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Summer food resource partitioning between four sympatric fish species in Central Spain (River Tormes)

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Abstract. Knowledge of food resource partitioning between sympatric fish species is critical for understanding the fish communities functioning. Four sympatric fish species (*Salmo trutta*, *Pseudochondrostoma duriense*, *Squalius carolitertii* and *Barbus bocagei*) were captured in August 2010 in the River Tormes (Ávila, Central Spain) in order to study food resource partitioning between fish species such as a possible mechanism enabling their coexistence, using a fuzzy principal component analysis (FPCA). Diet comparison among species shows that detritus are present in *P. duriense*, *B. bocagei* and *S. carolitertii*, although in different occurrence, showing that these species present typically omnivorous feeding habits. Regarding prevalent food, in all species, benthic prey constituted the most important prey in abundance terms, and terrestrial invertebrates were only consumed by *S. trutta*, *S. carolitertii* and *P. duriense*. High overlap values (Schoener's index from 0.8 up to 1) were found, but it may not indicate competition, since species can adopt different strategies to overcome competence. Thus, prey traits analyses suggest that differences in macrohabitat use, drift behaviour of prey and prey size are important adaptive features that may reduce the inter-specific competition in the fish community and permit the food partitioning that allows coexistence.

Key words: prey traits, multivariate approaches, coexistence, Iberian Peninsula

Introduction

In the Iberian Peninsula, the most of the researchers have studied the diet of fish species separately (e.g. Encina et al. 1999, Blanco-Garrido et al. 2003, Oscoz et al. 2005, Sánchez-Hernández et al. 2011a), and less abundant are the studies that investigated the food resource partitioning between co-occurring fish species (e.g. Encina et al. 2004, Oscoz et al. 2006, Sánchez-Hernández et al. 2011b). On the other hand, competition can play a critical role in influencing the habitat selection, foraging behaviour, growth and survival of fish stream communities (e.g. Haury et al. 1991, Elliott 1994, Hilderbrand & Kershner 2004, David et al. 2007). Hence, knowledge of predator-prey trophic interactions is critical for understanding the fish communities functioning (Jackson et al. 2001, Jaworski & Ragnarsson 2006).

Special attention has been given to the multivariate

approaches in order to clarify the mechanisms involved in predator-prey relationships, such as prey trait analysis (de Crespín de Billy & Usseglio-Polatera 2002, de Crespín de Billy et al. 2002), and recently, prey trait analysis has been employed to study the food resource partitioning between sympatric fish species (Sánchez-Hernández et al. 2011b). The current study was focused on the feeding habits of four co-occurring fish species in a temperate area (Central Spain): *Salmo trutta* Linnaeus, 1758, *Pseudochondrostoma duriense* (Coelho, 1985), *Squalius carolitertii* (Doadrio, 1988) and *Barbus bocagei* Steindachner, 1865. In this context, knowledge of feeding habits is essential to understand the ecological role and the productive capacity of fish populations, and the understanding of these mechanisms is critical to the development of conservation and management plans (Teixeira & Cortes 2006). Thus, the purposes of the present study are: 1)

to study the trophic ecology of these fish species; 2) to analyse macrohabitat, behavioural feeding and handling efficiency of fishes using prey trait analysis, thus helping to explain the food partitioning between species.

Study Area

The study area (altitude 1051 m) was located in the River Tormes (Ávila, Central Spain; UTM: 30T 288707 4466342), a tributary of the River Duero (897 km total length) (Fig. 1). The River Tormes has a catchment area of 7096 km² and a total length of 284 km. Geologically, the study basin is located in a great batholith with relatively uniform mineralogical granite composition (Alonso-González et al. 2008). The Tormes basin includes a mixture of agricultural and relatively undisturbed areas, with small rural areas interspersed. The vegetation structure comprises a series of extended grazing lands with Scots pine (*Pinus sylvestris*) and rebollo oak (*Quercus pyrenaica*) forests. The climate is typically continental, with higher differences between extreme temperatures in summer and winter. The studied site does not have any significant flow regulation structure, and flow regime has a great variability (Alonso-González et al. 2008).

