

## Feeding ecology of a vertebrate assemblage inhabiting a stream of NW Spain (Riobo; Ulla basin)

J. Santamarina

Area de Ecología, Facultad de Biología, Universidad de Santiago, Spain

**Key words:** fish, birds, mammals, stream, diet, overlap

### Abstract

The food resource use of a stream in NW Spain by fish (*Salmo trutta* L. and *Anguilla anguilla* L.), birds (*Cinclus cinclus* L. and *Motacilla cinerea* L.) and mammals (*Galemys pyrenaicus* G. and *Neomys anomalus* C.) was studied. Data on seasonal diets and stream benthos prey were used to determine prey selection patterns.

Caddisfly larvae are the main resource for *Cinclus* and *Galemys*, but these predators also consumed other benthic prey. *Salmo* fed on a wide range of benthic invertebrates, emergent pupae and terrestrial prey, whereas *Anguilla* consumed primarily benthic invertebrates, especially Lumbricids. *Neomys* fed mainly on terrestrial prey (Gasteropods and Lumbricids), but also consumed aquatic prey. *Motacilla* captured aquatic insects both in larval and aerial stages, as well as terrestrial prey.

Both prey availability and selection led to seasonal differences in the use of food resources. All species showed a marked prey selection of aquatic taxa. Prey size plays an important role in this selection, most species consuming the largest of available prey sizes. In spite of the fact that all species feed upon freshwater invertebrates, substantial resource partitioning was observed in all seasons. This partitioning may be attributable to morphological and physiological differences. Nevertheless, *Anguilla* and *Galemys*, two quite different animals, did feed on the same prey much of the time.

### Introduction

During the last decade, studies on resource partitioning of freshwater fish have increased greatly (review in Ross, 1986). At present, however, little is known about other vertebrate species that consume lotic prey (Ormerod, 1985; Santamarina & Guitián, 1988).

Nonetheless, studies of resource partitioning are important aspects of attempts to determine the potential importance of biological interactions to stream vertebrates. One of the most peculiar characteristics of many streams in North Spain is the coexistence of fish with birds (dipper *Cinclus*

*cinclus* L. grey wagtail *Motacilla cinerea* L.) and mammals (Pyrenean desman *Galemys pyrenaicus* G., Miller's water shrew *Neomys anomalus* C.). All of these species feed upon similar prey: freshwater invertebrates. Most studies on resource partitioning in streams compare closely related species. However, some investigations have demonstrated substantial similarities in diet, and even competition between different classes of vertebrates and between vertebrates and invertebrates (Brown & Davidson, 1977; Wright, 1979; Brown *et al.*, 1979).

This led me to investigate the resource use of insectivorous fish (brown trout *Salmo trutta* L.,

eel *Anguilla anguilla* L.), birds (dipper, grey wagtail) and mammals (Pyrenean desman, Miller's water shrew) inhabiting a small stream in Galicia, NW Spain. I attempt to determine whether the use of food may be important in influencing co-existence among these species. Such a study requires not only enumeration of species' resource use patterns, but also quantification of the relative abundances and availabilities of the resource in question.

## Methods

### Study site

The Riobo is a small tributary (5–7 m wide) of the river Ulla, a major river in NW Spain flowing into the Atlantic Ocean (Fig. 1). Altitude ranges from 150 to 20 m above sea-level. The climate of this

area is perhumid mesothermic according to the classification of Thornwaite (1933). The section that was studied is 3 km long, having an average gradient of  $35 \text{ m km}^{-1}$ . The stream is fed by springs, and the substrate of its basin is made of metamorphic granite.

Maximum and minimum water temperature are 9 and  $16^\circ\text{C}$ . Water pH ranges from 6.7 to 7.0 and conductivity from  $87.4$  to  $115.0 \mu\text{ohm cm}^{-1}$ . The substrate consists mainly of stones and rocks, while sand predominates in pools, frequently covered by vegetal detritus. The stream flows through a small wooded valley with scattered meadows. The bankside vegetation, which consists mainly of alder (*Alnus glutinosa*), willows (*Salix spp*) and ash (*Fraxinus angustifolia*), shades the stream. Aquatic vegetation is scarce, consisting of mosses and a few umbellifers (mainly *Oenanthe crocata*).

The fish community of Riobo consists of brown trout (mean biomass;  $127 \text{ kg ha}^{-1}$ ) and eel (mean biomass:  $10 \text{ kg ha}^{-1}$ ) (Santamarina, 1991). The densities of dippers and grey wagtails during the breeding season were respectively 6 and 5 pairs per 10 km of stream. No data about the abundance of mammals are available.

### Collection of samples

I based dietary analyses on stomach and intestinal contents of fish and mammals. Avian diets were described through analyses of faecal remains and regurgitated pellets.

Fish were collected by electro-fishing with a 350 V DC current. I captured the desman using two different techniques: funnel traps and electro-fishing. Water shrews were captured using spring-jaw traps baited with live worms (*Lumbricus spp*).

Faecal samples of the grey wagtail and the dipper were collected by checking underneath roosts for faecal pellets. Regurgitated pellets of the dipper were also located by checking under roosts.

I sampled the availability of prey in the river benthos using a Surber sampler ( $0.1 \text{ m}^2$ ). I collected 13–15 samples during each season studied. Riffles and pools were sampled separately. Table 1 summarizes the sampling features.

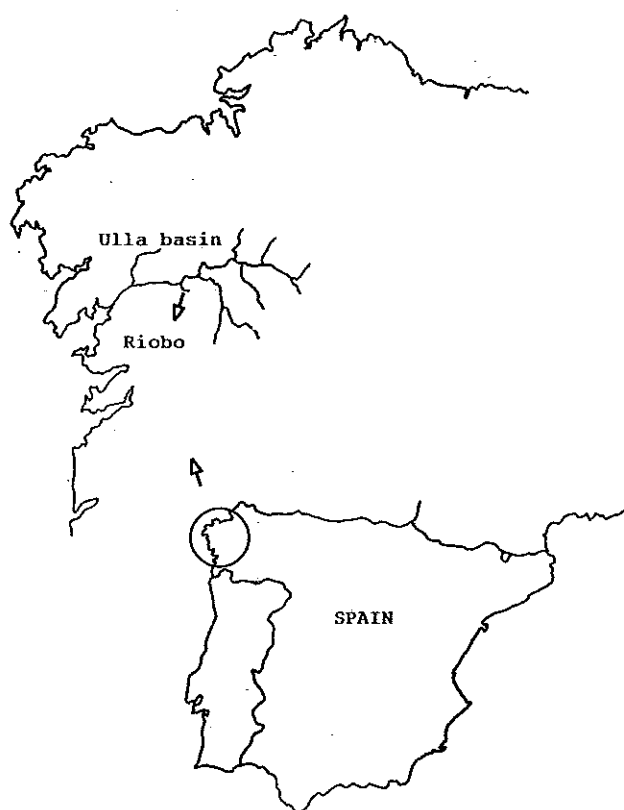


Fig. 1. Geographic location of the studied stream.

Table 1. Sampling features: source, date and sample size. Average lengths ( $\pm$  SD) of fish are indicated.

