10.1 ± 0.4	9.9 ± 0.4	2.361	0.124
pH	7.9 ± 0.2	8.0 ± 0.2	4.931	0.026
Flow (m^3/s)	0.2 ± 0.1	0.1 ± 0.1	7.103	0.007

Water values are averaged from the two points on each side of the dam sampled in three different seasons (autumn, winter and spring) over 2 years, giving six replicates between 2018 and 2020. Also shown are the results of the ANOVA analysis of these variables, derived from a Linear Mixed-Effects model, comparing the positions of sampling points in relation to the dam. The degrees of freedom were one. Variables were transformed using log10, square root or Box–Cox to reach normality. Adapted from López-de Sancha et al. (2022)

point in proportion to the distribution of each microhabitat type: one sampling unit for each 10% of microhabitat coverage, plus an extra half sampling unit for minority habitats (< 5%). Samples were taken using a using a 25-cm wide and 500-µm mesh-size hand net and then stored in plastic containers with ethanol 80% until processing and analysis in the laboratory.

Macroinvertebrates were identified using a stereoscopic microscope (Optika SZR-10) and identification keys (Campaioli et al. 1999; Malicky 2004; Tachet et al. 2010; Oscozet al. 2011; Osorio et al. 2021). The taxonomic resolution was based on the IBMWP Biological Quality Index (Alba-Tercedor et al. 2002), in which taxa other than Nematoda, Nematomorpha, Oligochaeta, Ostracoda, Hydracarina, Collembola, Nemouroidea and Perloidea were identified to family level. For each sample, a fraction of at least 300 individuals was identified and counted. All the individuals of the taxa not present in the analysed fraction but present in the rest of the sample were also counted. The abundance of each taxon was calculated by extrapolating the abundance of all individuals present in the analysed fraction plus the number of individuals in the rest of the sample. The results were expressed as densities (individuals/m^2) based on the size of the sampled area.

Insectivorous semi-aquatic vertebrates in the Catllar stream

The presence of the studied predators and their distribution in the Catllar stream had been determined previously (personal communication). Despite the coexistence of two water shrew species in the basin of the river Ter, only *N. fodiens* has ever been detected in the Catllar stream (via molecular analyses) and so all water shrew diet samples were attributed to this species. Whilst *N. fodiens* was frequent along the whole length of the stream, the Pyrenean desman *G. pyrenaicus* was only found upstream of the dam. This subpopulation of Pyrenean desman forms part of the highly endangered desman population in the Alt Ter basin (NE extreme of its range), which is composed of small, somewhat isolated subpopulations. Although both mammals were detected all year round in similar abundances, the numbers of dippers *C. cinclus* fluctuated seasonally, and were commonest in spring and summer.

Diet samples

To determine the use of benthic stream macroinvertebrates *G. pyrenaicus*, *N. fodiens* and *C. cinclus*, diet samplings were performed three times per season between March 2018 and November 2021 (but not in 2020 or in winter), resulting in nine samplings per year. Six transects of 200 m each, three below and three above the dam, were walked and diet pellets and depositions were visually searched for on projecting objects (i.e. rocks and roots) and in cavities. The macroinvertebrate sampling points were within the diet sampling transects. A standardised transect length of samplings for detecting *G. pyrenaicus* (Queiroz et al. 1998; Aymerich and Gosàlbez 2014) was used and is also appropriate for *N. fodiens* (Aymerich and Gosàlbez 2004), as repeated visits to the same sites increase the detection probabilities of both species (Charbonnel et al. 2014). The identification of the diet samples of each species was based on the expert criteria of the investigators taking into account where they were found and their size, colour and smell. The obtained samples were preserved in ethanol until analysis, when they were disaggregated using hydrogen peroxide, and macroinvertebrate mouthparts and key sclerites were separated, counted to determine the abundance of individuals per sample, and identified to the same taxonomic level as the macroinvertebrate abundance samplings. For identification, a reference collection of mouthparts and sclerites from the macroinvertebrate abundance samplings was used. Oligochaeta individuals were counted as a single individual when chaetae were found, whilst molluscs were identified through parts of their shields. All the data used for the prey electivity and trophic overlap analyses corresponded to the aquatic taxa found in the diet samples as no data on the availability of terrestrial prey were obtained.

Trophic overlap analyses

Aquatic prey counts were used to calculate the Pianka niche overlap index (Pianka 1974) to determine the degree of trophic overlap between the three analysed predator species in the stream (not including terrestrial taxa). This index ranges from 0 (no trophic resources used in common) to 1 (full dietary overlap). The same counts were used to generate a Venn diagram showing the number of different prey taxa unique to each predator, together with the taxa shared by these predators.

Ivlev's electivity index (Ivlev 1961) was calculated using the *Electivity* R package (Quintans 2019). The average abundance of each prey item found in the diet samples for each predator was compared to its average availability in the stream. The resulting index value was represented as a heatmap with an average linkage clustering method and a Euclidean distance measurement method. This index ranged from − 1, indicating that a prey item was abundant in the stream but avoided by the predators, to + 1, indicating that the prey taxon was rare in the stream but preferred by the predators; 0 indicates random feeding. All analyses were performed using the RStudio software version 1.2.5033 (RStudio Team 2019).

Results

During the macroinvertebrate samplings, similar abundance densities were found in all seasons. The highest average abundance in the stream of taxa consumed by predators was the ephemeropterans Baetidae and Heptageniidae, and the water beetles Elmidae. Intermediate abundances of the plecopterans Nemuroidea, the trichopterans Hydropsychidae, Limnephillidae, Brachycentridae and Odontoceridae, and the ephemeropterans Ephemerellidae were also found (Fig. 2).