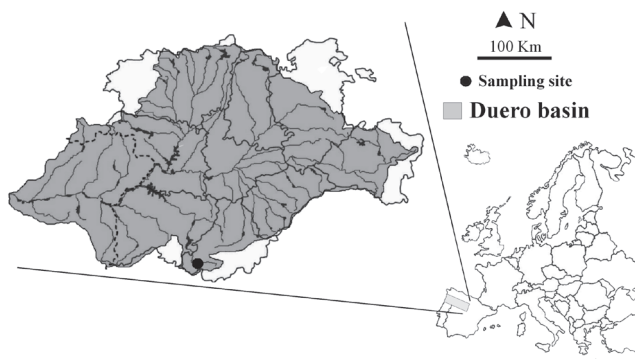


Fig. 1. Map of Europe and Duero basin (Iberian Peninsula) showing the sampling site in the River Tormes.

At the moment of survey, water temperature was *circa* 18 °C and conductivity and pH was 28.8 μS/cm and 6.4 respectively. Dissolved oxygen levels were high (91.5 % and 8.7 mg/l). Deciduous riparian vegetation was principally composed of alder (*Alnus glutinosa*), ash (*Fraxinus angustifolia*) and willow (*Salix* spp.), and substrate consisted of boulders, gravel and sand.

Material and Methods

Samples were collected in August 2010. Fishes were collected using pulsed D.C. backpack electrofishing equipment (Hans Grassl GmbH, ELT60II). Five

fish species were recorded in this study, three of which are endemic species in the Iberian Peninsula (*S. carolitertii*, *B. bocagei* and *P. duriense*). For Iberian endemic freshwater fishes we have employed the international standardization of common names of Leunda et al. (2009), being *S. carolitertii* or Northern Iberian chub, *B. bocagei* or Iberian barbel and *P. duriense* or Northern straight-mouth nose. The fish community was dominated by Northern straight-mouth nose (*P. duriense* = 0.65 fish/m², *S. carolitertii* = 0.23 fish/m², *S. trutta* = 0.15 fish/m², *B. bocagei* = 0.02 fish/m² and *Anguilla anguilla* = 0.003 fish/m²).

For the purpose of the study 156 fishes captured were killed immediately by an overdose of anaesthetic (benzocaine), and transported in coolboxes (approx. 4 °C) to the laboratory, where they were frozen at -30 °C until processing. Thus, individuals selected were: brown trout (*n* = 43, mean fork length = 14 cm ± 1.03 SE), Northern straight-mouth nose (*n* = 47, mean fork length = 9.1 cm ± 0.41 SE), Northern Iberian chub (*n* = 57, mean fork length = 6.5 cm ± 0.28 SE) and Iberian barbel (*n* = 9, mean total length = 6.6 cm ± 1.97 SE). *A. anguilla* was not included in the diet analysis due to only one specimen was captured.

Diet composition and feeding strategy of the four fish species were compared by the analysis of their stomach contents. Specimens were dissected and either stomach contents (Salmonidae) or contents of the gastrointestinal tract (Cyprinidae) were removed (Encina et al. 2004). For the description of the diet, data are offered on relative abundance of preys ($A_i = (\sum S_i / \sum S_j) \times 100$, where S_i is the stomach content [number] composed by prey *i*, and S_j the total stomach content of all stomachs in the entire sample) and frequency of occurrence of preys ($F_i = (N_i / N) \times 100$, where N_i is the number of fishes with prey *i* in their stomach and *N* is the total number of fishes with stomach contents of any kind). The abundance of detritus and vegetal rests was not quantified because it was impossible to count individual items, and only the number of stomachs in which they appeared was noted. Animal prey items were identified to the lowest taxonomic level possible, and the food items of each specimen were counted and measured (total length) with a digital micrometer (Mitutoyo Absolute, 0.01mm resolution, Japan) to determine differences on size consumption between species. When fragmented or partially digested, the number of items was estimated by counting body parts resistant to digestion. In those cases, prey length was estimated from the width of the cephalic capsule (see Rincón & Lobón-Cerviá 1999), which was normally the best preserved part. Moreover, the niche breadth