Dietary sample:	Benthos (Lotic)		Benthos (Lentic)	<i>G. pyrenaicus</i>	<i>N. anomalous</i>	<i>C. cinclus</i>	<i>M. cinerea</i>	<i>S. trutta</i> (juvenile)	<i>S. trutta</i> (adult)	<i>A. anguilla</i>
	Surber	Surber	Surber	Specimens E+1	Specimens E+1	Fecal/Regurgitated remains	Fecal remains	Specimens E+1	Specimens E+1	Specimens E+1
SPRING										
Date #	16-5	16-5	16-5			16, 25-5	27-4/19-5		28-3/20-4	28-3
Sample size	8	5	5			18/3	29		20	18
Length (mm) $\pm$ SD									147 $\pm$ 29	274 $\pm$ 76
Prey	1615	834				765	277		1660	378
SUMMER										
Date #	18-7	18-7	18-7	15, 18-7		8, 20, 28-7	20-7/12-8	19-7	13, 19-7	13, 19-7
Sample size	7	7	7	2		4/18	18	15	20	20
Length (mm) $\pm$ SD								66 $\pm$ 7	167 $\pm$ 43	297 $\pm$ 54
Prey	1575	903		192		978	202	375	2810	260
AUTUMN										
Date #	25-10	25-10	25-10	20, 25-10	18-10	6, 27-10	7, 25-10		20-10/5-12	20-10
Sample size	7	7	7	2	1	20/0	30		20	15
Length (mm) $\pm$ SD									163 $\pm$ 43	293 $\pm$ 50
Prey	1330	1188		565	18	789	291		1408	215
WINTER										
Date #	8-2	8-2	8-2	10, 21-1	11, 17-1/15-3	11, 21-1/17-3		8, 14-2	11-1/8, 14-2	8-2
Sample size	8	7	7	2	15	20/0		15	18	13
Length (mm) $\pm$ SD								106 $\pm$ 12	186 $\pm$ 37	298 $\pm$ 61
Prey	1013	1352		538	540	978		294	1894	3

E + I: stomachs + intestines; SD: standard deviation; # day, day-month (1988-1989).

### *Analysis of samples*

For availability samples, I identified invertebrates to family and calculated the volume of each family by immersion in water using a 5 cc graduated cylinder.

I placed dietary samples in a Petri disk and examined them microscopically at magnification 10–40. I estimated the number of prey consumed by counting calcareous or chitinous body parts. Body parts were obtained from the gut of organisms, pellets or faecal samples.

I identified *Oligochaeta* by chaeta. To have a standard reference for the number of chaetae per individual, an oligochaete was semidigested using HCl and the number of recognizable chaetae was counted at  $40\times$ . Then I divided the total number of chaetae in a dietary sample by this number to derive the number of *Oligochaeta* in the sample.

Molluscs were identified by their shells or opercula and crustaceans by chitinous body parts (in Gammaridae typically antennal bases). I identified most insect larvae (Ephemeroptera, Plecoptera, Odonata, Trichoptera, Diptera) by counting the number of mandibles in a dietary sample, but Odonata were identified to family using the labium, and I used cephalic capsules for Hemiptera and some Diptera (Chironomidae, Tipulidae). Caddisfly pupae were identified by mandibles but dipteran pupae and insect imagines by their thorax and wings. I examined body remains to confirm identifications based only on body parts.

Depending on the taxon, I used different body parts to classify terrestrial prey: Gasteropoda-radula; Myriapoda, Isopoda-scleritis; Hymenoptera, Orthoptera-mandibles; Diptera, Hymenoptera,...wings; Coleoptera-elytra. Vertebrates were detected by their bones, and tadpoles by remains of the labium.

To obtain a more accurate measure of the energetic importance of prey I reconstructed prey volumes from body part size-prey size regressions (Table 2). For each family of aquatic prey, specimens collected in Surber samples were classified according to the size of a body part. Then, the volume of each group was calculated by immer-

sion and I regressed average volume of the specimens against body part size.

For the remaining prey I reconstructed volumes using formulae to get volumes for objects of similar shape. To estimate the size of *Oligochaeta* I arbitrarily separated specimens into 4 volume classes and reconstructed volumes based on average chaetae size of the basic classes.

Prey that did not have calcareous or chitinous body parts may have been underestimated in my analyses (e.g. smaller *Oligochaeta*, Achaeta, eggs and small fishes). If this bias was strong, then easily digestible prey would have been common in the stomachs than in the intestines. This was not the case, and there were neither significant differences between the contents of stomachs and intestines nor between the contents of faecal and those of regurgitated pellets for dipper (Wilcoxon test, all  $p > 0.05$ ).

### *Analyses of data*

For each seasonal sample, I expressed availability and dietary data in numerical and volumetric percentages. Prey items comprising less than 2% of both, volumetric and numerical percentage, were deleted from tables. Prey selection by number was quantified using the index (C) of Pearre (1982). I used this index to compare aquatic prey in diet of predators to the abundance of prey from benthic samples. This ranges from  $-1$  (complete avoidance) to  $+1$  (complete selection). This index is neither linear nor stable (Lechowicz, 1982; for a discussion of these properties). Because of this behaviour I classified values of C as follows: values  $< 0$  with a significant  $p < 0.01$ , negative selection;  $0-0.2$  no selection or weak positive selection,  $0.2-0.4$  moderate positive selection,  $> 0.4$  strong positive selection.

Diet overlap was quantified using Schoener's index (Schoener, 1968):

$$R_0 = 1 - 0.5 \sum_{i=1}^n [P_{ij} - P_{j\bar{j}}],$$

where  $P_{ij}$  and  $P_{j\bar{j}}$  are the volumetric percentages in both diets of the  $j$ th food item. These food

Table 2. Regression between body part size and volume of invertebrate individuals.

*n*: number of determinations. *m*: slope. *b*: Y axis interception point. *SD*: standard deviation. *R*<sup>2</sup>: determination coefficient. Significance levels: *p* < 0.01.

	Variable (x)	<i>n</i>	<i>m</i>	<i>SD</i>	<i>b</i>	<i>SD</i>	<i>R</i> <sup>2</sup>
<b>EPHEMEROPTERA</b>							
<i>Ephemeridae</i>	w.m.	10	2.79 ± 0.27		- 1.16 ± 0.06		0.97
<i>Heptageniidae</i>	w.m.	10	3.11 ± 0.23		- 0.80 ± 0.12		0.97
<i>Baetidae</i>	w.m.	10	3.16 ± 0.45		- 0.73 ± 0.11		0.94
<i>Ephemerellidae</i>	w.m.	10	2.85 ± 0.44		- 1.19 ± 0.13		0.88
<b>PLECOPTERA</b>							
<i>Nemouridae</i>	l.m.	6	2.80 ± 0.06		- 0.60 ± 0.01		0.99
<i>Leuctridae</i>	l.m.	6	1.04 ± 0.44		- 1.90 ± 0.09		0.85
<i>Nemouridae/Leuctridae</i>	l.m.	12	1.56 ± 0.75		- 1.49 ± 0.27		0.52
<b>ODONATA</b>							
<i>Aeschnidae</i>	l.l.	10	2.31 ± 0.15		- 0.88 ± 0.04		0.99
<i>Cordulegastridae</i>	l.l.	10	2.06 ± 0.31		- 1.48 ± 0.26		0.96
<i>Gomphidae</i>	l.l.	8	2.94 ± 0.49		- 0.95 ± 0.19		0.90
<i>Calopterygidae</i>	l.l.	8	3.55 ± 0.68		- 1.37 ± 0.17		0.90
<b>HEMIPTERA</b>							
<i>Aphelocheiridae</i>	l.c.	10	1.55 ± 0.34		- 1.92 ± 0.16		0.95
<b>TRICHOPTERA</b>							
<i>Hydropsychidae</i>	l.m.	10	3.17 ± 0.16		- 1.05 ± 0.08		0.98
<i>Rhyacophilidae</i>	l.m.	10	3.80 ± 2.13		- 0.75 ± 0.34		0.44
<i>Philopotamidae</i>	l.m.	10	2.08 ± 0.43		- 1.47 ± 0.19		0.86
<i>Polycentropodidae</i>	l.m.	10	2.68 ± 0.77		- 1.50 ± 0.17		0.75
<i>Lepidostomatidae</i>	l.m.	10	2.76 ± 0.60		- 0.66 ± 0.16		0.88
<i>Limnephilidae</i>	l.m.	10	2.74 ± 0.48		- 0.48 ± 0.12		0.87
<i>Sericostomatidae</i>	l.m.	10	2.97 ± 0.50		- 0.85 ± 0.10		0.90
<b>DIPTERA</b>							
<i>Tipulidae</i>	l.c.	8	3.32 ± 1.11		- 4.01 ± 0.24		0.90
<i>Simuliidae</i>	w.c.	20	3.53 ± 0.19		- 1.85 ± 0.08		0.79
<i>Chironomidae</i>	w.c.	20	3.83 ± 0.37		- 1.57 ± 0.07		0.58
<i>Athericidae</i>	t.l.	10	2.03 ± 0.18		- 2.37 ± 0.05		0.99

Log (y) = *m* Log (x) - *b*

(x) w.m.: width of right mandible.

l.m.: length of right mandible.

l.l.: length of labium.

l.c.: length of cephalic capsule.

w.c.: width of cephalic capsule.

t.l.: total length.