During the diet characterisation samplings, a total of 1996 prey items were identified in 75 samples, 1012 for *G. pyrenaicus* (28 depositions), 309 for *N. fodiens* (32 depositions)

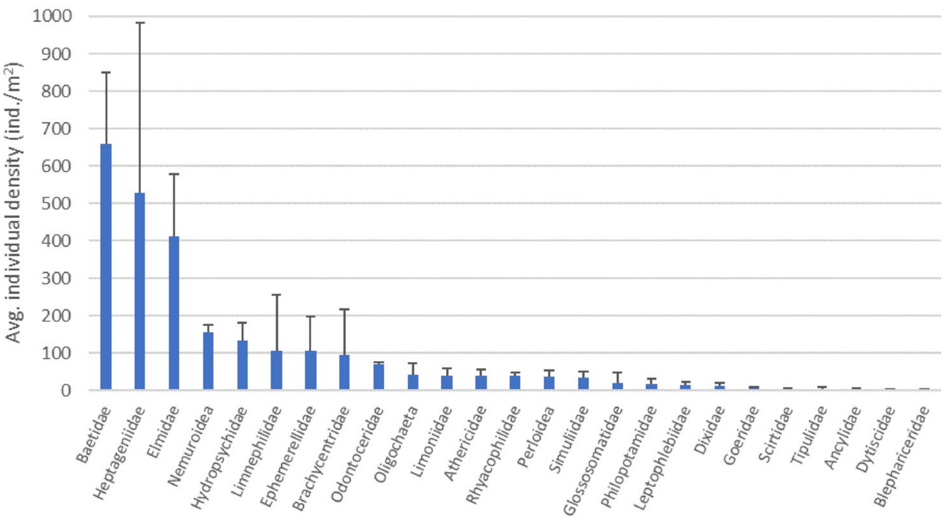

Fig. 2 Average values (individuals/m^2) with standard errors of the macroinvertebrate prey availability in the Catllar stream found during the seasonal samplings (spring, summer and autumn). Values include only the availability of the terrestrial taxa consumed by the analysed vertebrate predators

and 675 for *C. cinclus* (14 pellets). The average abundance values of prey taxa for each predator are shown in Table 2. The data indicate that the main components of the diet of *G. pyrenaicus* were ephemeropterans (33.1%) and trichopterans (29.5%). This species thus fed almost exclusively on taxa in aquatic life stages as less than 0.2% of its diet was composed

Table 2 Average abundance (individuals/sample) with the standard deviation of each taxon found in the diet samples of *Galemys pyrenaicus*, *Neomys fodiens* and *Cinclus Cinclus*

Prey taxa		*G. pyrenaicus*	*N. fodiens*	*C. cinclus*
Oligochaeta	*Indeterminate*	0.07 ± 0.26	0.03 ± 0.17	–
Mollusca	Ancylidae	–	0.03 ± 0.17	0.93 ± 2.94
Ephemeroptera				
	Baetidae	7.28 ± 7.82	1.48 ± 2.29	2.50 ± 2.56
	Ephemerellidae	1.68 ± 2.45	0.21 ± 0.48	7.43 ± 8.46
	Heptageniidae	2.79 ± 2.83	0.51 ± 0.57	4.79 ± 6.59
	Leptophlebiidae	0.04 ± 0.19	0.06 ± 0.24	0.07 ± 0.26
	Indeterminate	0.18 ± 0.95	–	–
Plecoptera				
	Nemouroidea	4.64 ± 6.72	1.24 ± 2.42	1.86 ± 1.91
	Perloidea	1.93 ± 1.86	0.36 ± 0.55	3.14 ± 3.06
Coleoptera				
	Elmidae	1.11 ± 1.72	0.06 ± 0.24	1.00 ± 1.71
	Scirtidae	0.29 ± 0.66	0.06 ± 0.24	–
	Dytiscidae	–	–	0.21 ± 0.80
	Indeterminate	–	0.03 ± 0.03	–
Trichoptera				
	Brachycentridae	–	–	11.07 ± 36.41
	Glossosomatidae	–	0.03 ± 0.17	0.14 ± 0.36
	Goeridae	0.03 ± 0.19	0.03 ± 0.17	1.14 ± 1.99
	Hydropsychidae	4.32 ± 4.08	0.79 ± 0.99	2.00 ± 2.11
	Limnephilidae	0.71 ± 0.94	0.97 ± 1.99	3.71 ± 2.52
	Odontoceridae	3.96 ± 3.60	0.58 ± 1.22	2.14 ± 2.62
	Philopotamidae	0.61 ± 1.60	0.27 ± 0.94	–
	Rhyacophilidae	0.93 ± 1.05	0.21 ± 0.48	4.28 ± 2.84
	Indeterminate	0.07 ± 0.38	0.12 ± 0.54	0.14 ± 0.36
Diptera				
	Athericidae	0.04 ± 0.19	–	0.07 ± 0.27
	Blephariceridae	0.04 ± 0.19	–	–
	Dixidae	2.43 ± 3.99	0.63 ± 1.69	0.14 ± 0.53
	Limoniidae	0.25 ± 0.52	0.12 ± 0.33	–
	Simuliidae	1.32 ± 3.69	0.24 ± 0.61	0.21 ± 0.58
	Tipulidae	1.32 ± 2.88	0.24 ± 0.61	0.29 ± 0.46
	Indeterminate	0.04 ± 0.19	0.09 ± 0.38	–
Terrestrial groups				
	Miriapoda	–	0.12 ± 0.33	–
	Heteroptera	–	0.06 ± 0.35	–
	Coleoptera	–	0.18 ± 0.46	0.21 ± 0.58
	Diptera	0.4 ± 0.19	0.06 ± 0.35	–
	Formicidae	–	0.18 ± 0.53	0.21 ± 0.58
	Araneidae	–	0.03 ± 0.17	–
	Indeterminate	–	0.03 ± 0.63	0.50 ± 0.76
Total consumed individuals		1012	309	675
Total consumed taxa		25	31	24
Number of diet samples		28	32	14
Average prey species per sample		9.57 ± 3.43	5.42 ± 3.26	9.85 ± 2.18