of the individuals was estimated using the Shannon diversity index ($H' = -\sum P_i \log_2 P_i$, where P_i is the proportion of the prey item i among the total number of preys). In order to evaluate diet specialization, evenness index ($E = H'/H'_{max}$) was used considering that values close to zero mean a stenophagous diet (i.e. individuals eat a limited range of prey) and those closer to one a more euryphagous diet (i.e. individuals eat a diverse range of prey) (Oscoz et al. 2005).

To assess the feeding strategy between fish species studied, the modified Costello (1990) graphical method (Amundsen et al. 1996) was used. In this method, the prey-specific abundance (A_i) (y – axis) was plotted against the frequency of occurrence (F_i) (x – axis). According to Amundsen et al. (1996), the interpretation of the diagram (prey importance, feeding strategy and niche breadth) can be obtained by examining the distribution of points along the diagonals and axes of the graph. Moreover, a Tokeshi plot (Tokeshi 1991) was constructed to graphically examine differences in individual *versus* population feeding habits, plotting mean individual diet diversity (H'_{ind}) against group diet diversity (Oscoz et al. 2006). Food overlap among the four species was assessed with Schoener's overlap index (Schoener 1970). The overlap index has a minimum of 0 (no prey overlap), and a maximum of 1 (all items in equal proportions), and diet overlap is usually considered significant when value of the index exceeds 60 % (Wallace 1981). The abundance of detritus and vegetal rests was not quantified, and only invertebrates were used for analysis of diet overlap.

Statistical analyses were conducted using the programme PASW Statistics 18. Kruskal-Wallis tests for non-normal data were used for detecting differences among fish species, and were considered statistically significant at P level < 0.05 . Similarity analyses carried out on frequency of occurrence data were performed using the programme PRIMER statistical package version 6.0 to assess the degree of similarity in the diets between fish species from Bray-Curtis similarity, using a cluster mode of group average and Log (x + 1) transformation (Clarke & Gorley 2001). By means of the software R (version 2.11.1), a fuzzy principal component analysis (FPCA) was used to analyse macrohabitats, behavioural feeding and handling efficiency according to the prey items consumed by fishes. FPCA is a method for robust estimation of principal components that has been described with detail, for example, by Cundari et al. (2002), who found that this method diminishes the influence of outliers. The ADE4 library for analysis in

R can be freely obtained at <http://cran.es.r-projet.org/>. We used the same trait database and trait analyses as de Crespín de Billy (2001) and de Crespín de Billy & Usseglio-Polatera (2002). To evaluate the potential vulnerability of invertebrates to fish predation, de Crespín de Billy & Usseglio-Polatera (2002) created a total of 71 different categories for 17 invertebrate traits (see trait categories used in this study in Table 1). Information was structured using a 'fuzzy coding' procedure (Chevenet et al. 1994). A score was assigned to each taxon describing its affinity for each category of each trait, with '0' indicating 'no affinity' to '5' indicating 'high affinity'. The taxonomic resolution (order, family, genus) used in the classification process corresponded to the lowest possible level of determination of taxa in fish gut contents. When identification to genus was not possible or in the case of missing information for a certain genus, the value assigned for a trait was that of the family level, using the average profile of all other genus of the same family, as recommended by de Crespín de Billy & Usseglio-Polatera (2002) and Rodríguez-Capítulo et al. (2009). All of the taxa and their assigned scores for each category can be found at: <http://www.aix.cemagref.fr/htmlpub/divisions/Hyax/titres-publication.htm> (de Crespín de Billy & Usseglio-Polatera 2002). Advantage and disadvantage of traits analysis have been summarized by several authors (e.g. Vieira et al. 2006, Rodríguez-Capítulo et al. 2009, Statzner & Bêche 2010, Sánchez-Hernández et al. 2011b). Thus, Copepoda, Gomphidae, Corixidae, Gyrinidae and Leptoceridae were not included in the analysis because trait values are still not available.