(y) Volume/specimen.

items corresponded to the taxa; Family for aquatic prey, Order for terrestrial prey, and Subclass in annelids. Values lower than 0.3 were con-

sidered low overlap, between 0.3–0.6 moderate and between 0.6–1.0 high overlap.

To estimate niche breadth I used Levins' index

(Levins, 1968):

$$B = 1 / \sum_{i=1}^n P_i^2,$$

where  $P_i$  is the percentage in the diet of each food item.

## Results

I will describe seasonal changes in prey availability and diets based on volumetric data because they are more representative of the energy in the system. Prey selection based on numerical data will also be described.

### *Surber samples (Benthos)*

The composition of the benthos showed no significant correlations (Spearman's  $r$  all  $p$ 's > 0.05) between lotic and lentic zones. Consequently, these results are presented separately.

In riffles, hydrobiid snails (*Potamopyrgus jenkinsi*) represented close to a quarter of the total seasonal volume (Table 3, Fig. 2). Gammarid amphipods were especially abundant in autumn. Among mayflies, baetids (*Baetis*), ephemereids (*Ephemerella*) and heptageniids, were abundant or common. So were hydropsychid (*Hydropsyche*) or rhyacophilids (*Rhyacophila*) caddisflies. Dragonflies, particularly cordulegasterids (*Cordulegaster* sp.), aeschnids (*Boyeria irene*) and gomphids, reached some volumetric importance in summer and spring.

In pools, the volumetric proportion of hydrobiids was lower than in riffles. Gammarids were of minor importance, whereas Oligochaeta were sometimes abundant. In this habitat, the only common mayfly was *Ephemera* (ephemerid), but in spring and summer this genus dominated benthic samples. *Cordulegaster* was always common and, on occasion, abundant. The caddisflies present in pools differed from those in riffles; sericostomatids, lepidostomatids and limnephilids were the most abundant.

## Dietary data

### *Pyrenean desman Galemys pyrenaicus*

The number of specimens captured was very low because this species is protected by Spanish law (specimens captured under permit). I was unable to obtain specimens during spring. In summer the desman consumed mainly Sericostomatidae and *Ephemera* (Table 3, Fig. 2), whereas during autumn it preyed upon Gammaridae, Lumbricidae, Philopotamidae and Tipulidae. The winter diet of the desman was dominated by caddisflies: Sericostomatidae, Limnephilidae, Lepidostomatidae and Hydropsychidae.

The desman exhibited a moderate positive selection for Sericostomatidae and *Ephemera* in summer, for Philopotamidae and Simuliidae in autumn, and for Simuliidae in winter (Table 4). The desman exhibited negative selection for Hydrobiidae, Elmidae and Chironomidae in all seasons examined. They also avoided Ephemerellidae (autumn) and Leptoceridae (winter).

### *Miller's water shrew Neomys anomalus*

Water shrews were only captured during winter. They fed mainly on terrestrial Gasteropoda and Oligochaeta (both aquatic and terrestrial), however they also consumed aquatic prey (Tipulidae, Gammaridae) (Table 3).

Among aquatic prey, the water shrew exhibited a weak positive selection for Tipulidae, Simuliidae, Gammaridae, Dixidae and Oligochaeta (most of these were probably captured outside the water). Water shrews avoided Hydrobiidae, most caddisflies. Elmidae and Chironomidae.

### *Dipper Cinclus cinclus*

During spring and summer the dipper fed mainly on Hydropsychidae and other caddisflies (Limnephilidae, Goeridae, Sericostomatidae, *Rhyacophila*), dragonflies (*Cordulegaster*) and mayflies (*Ephemerella*) (Table 3, Fig. 2). The diet in autumn consisted mainly of hydrobiid snails and

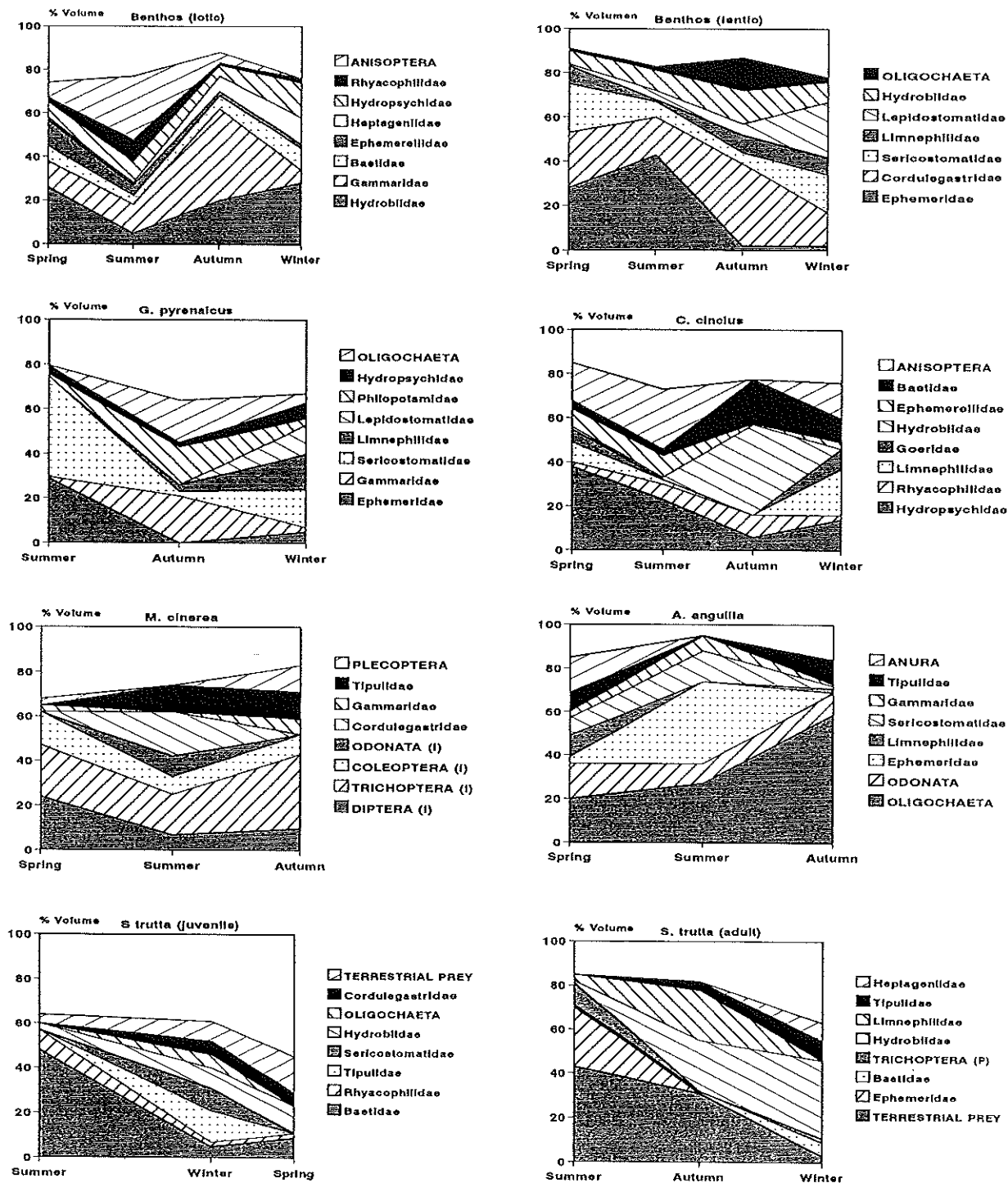


Fig. 2. Seasonal relative composition in volume of diets and benthos. On the right of the figures prey types are indicated in an orderly way (symbols as in Table 3). Spring data of adult trout (age  $>0+$ ) are included in the juvenile figure (most specimens have reached 1+ age recently) to show the evolution of the diet of juveniles. For insects I: imagines; P: pupae; no indication: larval stages.