of terrestrial prey. Similarly, the diet of *N. fodiens* was based on trichopterans (32.0%) and ephemeropterans (24.3%), but did also include a relevant proportion of terrestrial prey (10.0%). Both mammals included around 14–15% of dipterans and 17–18% of plecopterans in their diets. Finally, *C. cinclus* based its diet on trichopterans (51.1%) and ephemeropterans (30.7%), with just 1.9% of its diet consisting of terrestrial prey.

The Pianka niche overlap index based only on aquatic prey reveals that there was a clear diet overlap between *G. pyrenaicus* and *N. fodiens* (0.928). By comparison, the diet overlap of these two mammals with the dipper *C. cinclus* was not that strong (Pianka value = 0.446 in both cases; Table 3). A similar pattern was observed in the Venn diagram (Fig. 3): all predators shared 14 prey taxa, *G. pyrenaicus* and *N. fodiens* shared five taxa, *N. fodiens* only shared one group with *C. cinclus*, and *G. pyrenaicus* shared two groups with the dipper.

Table 3 Results of the Pianka dietary niche overlap index between the mammals *G. pyrenaicus* and *N. fodiens*, and the bird *C. cinclus*

Species compared	*Galemys–Neomys*	*Neomys–Cinclus*	*Cinclus–Galemys*
Pianka's Index value	0.928	0.446	0.446

Values close to 0 indicate no trophic resources were used in common, whilst values close to 1 indicate a full dietary overlap. These values do not include the proportion of terrestrial taxa

Ivlev's electivity index (Fig. 4) compares the selection of aquatic prey by the three analysed predators and prey availability in the stream. All three actively shared and positively selected the trichopterans Odontoceridae and Rhyacophilidae, and the plectopterans Perloidea. However, many abundant taxa in the stream were not positively selected but were still actively consumed: the trichopterans Glossosomatidae, the ephemeropterans Heptageniidae and Baetidae, the dipterans Athericidae and Limoniidae, the coleopterans Elmidae, and Oligochaeta worms. Despite these similarities, there were notable differences between each predator in terms of their prey electivity.

Cinclus cinclus clearly differed from the other predators as it actively selected groups, such as the beetles Dytiscidae and the trichopterans Brachycentridae, Goeridae and Limnephillidae, and the ephemeropterans Ephemerellidae, as well as the molluscs Ancylidae that were avoided—or only randomly captured—by the mammals. It avoided scarce taxa, such as Scirtidae and Philopotamidae. Conversely, although *G. pyrenaicus* and *N. fodiens* shared a positive electivity for many prey items, *N. fodiens* also positively selected the trichopterans Goeridae and Limnephillidae and the molluscs Ancylidae, which were not actively selected by *G. pyrenaicus* and only preyed upon somewhat randomly.

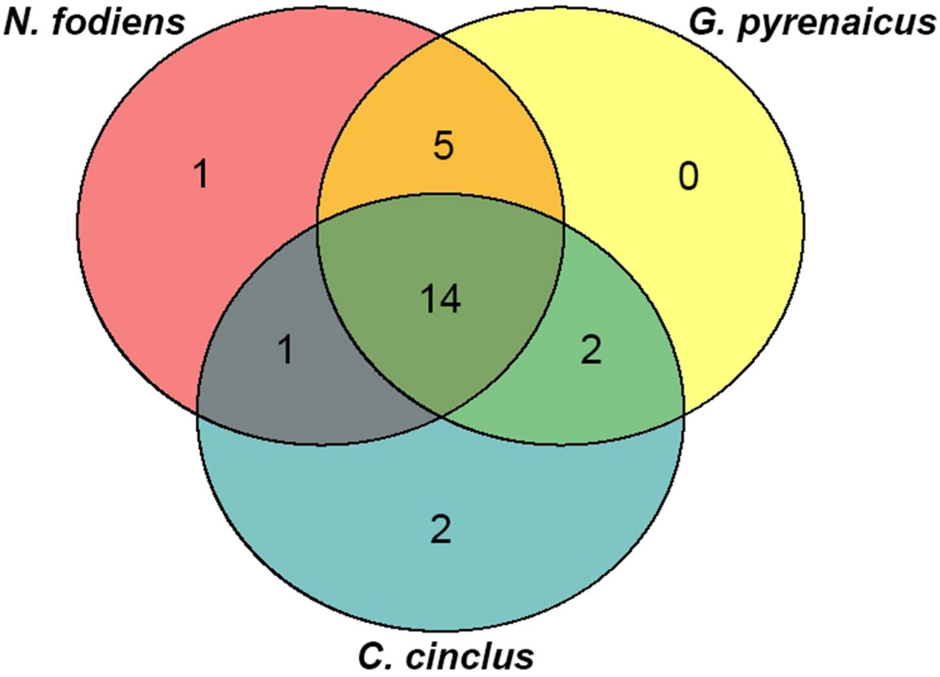

Fig. 3 Venn diagram showing the number of unique and shared prey taxa found in the diet samples of each predator (*N. fodiens, G. pyrenaicus* and *C. cinclus*)