In the present study, sixteen macroinvertebrate ecological traits were chosen for the analysis of trophic ecology of co-occurring fish species. Thus, invertebrate preferences ('macrohabitat trait' and 'current velocity trait') were defined at the macrohabitat scale and were used in this study to obtain information on the preferential use of feeding habitat of the four fish species (see trait categories in Table 1). The tendency of different invertebrate taxa to utilize different types of substratum ('substratum trait') and different flow conditions ('flow exposure') was used to estimate their conspicuousness and accessibility to fishes at the meso- and micro-scales. Meso-scale applies to channel features within a section, and micro-scale is related to characteristics within features, here related to the aquatic habitat of macroinvertebrates (Newson & Newson 2000). For instance, Heptageniidae nymphs that use exposed microhabitats were more likely to be dislodged from the substratum and enter

Table 1. Traits, categories and codes used in analyses and graphics. Based on de Crespin de Billy & Usseglio-Polatera (2002).

Trait	Categories	Code	Traits (continued)	Categories	Code	Traits (continued)	Categories	Code
(1) Macrohabitat	Hypotheic 'burrower'	hypo-b	(5) Tendency to drift in the water column	None	none	(12) Potential size (mm)	≤ 2	< 2
	Hypotheic 'interstitial'	hypo-i		Weak	weak		$> 2-4$	2-4
	Epibenthic depositional	epi-d	(6) Tendency to drift at the water surface	Medium	med	(13) Concealment	$> 4-8$	4-8
	Epibenthic erosional	epi-e		High	high		$> 8-16$	8-16
(2) Current velocity (cm/s)	Water column	water	(7) Diel drift behaviour	None	none	(14) Body shape (including cases/tubes)	$> 16-32$	16-32
	Still (0-5)	0-5		Weak	weak		> 32	> 32
(3) Substratum (mm)	Slow (5-25)	5-25	(8) Trajectory on the bottom substratum or in the drift	Medium	med	(15) Body flexibility (including cases/tubes)	Fixed accessory (nets, retreats)	net
	Moderate (25-75)	25-75		High	high		Movable accessory (cases/tubes)	case
	Fast (> 75)	> 75	(9) Movement frequency	None	none	(16) Morphological defences	Solidly coloured	sold-c
	Mud	mud		Nocturnal	noct		Variable	var-c
	Silt (0.001-0.2)	silt	(10) Agility	Dawn	dawn	(11) Aggregation tendency	Patterned	patt-c
	Sand (0.2-2)	sand		Daylight	d-light		Cylindrical	cyl
	Fine gravel (2-8)	gravel	(11) Aggregation tendency	Twilight	t-light	(11) Aggregation tendency	Spherical	sph
	Gravel-Cobble (8-256)	cobble		None	none		Conical	con
	Blocks (> 256)	bloc	(11) Aggregation tendency	Linear	lin	(11) Aggregation tendency	Flattened	flat
	Bryophytes	bryo		By random	rand		Streamlined	strl
	Other macrophytes	bryo-o	(11) Aggregation tendency	Oscillatory	oscil	(11) Aggregation tendency	None ($< 10^\circ$)	none
	Roots	root		Continuous	cont		Weak ($10-45^\circ$)	weak
(4) Flow exposure	Litter, organic detritus	detr	(11) Aggregation tendency	Discontinuous	disc	(11) Aggregation tendency	High ($> 45^\circ$)	high
	Protected	protect		None (sluggish)	none		Cerci, silk, spine	si-spi
	Exposed	expos	(11) Aggregation tendency	Weak	weak	None	none	
				High	high			
				Weak	weak			
				High	high			