Table 3 (A, B, C, D). Seasonal relative composition of diets and availability in benthos: (%N) number, (%V) volume. The niche breadth values (B. Levins' index) are also indicated.

For insects I: imagines, P: pupae, L: larvae. No indication refers to larval stages (except Hemiptera and Orthoptera).

SPRING	Benthos lotic		Benthos lentic		<i>C. cinclus</i>		<i>M. cinerea</i>		<i>S. trutta</i>		<i>A. anguilla</i>	
	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V
MOLLUSCA												
Sphaeriidae	—	—	2	2	—	—	—	—	—	—	—	—
Hydrobiidae	34	26	40	6	2	1	—	—	18	12	—	—
ACHAETA	0	3	—	—	—	—	—	—	—	—	—	—
OLIGOCHAETA	2	1	9	3	—	—	—	—	—	—	2	20
CRUSTACEA												
Gammaridae	13	12	3	1	—	—	4	3	—	—	8	3
EPHEMEROPTERA (I)	—	—	—	—	—	—	—	—	2	4	—	—
Ephemeridae	—	—	5	28	—	—	—	—	1	3	3	3
Heptageniidae	0	1	—	—	—	—	—	—	2	4	—	—
Baetidae	10	7	—	—	20	4	16	5	15	9	10	1
Ephemerellidae	17	22	1	1	20	8	6	4	9	8	18	4
PLECOPTERA												
Nemouridae/Leuctridae	—	—	—	—	—	—	4	3	2	2	3	0
ODONATA												
Aeschnidae	—	—	—	—	1	5	—	—	—	—	—	—
Cordulegastridae	0	1	1	25	1	8	—	—	0	6	0	2
Gomphidae	0	6	—	—	—	—	—	—	—	—	—	—
Calopterygidae	—	—	—	—	1	3	—	—	—	—	4	7
COLEOPTERA												
Elmidae (L + I)	11	4	22	2	—	—	4	0	—	—	—	—
TRICHOPTERA (P)	0	1	—	—	—	—	—	—	2	6	—	—
TRICHOPTERA (I)	—	—	—	—	—	—	6	23	—	—	—	—
Rhyacophilidae	0	2	—	—	1	2	1	3	1	2	4	2
Hydropsychidae	1	7	—	—	27	38	1	2	2	4	—	—
Philoptamidae	—	—	—	—	—	—	2	2	2	3	—	—
Limnephilidae	—	—	1	8	1	9	0	4	0	4	2	10
Gocridae	0	1	—	—	10	6	—	—	—	—	—	—
Sericostomatidae	0	1	6	22	4	7	—	—	—	—	7	8
DIPTERA												
Tipulidae	—	—	—	—	—	—	—	—	—	—	0	9
Simuliidae	3	1	1	0	—	—	3	0	5	1	23	1
Chironomidae (L + P)	4	1	6	0	—	—	—	—	16	3	5	0
AMPHIBIA												
TERRESTRIAL PREY												
MYRIAPODA	—	—	—	—	—	—	—	—	0	4	1	3
HEMIPTERA	—	—	—	—	—	—	2	4	—	—	—	—
LEPIDOPTERA (L)	—	—	—	—	—	—	—	—	0	3	—	—
HYMENOPTERA (I)	—	—	—	—	5	2	—	—	—	—	—	—
DIPTERA (I)	—	—	—	—	—	—	34	24	7	6	—	—
COLEOPTERA (I)	—	—	—	—	—	—	9	15	2	3	—	—
B	5	7	4	5	6	5	6	7	9	18	9	10



Table 3 (B).

SUMMER	Benthos lotic		Benthos lentic		<i>G. pyrenaicus</i>		<i>C. cinclus</i>		<i>M. cinerea</i>		<i>S. trutta</i> (juvenile)		<i>S. trutta</i> (adult)		<i>A. anguilla</i>	
	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V
MOLLUSCA																
Sphaeriidae	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—
Hydrobiidae	9	5	32	9	—	—	2	1	—	—	3	3	3	1	5	0
OLIGOCHAETA	—	—	4	2	—	—	—	—	—	—	—	—	—	—	4	27
CRUSTACEA																
Gammaridae	13	5	3	0	2	0	4	2	—	—	2	2	2	1	25	7
EPHEMEROPTERA (I)	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—	—
Ephemeridae	0	2	7	43	35	29	—	—	—	—	—	—	8	27	31	38
Heptageniidae	1	1	—	—	4	2	2	1	—	—	4	7	—	—	—	—
Baetidae	13	4	2	0	2	0	12	3	13	3	51	48	2	0	—	—
Ephemerellidae	8	5	4	1	2	0	25	9	9	3	3	3	—	—	2	0
PLECOPTERA																
Nemouridae/Leuctridae	2	1	1	0	—	—	6	2	—	—	—	—	—	—	—	—
ODONATA	—	—	—	—	—	—	—	—	1	9	—	—	—	—	—	—
Aeschnidae	0	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cordulegastridae	0	17	1	19	3	11	2	18	2	20	—	—	—	—	1	4
Gomphidae	0	3	0	4	1	3	0	3	—	—	—	—	—	—	1	5
COLEOPTERA (I)	—	—	—	—	—	—	—	—	3	2	—	—	—	—	—	—
Elmidae (L + I)	18	5	19	1	—	—	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA (P)	1	11	—	—	2	1	—	—	—	—	—	—	5	10	—	—
TRICHOPTERA (I)	—	—	—	—	—	—	—	—	7	18	0	3	—	—	—	—
Rhyacophilidae	2	10	—	—	2	2	5	7	—	—	6	9	3	5	2	1
Hydropsychidae	7	10	—	—	10	4	13	23	2	4	1	4	—	—	—	—
Philoptamidae	1	2	—	—	4	1	—	—	—	—	—	—	—	—	3	0
Brachycentridae	—	—	—	—	—	—	6	3	—	—	—	—	—	—	—	—
Limnephilidae	—	—	0	1	—	—	0	2	0	4	—	—	1	3	—	—
Goeridae	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—
Lepidostomatidae	—	—	4	4	—	—	0	1	—	—	—	—	—	—	—	—
Sericostomatidae	1	3	3	7	30	45	2	3	—	—	—	—	1	2	14	14
DIPTERA																
Tipulidae	—	—	—	—	—	—	0	3	2	12	—	—	—	—	—	—
Simuliidae	14	4	1	0	—	—	6	1	18	2	6	4	—	—	—	—
Chironomidae	9	1	15	1	—	—	—	—	—	—	12	5	—	—	5	0
AMPHIBIA	—	—	—	—	—	—	0	3	—	—	—	—	—	—	—	—
TERRESTRIAL PREY																
ARANEAE	—	—	—	—	—	—	—	—	2	2	—	—	—	—	—	—
HEMIPTERA	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—
HYMENOPTERA (I)	—	—	—	—	—	—	5	2	2	1	2	4	58	37	—	—
DIPTERA (I)	—	—	—	—	—	—	—	—	15	7	—	—	3	2	—	—
COLEOPTERA (L)	—	—	—	—	—	—	—	—	4	2	—	—	—	—	—	—
COLEOPTERA (I)	—	—	—	—	—	—	—	—	9	6	—	—	1	2	—	—
B	9	12	6	4	4	3	9	9	10	9	3	4	3	5	5	4

Table 3 (C).