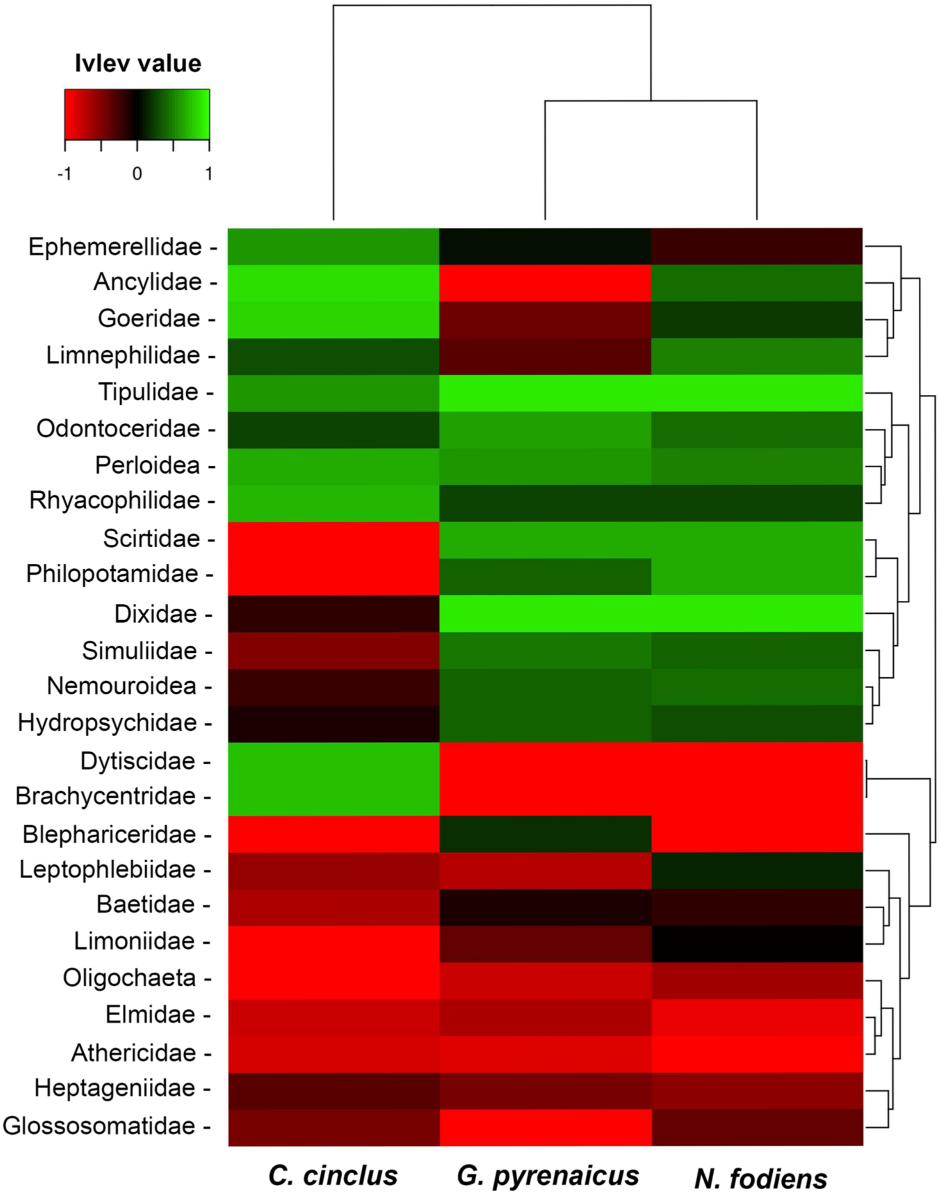

Fig. 4 Ivlev's electivity index for the macroinvertebrate prey consumed by each predator (*N. fodiens, G. pyrenaicus* and *C. cinclus*) represented as a heatmap. The electivity ranges from − 1 (red), indicating that a prey item is abundant in the stream but avoided by the predator, to + 1 (green), indicating that the prey item is rare in the stream but is preferred by the predator. Values near 0 (black) indicate random feeding

Discussion

The diet analysis of these three stream vertebrates revealed a clear overlap that gives rise to interspecific trophic competition, especially between *G. pyrenaicus* and *N. fodiens*. General tendencies were observed including the negative electivity of groups that are scarce in the stream (e.g. Leptophlebiidae), had a low energy yield due to their low digestibility (e.g. Athericidae, Limoniidae), or belonged to highly chitinous (e.g. Elmidae) or hard-cased (e.g. Glossomatidae) families. Groups that were difficult to access due to their habitat selection (e.g. Blephariceridae, Oligochaeta) were also avoided (Tachet et al. 2010; Biffi et al. 2017a). By contrast, the prey groups that were positively or randomly selected by all the predators were rheophile, abundant and energetically profitable taxa, mainly trichopterans but also ephemeropterans, plecopterans and the large dipterans Tipulidae. Despite these similarities, certain differences in prey electivity by each predator were observed, which prompted resource partitioning based on morphological and physiological differences.