the drift than Orthoclaudiinae larvae that use protected microhabitats (Rader 1997). The ‘tendency to drift in the water column trait’, ‘tendency to drift at the water surface trait’, ‘diel drift behaviour trait’, ‘trajectory on the bottom and in the drift trait’, ‘movement frequency trait’, ‘agility trait’ and ‘aggregation tendency trait’ were used to describe the behavioural feeding habits of the fish species, and finally, ‘potential size

trait’, ‘concealment trait’, ‘body shape trait’, ‘body flexibility trait’ and ‘morphological defences trait’ were used to analyse handling efficiency of fishes.

Results

Diet composition of Salmo trutta

Stomach contents showed that diet included a wide variety of prey items, with *Baetis* spp. (56 % of total

Table 2. Diet composition for each fish species in the Tormes River. Abundance (A_i %) and frequency of occurrence (F_i %).

	<i>S. trutta</i>		<i>S. carolitertii</i>		<i>B. bocagei</i>		<i>P. duriense</i>	
	A_i	F_i	A_i	F_i	A_i	F_i	A_i	F_i
Aquatic prey								
Lumbriculidae	0.2	2.4	-	-	-	-	-	-
<i>Ancylus fluviatilis</i>	0.5	7.3	-	-	-	-	-	-
Hydracharina*	0.8	9.8	6.7	8.8	-	-	-	-
Copepoda*	-	-	0.3	1.8	-	-	-	-
<i>Baetis</i> spp.	56	92.7	46.6	49.1	20.3	77.8	42.1	27.7
<i>Ephemerella</i> spp.	-	-	-	-	-	-	-	-
<i>Ecdyonurus</i> spp.	2.6	31.7	-	-	-	-	0.2	2.1
<i>Epeorus</i> spp.	6.2	36.6	2.7	15.8	-	-	2.2	14.9
<i>Habrophlebia</i> sp.	-	-	0.5	1.8	-	-	-	-
<i>Leuctra geniculata</i>	-	-	0.3	1.8	-	-	0.5	4.3
<i>Ophiogomphus</i> sp.	0.5	2.4	-	-	-	-	-	-
<i>Aphelocheirus aestivalis</i>	0.5	7.3	0.8	5.3	2.7	22.2	-	-
<i>Micronecta</i> sp.	0.3	2.4	-	-	-	-	0.2	2.1
Gerridae	0.2	2.4	-	-	-	-	-	-
<i>Elmis</i> sp.	-	-	0.5	3.5	1.4	11.1	-	-
<i>Orectochilus</i> sp.	0.3	2.4	-	-	-	-	-	-
<i>Hydropsyche</i> spp.	2	19.5	2.4	14	17.6	55.6	0.7	4.3
Leptoceridae	0.2	2.4	0.3	1.8	-	-	-	-
<i>Allogamus</i> sp.	2.3	19.5	2.2	7	4.1	33.3	-	-
<i>Chimarra marginata</i>	0.2	2.4	0.3	1.8	-	-	0.5	4.3
<i>Polycentropus</i> sp.	0.2	2.4	1.1	7	-	-	-	-
<i>Rhyacophila</i> spp.	3.4	31.7	1.6	10.5	21.6	33.3	0.7	4.3
<i>Atherix</i> sp.	0.2	2.4	-	-	-	-	-	-
Tanypodinae	2.6	22	3	14	32.4	77.8	1.5	12.8
Prosimuliini	9.1	41.5	22.9	40.4	-	-	49.8	21.3
Terrestrial prey								
Trichoptera*	5	26.8	1.9	8.8	-	-	-	-
Ephemeroptera*	3.7	34.2	0.5	3.5	-	-	-	-
Asilidae	-	-	-	-	-	-	-	-
Chironomidae	0.3	4.9	-	-	-	-	-	-
Empididae	0.2	2.4	-	-	-	-	-	-
Simuliidae	0.3	4.9	-	-	-	-	-	-
Diptera*	-	-	0.5	3.5	-	-	0.2	2.1
Formicidae	2.1	19.5	3.2	17.5	-	-	1.0	4.3
Coleoptera*	0.2	2.4	0.5	3.5	-	-	0.2	2.1
Arachnida*	-	-	0.8	5.3	-	-	-	-
Other prey items								
<i>P. duriense</i>	0.2	2.4	0.3	1.8	-	-	-	-
Detritus	-	-	-	57.9	-	77.8	-	85.1
Plant material	-	-	-	-	-	-	-	36.2