AUTUMN	Benthos lotic		Benthos lentic		<i>G. pyrenaicus</i>		<i>C. cinclus</i>		<i>M. cinerea</i>		<i>S. trutta</i> (adult)		<i>A. anguilla</i>	
	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V
MOLLUSCA														
Hydrobiidae	17	20	33	15	—	—	54	41	—	—	46	23	—	—
OLIGOCHAETA	—	—	3	15	1	19	—	—	—	—	—	—	4	59
CRUSTACEA														
Gammaridae	34	42	3	1	32	21	—	—	11	7	—	—	7	1
EPHEMEROPTERA														
Ephemeridae	—	—	3	2	—	—	—	—	—	—	—	—	—	—
Heptageniidae	5	7	—	—	4	3	1	2	—	—	—	—	—	—
Baetidae	13	6	—	—	11	3	23	20	9	4	3	1	—	—
Ephemerellidae	7	2	2	0	—	—	—	—	—	—	—	—	—	—
PLECOPTERA (I)	—	—	—	—	—	—	—	—	6	5	—	—	—	—
Nemouridae/Leuctridae	9	5	3	2	6	4	—	—	11	7	—	—	3	1
ODONATA														
Cordulegastridae	—	—	1	37	—	—	—	—	—	—	—	—	1	10
Gomphidae	0	5	—	—	—	—	—	—	—	—	—	—	—	—
COLEOPTERA (I)	—	—	—	—	—	—	—	—	2	3	—	—	—	—
Elmidae (L + I)	7	3	3	0	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA (I)	—	—	—	—	—	—	—	—	13	33	—	—	—	—
Rhyacophilidae	1	1	—	—	1	3	3	10	—	—	—	—	—	—
Hydropsychidae	1	5	—	—	2	2	4	6	—	—	—	—	2	1
Philoptamidae	—	—	—	—	18	17	—	—	—	—	2	1	52	8
Limnephilidae	—	—	3	8	1	3	—	—	—	—	4	23	3	2
Goeridae	—	—	—	—	—	—	—	—	—	—	4	4	—	—
Lepidostomatidae	—	—	8	5	—	—	—	—	—	—	—	—	—	—
Leptoceridae	1	0	3	1	—	—	—	—	—	—	—	—	—	—
Sericostomatidae	—	—	6	5	2	2	1	4	—	—	—	—	3	1
DIPTERA														
Tipulidae	—	—	—	—	1	9	0	7	1	12	0	4	2	11
Dixidae	—	—	—	—	—	—	—	—	10	2	—	—	—	—
Simuliidae	2	1	1	0	14	2	3	1	2	0	3	1	10	0
Chironomidae	1	1	23	4	2	0	—	—	—	—	5	0	5	0
Athericidae	—	—	2	2	—	—	—	—	—	—	—	—	—	—
TERRESTRIAL PREY														
GASTEROPODA	—	—	—	—	—	—	—	—	—	—	—	—	1	3
MYRIAPODA	—	—	—	—	—	—	—	—	—	—	1	3	—	—
HEMIPTERA	—	—	—	—	—	—	—	—	—	—	8	11	—	—
LEPIDOPTERA (L)	—	—	—	—	—	—	—	—	—	—	1	11	—	—
HYMENOPTERA (I)	—	—	—	—	—	—	—	—	4	3	2	2	—	—
DIPTERA (I)	—	—	—	—	—	—	—	—	15	10	6	2	—	—
COLEOPTERA (I)	—	—	—	—	—	—	—	—	6	6	—	—	—	—
B	6	4	6	5	6	8	3	4	10	6	4	7	3	3

baetid mayflies, whereas in winter it was dominated by Limnephilidae, Hydropsychidae, *Cordulegaster* and *Baetis*.

The dipper exhibited strong positive selection for Hydropsychidae in spring and moderate positive selection for Goeridae and *Baetis* (summer

Table 3 (D).

WINTER	Benthos lotic		Benthos lentic		<i>G. pyrenaicus</i>		<i>N. anomalus</i>		<i>C. cinclus</i>		<i>S. trutta</i> (juvenile)		<i>S. trutta</i> (adult)	
	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V	%N	%V
MOLLUSCA														
Sphaeriidae	—	—	2	1	—	—	—	—	—	—	2	1	—	—
Hydrobiidae	26	28	16	9	—	—	—	—	—	—	11	9	36	35
ACHAETA	—	—	—	—	1	3	—	—	—	—	—	—	—	—
OLIGOCHAETA	1	2	4	2	0	4	5	23	—	—	1	6	—	—
CRUSTACEA														
Gammaridae	4	6	3	3	4	2	10	3	—	—	15	2	3	2
EPHEMEROPTERA														
Ephemeriidae	—	—	1	2	2	5	—	—	—	—	2	1	—	—
Heptageniidae	7	12	—	—	8	7	—	—	2	1	1	2	5	8
Baetidae	14	10	—	—	10	3	5	1	31	11	6	5	7	6
Ephemerellidae	9	2	—	—	—	—	—	—	9	3	2	1	—	—
Leptophlebiidae	—	—	—	—	—	—	—	—	—	—	2	2	—	—
PLECOPTERA														
Nemouridae/Leuctridae	5	7	1	1	3	1	2	1	14	7	4	2	7	5
ODONATA														
Cordulegastridae	—	—	0	15	—	—	—	—	1	13	1	6	—	—
MEGALOPTERA														
Sialidae	—	—	—	—	—	—	—	—	—	—	1	7	—	—
COLEOPTERA														
Elmidae (L + I)	12	2	1	0	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA (P)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
TRICHOPTERA (I)	—	—	—	—	—	—	2	2	—	—	—	—	—	—
Rhyacophilidae	1	2	0	2	2	4	—	—	3	2	1	2	1	3
Glossosomatidae	4	1	—	—	—	—	—	—	—	—	—	—	—	—
Hydropsychidae	4	16	—	—	10	7	—	—	12	14	—	—	2	3
Philoptamidae	1	2	—	—	5	3	—	—	—	—	6	3	4	6
Limnephilidae	0	1	2	8	5	16	—	—	3	21	—	—	—	—
Goeridae	—	—	—	—	—	—	—	—	12	9	—	—	—	—
Lepidostomatidae	—	—	17	25	18	13	—	—	—	—	3	3	—	—
Leptoceridae	—	—	17	6	—	—	—	—	—	—	2	1	—	—
Sericostomatidae	1	1	7	17	11	17	—	—	4	6	3	10	0	2
DIPTERA														
BRACHYCERA	—	—	—	—	—	—	3	2	—	—	1	2	—	—
Tipulidae	—	—	—	—	—	—	3	14	—	—	1	14	0	9
Dixidae	—	—	—	—	—	—	2	0	—	—	—	—	—	—
Simuliidae	4	1	—	—	12	2	7	1	2	—	—	—	—	—
Chironomidae (L + P)	5	1	24	2	—	—	5	0	—	—	18	3	22	4
TERRESTRIAL PREY														
GASTEROPODA	—	—	—	—	—	—	4	40	—	—	—	—	—	—
MYRIAPODA	—	—	—	—	—	—	—	—	—	—	1	6	0	3
ARANEAE	—	—	—	—	—	—	3	2	—	—	—	—	—	—
HEMIPTERA	—	—	—	—	—	—	26	2	—	—	—	—	—	—
COLEOPTERA (L)	—	—	—	—	—	—	5	2	—	—	—	—	—	—
COLEOPTERA (I)	—	—	—	—	—	—	—	—	—	—	2	3	—	—
B	8	7	7	7	11	11	10	4	6	9	12	16	5	7

Table 4. Seasonal prey selection (Pearre index) in relation to availability in benthos. All values have a significance level  $p < 0.01$ , except those indicated with \* ( $p < 0.05$ ). Only taxa with the highest and lowest values are shown for each species and season.