Prey electivity in the white-throated dipper (*C. cinclus*) and water shrew (*N. fodiens*)

The generalist diet of the dipper, which is known to contain trichopterans as a staple (Santamarina 1990, 1993; Taylor and O'Halloran 2001), was reflected in the results of our study. This bird selected the most available and energetically profitable prey, and trichopterans were the most abundant fraction in its diet (i.e. high electivity values for families, such as Goeridae, Limnephilidae, Rhyacophyllidae, Brachycentridae and Odontoceridae). Trichoptera larvae are the largest macroinvertebrate group (in terms of biomass) available to dippers and are used by dippers to feed their nestlings (Taylor and O'Halloran 2001), which would explain their active selection of this group. The dippers in this stream also used ephemeropterans as an important food resource: some of the families of this group were actively selected (e.g. Ephemerellidae) or randomly captured if they were highly abundant (Baetidae and Heptagenidae). These results agree with available information for the typical diet of this bird (Santamarina 1990; Tyler and Ormerod 1991; Bertrand 1994; Taylor and O'Halloran 2001; Horváth 2002). The selection by dippers of Brachycentridae and Dytiscidae, two groups that were avoided by *N. fodiens* and *G. pyrenaicus*, could be due to the ecology of this species. Brachycentridae individuals are small and are mainly found in the moss on rocks, usually in large quantities. Unlike the two mammals analysed in the stream, dippers' beaks will allow them to efficiently select these groups. Similarly, Dytiscidae beetles, swimmers found in areas of low flow (Tachet et al. 2010), are vulnerable to visual detection by dippers; the mammals, on the other hand, move amongst the benthic rocks of the stream and detect prey mainly using their vibrissae.

The diet of the water shrew *N. fodiens* in the Catllar stream was based on abundant trichopterans and ephemeropterans but also included terrestrial prey, which agrees with previous categorisations of this mammals as a generalist predator (Castién and Gosálbez 1999; Churchfield and Rychlik 2006). Even so, it also actively selected various families of dipterans and other groups found in low abundances. Its prey preference was focussed on families that, on one hand, are easy to catch due to their low mobility and, on the other hand, are soft-bodied and so completely and easily digestible. This fact would also explain the avoidance of and random feeding tendencies on families that are highly chitinous, have hard cases, or are difficult to find (Tachet et al. 2010; Biffi et al. 2017a). Most of the aquatic taxa consumed by *N. fodiens* were also preyed on by *G. pyrenaicus*.

Trophic ecology and diet specialisation in *G. pyrenaicus*

The *G. pyrenaicus* population in the Catllar stream fed on the most abundant aquatic taxa of the stream (Baetidae, Nemouroidea, Hydropsychidae, Odontoceridae and Heptageniidae) but also selected low abundance families preyed upon by *N. fodiens* and *C. cinclus* (e.g. Tipulidae and Dixidae). Both mammals avoided the soft-bodied taxa that inhabit fine sediments (e.g. Athericidae, Limoniidae and Oligochaeta), a finding also reported in other studies of *G. pyrenaicus* (Esnaola et al. 2021). This situation illustrates the interspecific trophic competition occurring between *G. pyrenaicus* and the other analysed semi-aquatic predators, as well as the partial prey overlap, in which these predators co-exist by frequenting a different microhabitat determined by their specific morphological and physiological adaptations (Castién and Gosálbez 1999; Churchfield and Rychlik 2006).

The Pyrenean desman is considered a generalist that feeds on the most abundant prey (Biffi et al. 2017a; Hawlitschek et al. 2018; Esnaola et al. 2021) and only a few studies have ever reported a specialist diet for this species (Bertrand 1994). In our study, *G. pyrenaicus* focussed on aquatic, energetically profitable prey. Its physiological and morphological adaptations to diving (Richard and Micheau 1975) explain its prey electivity in the Catllar stream, which is characterised by its choice of rheophile, benthic, low mobility, soft-bodied and abundant groups, but also its rejection of families with a low energetic yield (Bertrand 1994; Biffi et al. 2017a) and avoidance of terrestrial prey. In this aquatic environment, the Pyrenean desman outcompetes both *N. fodiens* and *C. cinclus*. Although its avoidance of terrestrial prey observed in the Catllar stream matches other studies that have used a morphological approach for prey identification (Santamarina 1993; Bertrand, 1994; Castién and Gosálbez 1999), some studies based on a genetic approach (Biffi et al. 2017a, b; Esnaola et al. 2021) indicate that the desman actively consumes terrestrial groups. Both these approaches permit the identification of a wide range of prey items but it is, nevertheless, important to understand the biology of these prey species when assessing their use as food resources to avoid misleading interpretations.

For instance, in many recent studies (Biffi et al. 2017a, b; Esnaola et al. 2021), the Diptera family Psychodidae has been reported to be an important component of the diet of the Pyrenean desman. In our study, individuals of this family were found in the analysed faecal samples but were also observed alive in faeces and later identified at the larval stage with no signs of having been digested. Given the biology of this family, we decided that this taxon should not be included as prey because the adults of many of its members lay their eggs in fresh depositions (Arnett 2000; Tachet et al. 2010). Thus, the finding of full-bodied, undigested individuals from this family does not indicate that they were used as a food resource. Hence, we believe it to be essential to collect as fresh as possible diet samples to avoid this kind of environmental contamination, and to undertake a morphological examination of samples to rule out any possible misinterpretation of results. In conjunction with the morphological identification of prey groups, genetic diet studies can confirm the importance of soft-bodied prey groups that are often missed by morphological studies (Biffi et al. 2017a; Hawlitschek et al. 2018; Esnaola et al. 2021). For example, the molluscs Ancylidae and the Oligochaeta worms are difficult to detect morphologically after digestion due to their soft bodies, and their morphological identification is based on chaeta and shield parts that diminish their relative abundance in the diet of *G. pyrenaicus* and other stream predators.

Further research is still needed to fully understand prey electivity and diet specialisation in *G. pyrenaicus* and the role terrestrial prey items play therein. The benefits and limitations of both genetic and morphological approaches must be taken into account when designing studies aimed at assessing the diet of stream vertebrates such as *G. pyrenaicus* to avoid misleading interpretations.

Conservation of *G. pyrenaicus*: impacts of damming and the need for action

The Pyrenean desman is restricted to productive, relatively pristine and well-preserved habitats in mountainous regions due to its sensibility to many anthropogenic stressors and its need for regular food availability throughout the year. Local population declines and extinctions have been reported in all the fluvial basins in its range. This has been attributed to the interaction of multiple anthropogenic stressors, of which those linked to hydrological alterations—above all, damming—are thought to be one of the main threats (Nores 2007; Aymerich and Gosàlbez 2018; Esnaola et al. 2021).