SPRING					
<i>C. cinchus</i>	<i>M. cinerea</i>	<i>S. trutta</i>	<i>A. anguilla</i>		
0.46 Hydropsychidae	0.15 PLECOPTERA	0.22 Chironomidae	0.32 Simuliidae		
0.28 Goeridae	0.11 Baetidae	0.20 Baetidae	0.17 Calopterygidae		
0.21 Baetidae	0.11 Philopotamidae	0.13 Philopotamidae	0.16 Rhyacophilidae		
0.11 Ephemerellidae	0.05 Rhyacophilidae	0.12 Heptageniidae	0.12 PLECOPTERA		
0.07 Rhyacophilidae		0.10 Simuliidae	0.09 Sericostomatidae		
0.06 Aeschnidae		0.09 PLECOPTERA	0.09 Limnephilidae		
-0.06 Ephemeridae	-0.04*Sericostomatidae	-0.04 Sphaeriidae	-0.12 Elmidae		
-0.07 Simuliidae	-0.05*Ephemerellidae	-0.04*Brachycentridae	-0.22 Hydrobiidae		
-0.10 OLIGOCHAETA	-0.05*Gammaridae	-0.08 Sericostomatidae			
-0.10 Chironomidae	-0.06 OLIGOCHAETA	-0.11 OLIGOCHAETA			
-0.15 Gammaridae	-0.07 Chironomidae	-0.15 Hydrobiidae			
-0.19 Elmidae	-0.08 Elmidae	-0.18 Gammaridae			
-0.23 Hydrobiidae	-0.23 Hydrobiidae	-0.22 Elmidae			
SUMMER					
<i>G. pyrenaicus</i>	<i>C. cinchus</i>	<i>M. cinerea</i>	<i>S. trutta</i> 0 +	<i>S. trutta</i> > 0 +	<i>A. anguilla</i>
0.36 Sericostomatidae	0.28 Ephemerellidae	0.12 Tipulidae	0.40 Baetidae	0.14 Ephemeridae	0.37 Ephemeridae
0.33 Ephemeridae	0.20 Brachycentridae	0.09 Simuliidae	0.12 Heptageniidae	0.09 Sericostomatidae	0.24 Sericostomatidae
0.09 Heptageniidae	0.16 Hydropsychidae	0.07 Calopterygidae	0.12 Rhyacophilidae	0.07 Rhyacophilidae	0.15 Gammaridae
0.06 Cordulegastridae	0.14 Rhyacophilidae	0.05*Baetidae	0.11 Goeridae	0.05 Limnephilidae	0.06 OLIGOCHAETA
0.06 Philopotamidae	0.13 PLECOPTERA	0.05 Cordulegastridae			
0.05*Hydropsychidae	0.09 Heptageniidae				
-0.05*Limnephilidae	-0.06 OLIGOCHAETA	-0.04*Ephemeridae	-0.05*Ephemeridae	-0.13 Baetidae	-0.05*Chironomidae
-0.05*Goeridae	-0.06 Lepidostomatidae	-0.09 Gammaridae	-0.08 Gammaridae	-0.14 Gammaridae	-0.06 Hydropsychidae
-0.05*Gammaridae	-0.09 Ephemeridae	-0.10 Chironomidae	-0.11 Hydrobiidae	-0.18 Ephemerellidae	-0.09 Baetidae
-0.06 Simuliidae	-0.09 Gammaridae	-0.13 Hydrobiidae	-0.15 Elmidae	-0.21 Simuliidae	-0.09 Simuliidae
-0.07 Chironomidae	-0.20 Hydrobiidae	-0.13 Elmidae		-0.22 Hydrobiidae	-0.09 Hydrobiidae
-0.09 Hydrobiidae	-0.24 Elmidae			-0.24 Chironomidae	-0.13 Elmidae
-0.09 Elmidae				-0.31 Elmidae	
AUTUMN					
<i>G. pyrenaicus</i>	<i>C. cinchus</i>	<i>M. cinerea</i>	<i>S. trutta</i>	<i>A. anguilla</i>	
0.38 Philopotamidae	0.32 Hydrobiidae	0.30 Dixidae	0.28 Hydrobiidae	0.72 Philopotamidae	
0.26 Simuliidae	0.25 Baetidae	0.15 PLECOPTERA	0.17 Goeridae	0.13 Simuliidae	
0.14 Gammaridae	0.12 Hydropsychidae	0.10 Tipulidae	0.11 Philopotamidae	0.10 Sialidae	
0.07 Baetidae	0.10 Rhyacophilidae		0.09 Limnephilidae	0.10 Tipulidae	
0.06 Tipulidae	0.06 Brachycentridae		0.05 Simuliidae	0.05 OLIGOCHAETA	
0.06 Hydropsychidae	0.05*Simuliidae				
-0.06 Leptoceridae	-0.10 Lepidostomatidae	-0.06 Gammaridae	-0.10 Sericostomatidae	-0.05 Elmidae	
-0.10 Lepidostomatidae	-0.10 Ephemerellidae	-0.07 Lepidostomatidae	-0.11 Lepidostomatidae	-0.06 Baetidae	
-0.10 Ephemerellidae	-0.11 Elmidae	-0.07 Ephemerellidae	-0.12 Ephemerellidae	-0.07 Gammaridae	
-0.11 Elmidae	-0.13 PLECOPTERA	-0.08 Elmidae	-0.13 Elmidae	-0.13 Hydrobiidae	
-0.13 Chironomidae	-0.17 Chironomidae	-0.13 Chironomidae	-0.15 PLECOPTERA		
-0.26 Hydrobiidae	-0.23 Gammaridae	-0.20 Hydrobiidae	-0.27 Gammaridae		
WINTER					
<i>G. pyrenaicus</i>	<i>N. anomalus</i>	<i>C. cinchus</i>	<i>S. trutta</i> 0 +	<i>S. trutta</i> > 0 +	
0.21 Simuliidae	0.17 Tipulidae	0.36 Baetidae	0.18 Gammaridae	0.22 Hydrobiidae	
0.19 Hydropsychidae	0.15 Simuliidae	0.29 Goeridae	0.17 Philopotamidae	0.14 Philopotamidae	
0.16 Philopotamidae	0.15 Gammaridae	0.23 PLECOPTERA	0.12 Leptophlebiidae	0.11 PLECOPTERA	
0.11 Sericostomatidae	0.14 Dixidae	0.23 Hydropsychidae		0.11 Chironomidae	
0.11 Limnephilidae	0.07 OLIGOCHAETA	0.11 Ephemerellidae		0.05 Rhyacophilidae	
0.10 Lepidostomatidae		0.11 Rhyacophilidae		0.05*Heptageniidae	
-0.04*OLIGOCHAETA	-0.08 Ephemerellidae	-0.09 OLIGOCHAETA	-0.05*Lepidostomatidae	-0.10 OLIGOCHAETA	
-0.07 Ephemerellidae	-0.08 Sericostomatidae	-0.11 Gammaridae	-0.06 Elmidae	-0.11 Sericostomatidae	
-0.08 Elmidae	-0.10 Elmidae	-0.14 Elmidae	-0.06 Leptoceridae	-0.12 Ephemerellidae	
-0.11 Leptoceridae	-0.10 Chironomidae	-0.19 Leptoceridae		-0.15 Elmidae	
-0.15 Chironomidae	-0.13 Leptoceridae	-0.19 Lepidostomatidae		-0.20 Leptoceridae	
-0.18 Hydrobiidae	-0.13 Lepidostomatidae	-0.25 Chironomidae		-0.20 Lepidostomatidae	
	-0.20 Hydrobiidae	-0.29 Hydrobiidae		-0.15 Elmidae	

and winter), *Ephemerella* and Brachycentridae (autumn), and Nemouridae/Leuctridae and Hydropsychidae (winter). The dipper typically exhibited negative selection for elmids, gammarid amphipods, chironomid dipterans and hydrobiid snails (except in autumn) (Table 4).