Damming can directly impact the Pyrenean desman, on the one hand, by impairing the connectivity between its populations (Allan and Castillo 2007; Nores 2007) and, on the other hand, by causing a reduction in the water flow, and a decrease in the volume, area and depth of streams, thereby altering the velocity of its waters (Rolls et al. 2012). This reduces the heterogeneity of the stream habitat, as well as the availability of riffles, the fast-flowing sections of the stream that are a key requirement for the Pyrenean desman. They help it overcoming its natural buoyancy, allowing it to crawl down to the benthos and cling on with its strong claws as it feeds on its preferred prey (Nores 2007; Esnaola et al. 2021). The presence of a dam can also affect it indirectly by altering the availability of its food resources: the rheophile macroinvertebrate community of the stream. A reduction in the density and richness of rheophile prey species, especially those belonging to the Trichoptera, Plecoptera and Ephemeroptera orders, has been reported in many dam-impounded streams due to the negative effects these structures have on habitats (Lessard and Hayes 2001; Allan and Castillo 2007; Rolls et al. 2012; Martínez et al. 2013; Mor et al. 2018). Damming undoubtedly increases competition for their preferred resources, which is rheophile prey (Rolls et al. 2012).

A reduction in the density of stream macroinvertebrates caused by damming could, as a result of bottom–up processes (Livingston 1997; McIntosh et al. 2003; Hannah et al. 2007), intensify competitive trophic interactions between *G. pyrenaicus* and its competitors (Biffi et al. 2017a), thereby even further reducing the availability of resources for the Pyrenean desman's highly specialised diet. Considering that currently more than 115 hydropower dams exist in the Pyrenees (Durban 2011), this situation, along with other factors, could be contributing to current population declines in *G. pyrenaicus*, as its very specific diet could prove to be a disadvantage compared to other predators that feed on a wider variety of prey. This effect will not have such a strong effect on populations of either *C. cinclus*, which can easily migrate to other areas with better conditions and feed on terrestrial prey, or on populations of *N. fodiens*, which have higher individual densities and can also feed on terrestrial macroinvertebrates. This situation has been hinted at in the central Pyrenees, where *G. pyrenaicus* is experiencing severe population declines and is now found in only 45% of possible streams, whereas *N. fodiens* is found in 94% (Aymerich and Gosàlbez 2015). One possible solution to this problem is the complete removal of dams since the release of 'environmental flows' from dammed streams is not enough to preserve the populations of this endangered species (Esnaola et al. 2021). In fact, dam removal operations in the Basque Country (northern Iberian Peninsula) have improved the situation of the desman populations in affected streams (Urquijo 2018; Yarzabal et al. 2018; Esnaola et al. 2021).

More awareness is needed of the current situation of the Pyrenean desman. Due to the increase in average temperatures and reduction in water flow in the Pyrenees caused by climate change, the distribution of *G. pyrenaicus* is expected to severely decline during the present century (OPCC-CTP 2018). As a characteristic species of an emblematic and threatened habitat, *G. pyrenaicus* could be used as a flagship species for protecting whole ecosystems, and management actions could be focussed on this single species. The European desman has been reported from 296 Natura 2000 sites and multiple European restoration projects have included actions in streams to improve the populations of this species. Despite this, its conservation is still being hindered by a lack of awareness in the human population of the situation of this threatened mammal (Hawlitschek et al. 2018; Esnaola et al. 2021). Bearing all this in mind, we believe that more research into how anthropogenic stressors affect the quality of suitable habitats for the Pyrenean desman is urgently required and so we encourage scientists to instigate effective communication programmes aimed at raising awareness of this vulnerable species.

Acknowledgements The authors would like to thank the Apatura Iris team for their support in this research and the facilities provided by the owners of the Catllar estate, and to Mike Lockwood for his revision of the language of this paper.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Declarations

Ethical approval This research was supported by the Government of Catalonia via the Secretaria d'Universitats i Recerca and the European Social Funds and the main author's doctoral scholarship (code 2020FI_B1 00098). Part of the research was also supported by Apatura Iris SL. All macroinvertebrate sampling and analysis were carried out in compliance with ethical guidelines set for animal experimentation. Meticulous efforts were made to ensure that animals suffered as little as possible and to reduce external sources of stress, pain and discomfort; only the minimum number of individuals were sampled.

References

Agència Catalana de l'Aigua (ACA) (2006) HIDRI, River Hydromorphologic Quality Evaluation Protocol. Departament de Medi Ambient de la Generalitat de Catalunya, Barcelona

Alba-Tercedor J, Jáimez-Cuéllar P, Álvarez M, Avilés J, Bonada N, Casas J, Mellado A, Ortega M, Pardo I, Prat N, Rieradevall M, Robles S, Sáinz-Cantero C, Sánchez-Ortega A, Suárez M, Toro M, Vidal-Abarca M, Vivas S, Zamora-Muñoz C (2002) Caracterización del estado ecológico de ríos mediterráneos ibéricos mediante el índice IBMWP (antes BMWP'). Limnetica 21:175–185

Allan J (1995) Stream ecology. Structure and function of running waters. Chapman and Hall, London

Allan J, Castillo M (2007) Stream ecology. Structure and function of running waters. Springer, Amsterdam

Arnet R (2000) American insects: a handbook of the insects of America North of Mexico, 2nd edn. CRC Press, Florida

Aymerich P, Gosálbez J (2004) La prospección de excrementos como metodología para el estudio de la distribución de los musganos (*Neomys*sp.). Galemys 16:83–90

Aymerich P, Gosàlbez J (2014) El desmán ibérico (*Galemyspyrenaicus*) en los Pirineos meridionales. Munibe Monogr Nat Ser 3:37–77

Aymerich P, Gosàlbez J (2015) Evidencias de regresión local del desmán ibérico en los Pirineos meridionales. Galemys 27:31–40

Aymerich P, Gosálbez J (2018) Regresión reciente y general del desmán ibérico en su límite noreste de distribución. Galemys 30:21–30

Bertrand A (1994) Répartition géographique et écologie alimentaire du desman des Pyrénées, *Galemys pyrenaicus* (Geoffroy, 1811) dans les Pyrénées françaises. Dissertation, Université Toulouse III Paul Sabatier

Biffi M, Laffaile P, Jabiol J, André A, Gillet F, Lamothe S, Michaux J, Buisson L (2017a) Comparison of diet and prey selectivity of the Pyrenean desman and the Eurasian water shrew using next-generation sequencing methods. Mamm Biol 87:176–184. https://doi.org/10.1007/s42991-021-00115-4

Biffi M, Gillet F, Laffaille P, Colas F, Aulagnier S, Blanc F et al (2017b) Novel insights into the diet of the Pyrenean desman (*Galemyspyrenaicus*) using next-generation sequencing molecular analyses. J Mammal 98:1497–1507. https://doi.org/10.1371/journal.pone.0208986

Bona F, Falasco E, Fenoglio S, Iorio L, Badino G (2008) Response of macroinvertebrate and diatom communities to human-induced physical alteration in mountain streams. River Res Appl 24:1068–1081. https://doi.org/10.1002/rra.1110

Campaioli S, Ghetti P, Minelli A, Ruffo S (1999) Manuale per il riconoscimento dei macroinvertebrati delle acque dolci Italiane. Vol. II. Provincia autonoma di Trento, Trento

Castién E, Gosálbez J (1999) Habitat and food preferences in a guild of insectivorous mammals in the Western Pyrenees. Acta Theriol 44:1–13

Charbonnel A, D'Amico F, Besnard A, Blanc F, Buisson L, Némoz M, Laffaille P (2014) Spatial replicates as an alternative to temporal replicates for occupancy modelling when surveys are based on linear features of the landscape. J Appl Ecol 51:1425–1433. https://doi.org/10.1111/1365-2664.12301

Charbonnel A, Laffaille P, Biffi M, Blanc F, Maire A, Némoz M, Sanchez-Perez J, Sauvage S, Buisson L (2016) Can recent global changes explain the dramatic range contraction of an endangered semi-aquatic mammal species in the French Pyrenees? PLoS ONE 11:e0159941. https://doi.org/10.1371/journal.pone.0159941

Churchfield S, Rychlik L (2006) Diets and coexistence in *Neomys* and *Sorex* shrews. J Zool 269:381–390. https://doi.org/10.1111/j.1469-7998.2006.00115.x

Dudgeon D (2010) Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. Curr Opin Environ Sustain 2:422–430. https://doi.org/10.1016/j.cosust.2010.09.001

Dudgeon D, Arthington A, Gessner M, Kawabata Z, Knowler D, Lévêque C, Naiman R, Prieur-Richard A, Soto D, Stiassny M et al (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81:163–182. https://doi.org/10.1017/S1464793105006950

Durban R (2011) La producción hidráulica al Pirineu. Les hidroelèctriques al Pirineu. University of Lleida. http://www.tremp.cat/public/153/file/LaproducciohidraulicaalPirineo.pdf. Accessed 10 Apr 2021

Esnaola A, Arrizabalaga-Escudero A, González-Esteban J, Elosegi A, Aihartza J (2018) Determining diet from faeces: selection of metabarcoding primers for the insectivore Pyrenean desman (*Galemyspyrenaicus*). PLoS ONE 13:e0208986. https://doi.org/10.1371/journal.pone.0208986

Esnaola A, Mata V, Arrizabalaga-Escudero A, González-Esteban J, Larrañaga A, Rebelo H, Elosegi A, Aihartza J (2021) It is the ambience, not the menu. Prey availability does not drive habitat selection by the endangered Pyrenean desman. Aquat Conserv Mar Freshw Ecosyst 31:1859–1872. https://doi.org/10.1098/rsbl.2018.0348

Giller P, Malmqvist B (1998) The biology of streams and rivers. Oxford University Press, Oxford

Gillet F (2015) Génétique et biologie de la conservation du desman des Pyrénées (*Galemys pyrenaicus*) en France. Dissertation, Université Paul Sabatier de Toulouse/Université de Liège

Hannah D, Brown L, Milner A, Gurnell A, McGregor G, Petts G, Smith B, Snook D (2007) Integrating climate–hydrology–ecology for alpine river systems. Aquat Conserv Mar Freshw Ecosyst 17:636–656. https://doi.org/10.1002/aqc.800

Hawlitschek O, Fernández-González A, Balmori-de la Puente A, Castresana J (2018) A pipeline for metabarcoding and diet analysis from faecal samples developed for a small semi-aquatic mammal. PLoS ONE 13(8):e0201763. https://doi.org/10.1371/journal.pone.0201763

Horváth R (2002) The diet of dippers (*Cinclus cinclus*) in the Aggtelek karst. Tiscia 33:59–66

Hutchinson G (1957) Concluding remarks. Cold Spring Harb Symp Quant Biol 22:415–427

Ivlev U (1961) Experimental ecology of the feeding of fish. Yale University Press, New Haven

Lessard J, Hayes D (2001) Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. River Res Appl 19:721–732. https://doi.org/10.1002/rra.713