#### *Grey wagtail Motacilla cinerea*

The grey wagtail consumed both terrestrial and aquatic prey, and its diet was dominated by winged insects of aquatic origin. In spring grey wagtails consumed mainly winged insects, with dipterans, caddisflies and beetles comprising most of the volume (Table 3, Fig. 2). The importance of aquatic prey increased in summer, when they fed mostly on larvae of *Cordulegaster* and Tipulidae, and imagines of caddisflies, dragonflies and dipterans. During autumn, the diet was dominated by imagines of caddisflies and dipterans, tipulid larvae, stoneflies and gammarids.

Among aquatic prey, the grey wagtail showed moderate positive selection for Dixidae (autumn) and weak positive selection for *Baetis* (spring), Nemouridae/Leuctridae (spring and autumn), Tipulidae (summer and autumn) and dragonflies (summer) (Table 4). The grey wagtail generally avoided Hydrobiidae, Elmidae, Chironomidae, Leptoceridae (only autumn) and Lepidostomatidae (only autumn).

#### *Brown trout Salmo trutta*

The trout fed on a wide range of prey, including benthic invertebrates, emergent pupae and terrestrial prey (Table 3, Fig. 2). I separated data for 0+ and older trout, mostly 1+ and 2+, because the diets of these age classes were not significantly correlated (Spearman's  $r$  all  $p$ 's > 0.05).

During spring, Hydrobiidae, *Baetis*, *Ephemerella*, *Cordulegaster*, winged dipterans and caddisfly pupae were the most abundant prey in the diet of trouts. During summer, almost half of 0+ trout's diet was comprised of *Baetis*, whereas older trout fed mainly on winged hymenoptera

(primarily ants), *Ephemerella* and emerging caddisflies. In autumn, adults consumed increasing amounts of Hydrobiidae and Limnephilidae, but terrestrial prey still were important to the diet. During winter, the diet of juveniles was broader than in summer. During this season the diet of adults differed from that of juveniles by the greater proportion of Hydrobiids and gastropods consumed by older trouts.

Considering aquatic taxa, adult trout exhibited moderate positive selection for Chironomidae and *Baetis* in spring, and for Hydrobiidae in autumn and winter. Juvenile trout exhibited strong positive selection for *Baetis* in summer but weak positive selections in winter. Juvenile and adult classes showed negative selection during all seasons for Elmidae, and they generally avoided *Ephemerella* and Lepidostomatidae, whereas most other prey changed from positive to negative selection depending on the season (Table 4).

#### *Eel Anguilla anguilla*

The diet of the eel was composed primarily of benthic invertebrates. During spring they fed on Lumbricidae, tadpoles, Limnephilidae, Tipulidae, Sericostomatidae and dragonflies, whereas in summer *Ephemerella*, Lumbricidae and Sericostomatidae dominated the diet. In autumn Lumbricidae comprised more than half of the ingested volume. The specimens captured in winter had no prey in either their stomachs or intestines.

The eel exhibited strong positive selection for Philopotamidae in autumn, and moderate positive selection for Simuliidae in spring, and for *Ephemerella* and Sericostomatidae in summer. Eels typically avoided Hydrobiidae and Elmidae in all seasons.

#### *Prey size*

Numerical prey availability samples were typically dominated by small invertebrates < 0.005 ml (Fig. 3). Most predators, however, generally consumed larger prey.

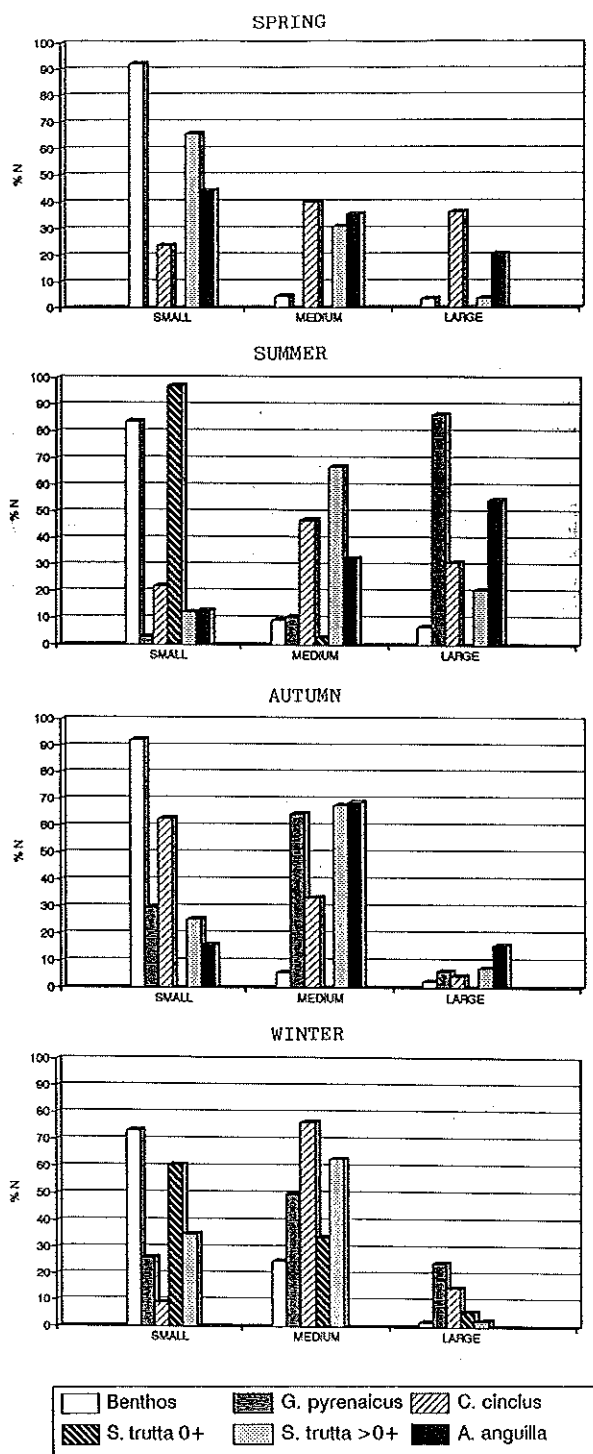


Fig. 3. Relative numeric composition of three prey size classes (benthos and diets). The size classes are as follow: small (volume <0.005 ml), medium (0.005–0.02 ml), and large (0.02–0.1 ml).

Juvenile trout were the unique individuals with a prey size distribution close to the available, and in summer they consumed a little higher proportion of small sized prey than available. Adult trout, eel, desmans and dippers preyed on higher percentages of medium or large sizes of prey (0.005–0.02 and 0.02–0.1 ml respectively) than available. Therefore, except for juvenile trouts, prey size plays an important role in prey selection, but it may be meaningless for resource partitioning unless taxonomic composition is considered.

#### Niche breadth

Juvenile and adult trout had the widest niche breadths (Fig. 4), but as it was not possible to take prey identifications to species, the results are not very revealing.

#### Niche overlap

Niche overlap values based on volumetric data indicated that most overlaps were from low to intermediate (Table 5). These values generally fluctuated seasonally but no general patterns were observed. Slighter higher values between several species (trout, eel, desman) in summer were attributable to the high relative abundance of Ephemeridae available in this season.

The species exhibiting the highest overlap were the desman and the eel (Schoener index 0.54 in summer and 0.47 in autumn). During summer the diet of juvenile trout was closer to other species (dipper) than to the adult of the same species.

In spite of low overlaps, the identification only to order of terrestrial and winged prey may have overestimated values between adult trout, water shrew and grey wagtail.