Livingston R (1997) Trophic response of estuarine fishes to long-term changes of river runoff. Bull Mar Sci 60:984–1004. https://doi.org/10.3389/fmars.2021.689950

López-de Sancha A, Roig R, Jiménez I, Vila-Gispert A, Guasch H (2022) Impacts of damming and climate change on the ecosystem structure of headwater streams: a case study from the Pyrenees. Inland Waters. https://doi.org/10.1080/20442041.2021.2021776

Malicky H (2004) Atlas of European Trichoptera, 2nd edn. Springer, Dordrecht

Martínez A, Larrañaga A, Basaguren A, Pérez J, Mendoza-Lera C, Pozo J (2013) Stream regulation by small dams affects benthic macroinvertebrate communities: from structural changes to functional implications. Hydrobiologia 711:31–34. https://doi.org/10.1007/s10750-013-1459-z

McIntosh M, Benbow M, Burky A (2003) Effect of water removal on introduced caddisflies from a tropical mountain stream. Int J Limnol 39:297–306. https://doi.org/10.1051/limn/2003024

Mendes-Soares H, Rychlik L (2009) Differences in swimming and diving abilities between two sympatric species of water shrews: *Neomys anomalus* and *Neomys fodiens* (Soricidae). J Ethol 27:317–325

Milner A, Petts G (1994) Glacial rivers: physical habitat and ecology. Freshw Biol 32:295–307. https://doi.org/10.1111/j.1365-2427.1994.tb01127.x

Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA) (2013) Protocol of laboratory and sampling of benthic invertebrates in streams. Secretaria General Técnica del MAGRAMA, Madrid

Mor J, Ruhí A, Tornés E, Valcárcel H, Muñoz I, Sabater S (2018) Dam regulation and riverine food-web structure in a Mediterranean river. Sci Total Environ 625:301–310. https://doi.org/10.1016/j.scitotenv.2017.12.296

Nores C (2007) *Galemys pyrenaicus* (E. Geoffroy Saint Hilaire, 1811). In: Palomo L, Gisbert J, Blanco J (eds) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad. SECEM–SECEMU, Madrid, pp 96–98

OPCC-CTP (2018). Climate change in the Pyrenees: impacts, vulnerabilities and adaptation. Bases of knowledge for the future climate change adaptation strategy in the Pyrenees. OPCC, Huesca

Oscoz J, Galicia D, Miranda R (2011) Identification guide of freshwater macroinvertebrates of Spain. Springer, Dordrecht

Osorio V, Bonada N, Puig M (2021) Macro invertebrats fluvials de Catalunya. Brau Edicions, Spain

Pianka E (1974) Niche overlap and diffuse competition. PNAS 71:2141–2145. https://doi.org/10.1073/pnas.71.5.2141

Quaglietta L (2021) *Galemys pyrenaicus*. The IUCN red list of threatened species 2021: e.T8826A200888614. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T8826A200888614.en. Accessed 6 Jan 2022

Queiroz A, Quaresma C, Santos C, Barbosa A, Carvalho H (1998) Bases para a Conservaçao da Toupeira-de-Água, *Galemys pyrenaicus*. Instituto de Conservaçao da Natureza, Lisboa

Quintans D (2019) Electivity: algorithms for electivity indices. R package version 1.0.2. https://github.com/DesiQuintans/electivity. Accessed 20 Nov 2021

Richard P, Micheau C (1975) Le carrefour trachéen dans l'adaptation du desmán des Pyrénées (*Galemys pyrenaicus*) à la vie dulc¸ aquicole. Mammalia 39:467–478. https://doi.org/10.1515/mamm.1975.39.3.467

Rolls R, Leigh C, Sheldon F (2012) Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshw Sci 31:1163–1186. https://doi.org/10.1899/12-002.1

RStudio Team (2019) RStudio: integrated development for R. RStudio, Inc., Boston

Santamarina J (1990) Alimentación del mirlo acuático (*Cinclus cinclus*) en ríos de Galicia. Misc Zool 14:207–215

Santamarina J (1993) Feeding ecology of a vertebrate assemblage inhabiting a stream of NW Spain (Riobo; Ulla basin). Hydrobiologia 252:175–191

Tachet H, Bournaud M, Richoux P, Usseglio-Polatera P (2010) Invertébrés d'eau douce: systématique, biologie, écologie. CNRS Editions, Paris

Taylor A, O'Halloran J (2001) Diet of dippers *Cinclus cinclus* during an early winter spate and the possible implications for dipper populations subjected to climate change. Bird Study 48:173–179. https://doi.org/10.1080/00063650109461215

Tyler S, Ormerod S (1988) The Dipper. Shire Natural History, London

Tyler S, Ormerod S (1991) Aspects of the biology of Dippers *Cinclus cinclus* minor in the Atlas Mountains of Morocco outside the breeding season. Bonn Zool Beitr 42:35–45

Urquijo A (2018) Hacia la recuperación la permeabilidad del río Leitzaran. Demolición de la presa de Inturia. In: Díez J, Ibisate A (eds) Retos y experiencias de restauración fluvial en el ámbito de la Red Natura 2000. Servicio Central de Publicaciones del Gobierno Vasco, Vitoria-Gasteiz, pp 194–203

Yarzabal A, Martín-Vide J, Elosegi A, Díez J (2018) El desmantelamiento de la presa de Enobieta: último obstáculo a la conectividad fluvial en Artikutza. In: Díez J, Ibisate A (eds) Retos y experiencias de restauración fluvial en el ámbito de la Red Natura 2000. Servicio Central de Publicaciones del Gobierno Vasco, Vitoria-Gasteiz, pp 180–193