#### Discussion

The community described in this paper commonly occurs in other rivers of NW Spain (Santamarina, 1991). In Riobo, fish coexist with mammals and birds, and all species are dependent upon a similar food resource.

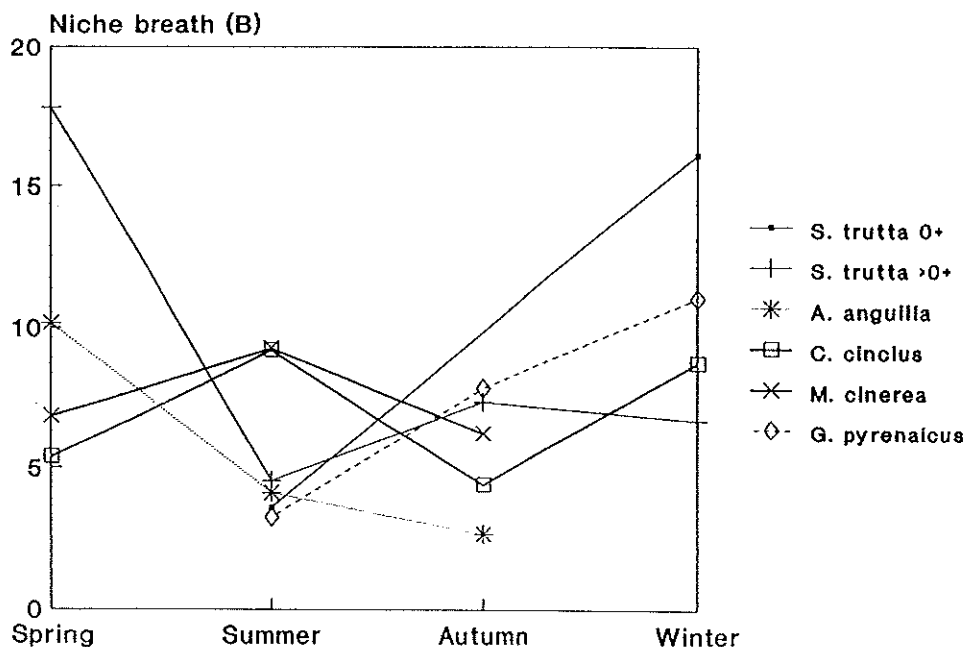


Fig. 4. Seasonal variation of niche breadth (Levins' index; volumetric data).

Table 5. Seasonal niche overlaps of diets (Schoener index; volumetric data)

#### SPRING

##### C. cinclus

0.23	M. cinerea
0.42	0.43 S. trutta >0+
0.36	0.24 0.35 A. anguilla

#### SUMMER

##### G. pyrenaicus

0.31	C. cinclus
0.18	0.44 M. cinerea
0.11	0.31 0.20 S. trutta 0+
0.45	0.27 0.18 0.20 S. trutta >0+
0.54	0.22 0.08 0.08 0.44 A. anguilla

#### AUTUMN

##### G. pyrenaicus

0.28	C. cinclus
0.32	0.20 M. cinerea
0.20	0.38 0.20 S. trutta >0+
0.47	0.14 0.19 0.14 A. anguilla

#### WINTER

##### G. pyrenaicus

0.17	N. anomalus
0.46	0.09 C. cinclus
0.41	0.34 0.33 S. trutta 0+
0.38	0.23 0.32 0.53 S. trutta >0+

Most of the predators consumed prey captured in the water; brown trout, eel, dipper and Pyrenean desman. My results indicate that they may be classified as either benthic feeders (eel, dipper

and desman) or water column-benthic feeders (trout). Among benthic feeders, the dipper fed more in riffles than in pools whereas the desman and the eel fed equally in both. These were the

species with more similar diet patterns, although there are some feeding differences.

The Miller's water shrew and the grey wagtail were only partially dependant on aquatic prey. Water shrews primarily ate soft-bodied terrestrial prey, which may occur on nearby stream banks, whereas grey wagtails consumed large amounts of winged insects, many of which had aquatic larval stages.

Substantial dietary information exists for many assemblage members (i.e. dipper, eel, trout), whereas little information is available for the water shrew, the desman and the grey wagtail. The basic pattern in the diets of the eel, the trout and the dipper is quite similar to that elsewhere in Europe, although there were differences probably attributable to differences in resource availability in Riobo. For example, the dipper fed on caddisflies and mayflies in this stream as well as in others (Jost, 1975; Ormerod, 1985; Spitznagel, 1985; Ormerod & Tyler, 1987), but in Riobo dragonflies were also an important prey. The desman in Riobo fed primarily upon caddisfly and mayfly larvae as has been shown for other streams in NW Spain (Santamarina, 1988). Some information is also available on the grey wagtail's diet during breeding season (Schifferli, 1972; Sonin & Anuchina, 1979; Ormerod & Tyler, 1987). These studies indicate that both winged and aquatic insects are important prey for this species.

My results indicate that the relative abundance of prey in the benthos and in the diet of the assemblage members varied seasonally. Nevertheless, perhaps because of the infrequency of my sampling, some of the observed differences could also be due to chance or to the dates and times when dietary samples were taken.

Dietary fluctuations tended not to be coincident with changes in prey availability, but they may be related to the fluctuations in their availability to a particular predator feeding at a particular time and place. Nevertheless, the abundance of a particular prey was sometimes reflected in the diet of several species. In summer, for example, the volumetrically dominant prey in benthos (*Ephemera* became a dominant prey type for desmans, eel and trout.

In the last decade, studies on resource partitioning in fish assemblages have increased greatly (review in Ross, 1986). At present, however, considerable disagreement exists over the major processes affecting assemblage organization in stream fishes (Herbold, 1984; Grossman *et al.*, 1985; Grossman & Freeman, 1987) and some investigators maintain that partitioning of resources may not be of general importance for stream fishes.

The Riobo fish assemblage is dominated both in number and biomass by brown trouts (Santamarina, 1991). Birds, and probably mammals, are scarce compared to fish abundance. Nevertheless, the rarity of mammals and birds may be linked to homeostatic ability. Homiotherms such as these have greater energy requirements and smaller densities than ectotherms.

The dietary differences probably arose from differential microhabitat selection, as well as from morphological abilities of predators to capture different prey, feeding periodicities and other factors related to prey preferences.

Some authors have shown the important role played by morphology in some vertebrates (Smartt, 1978; Gatz, 1981). Trout have a fusiform body which is efficient for rapid swimming and the role of vision in its feeding is well established. This should allow them to capture prey in the water column or on the stream bed. Eel have a very elongate and tubular body, which is effective in negotiating objects on the bottom. Eels have well developed olfactory organs (Hara, 1971) which allows them to locate prey in the bottom. The desman is well adapted to motion through streams, it has strong claws that may be used to turn bottom objects over, and a tromp with well developed tactile sensitivity (Richard, 1981; 1982). These adaptations may make it an efficient predator of prey residing in the stream bed. Dippers have less adaptations to aquatic environment (Goodge, 1960; Murrish, 1970), reaching the bottom with less energetic cost in riffles or shallow water. As other birds do, dippers locate prey by vision (Goodge, 1960). *Neomys anomalus* is less aquatic than the other European water shrew (*N. fodiens*) (Heinrich, 1948;



Spitzenberger, 1980), whereas the grey wagtail only introduces its legs into the water but is an efficient fly-catcher (Schifferli, 1961).

It is clear that these species converged to feed in some way on invertebrates from streams. As these vertebrates are morphologically and physiologically different, it is more likely that the observed shifts in food use were primarily due to their phylogenetic histories, rather than to coevolution within this particular community.

Finally, this study has shown that the diets of quite different fish, birds and mammals may overlap to a considerable extent, and future studies on predation on stream invertebrates should take into account the predation by birds and mammals as well as fish.

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