* Not identified. The abundance of detritus and vegetal rests was not quantified and only the number of stomachs in which they appeared was noted.

Table 3. Diet overlap (Schoener's index) among different fish species in the River Tormes.

	Schoener's index
<i>B. bocagei</i> - <i>S. carolitertii</i>	0.8
<i>B. bocagei</i> - <i>S. trutta</i>	0.9
<i>B. bocagei</i> - <i>P. duriense</i>	1
<i>S. carolitertii</i> - <i>S. trutta</i>	0.89
<i>S. carolitertii</i> - <i>P. duriense</i>	0.8
<i>S. trutta</i> - <i>P. duriense</i>	0.9

Table 4. Values of the Bray-Curtis index of diet similarity between fish species.

	<i>S. carolitertii</i>	<i>B. bocagei</i>	<i>P. duriense</i>
<i>B. bocagei</i>	47.8	-	-
<i>P. duriense</i>	60.4	41.1	-
<i>S. trutta</i>	56.5	42.9	29.4

prey) dominating. In total, 616 preys belonging to 28 taxa were identified, and the diets were dominated by aquatic invertebrates (87.9 % of total prey) (Table 2).

Diet composition of *Squalius carolitertii*

Diet composition was constituted by 23 types of prey, and a total of 371 preys were identified in the gastrointestinal tracts. Detritus were found in 33 fishes (57.9 % of occurrence). Nymphs of *Baetis* spp. were the most abundant prey (46.6 %) and were identified in the 49.1 % of the stomachs (Table 2). Terrestrial invertebrates were also present (7.4 % of total prey).

Table 5. Diet composition. Shannon diversity index (H') and evenness index (E) for each fish species (mean \pm SE).

	<i>S. trutta</i>	<i>S. carolitertii</i>	<i>B. bocagei</i>	<i>P. duriense</i>
Benthic prey (%)	85.9 \pm 3.09	88.1 \pm 3.30	100	91.8 \pm 5.43
Terrestrial invertebrates (%)	13.9 \pm 3.08	11.3 \pm 3.28	0	8.2 \pm 5.32
Fishes (%)	0.2 \pm 0.143	0.6 \pm 0.58	0	0
Shannon diversity index (H')	1.35 \pm 0.131	1.06 \pm 0.103	1.07 \pm 0.166	0.75 \pm 0.094
Evenness index (E)	0.51 \pm 0.046	0.38 \pm 0.037	0.38 \pm 0.059	0.27 \pm 0.034

Diet composition of *Barbus bocagei*

The occurrence of *Baetis* spp., Chironomidae and detritus were similar (77.8 % in all cases). Chironomid larvae were the most abundant prey (32.4 % of total prey). *Rhyacophila* spp. and *Baetis* spp. contributed 21.6 and 20.3 %, respectively, to the total abundance. In total, 74 preys were identified, and no terrestrial invertebrates were found in the diet (Table 2).

Diet composition of *Pseudochondrostoma duriense*

A total of 406 preys and 15 items were identified in the gastrointestinal tracts of Northern straight-mouth nase. Detritus was present in the majority of individuals, and occurred in 85.1 % of fishes. Simuliidae and *Baetis* spp. were the most prevalent food, accounting for 49.8 % and 42.1 %, respectively, of animal prey numbers (Table 2). Terrestrial invertebrates (1.4 % of total prey) and plant material (36.2 % of occurrence) were also present.

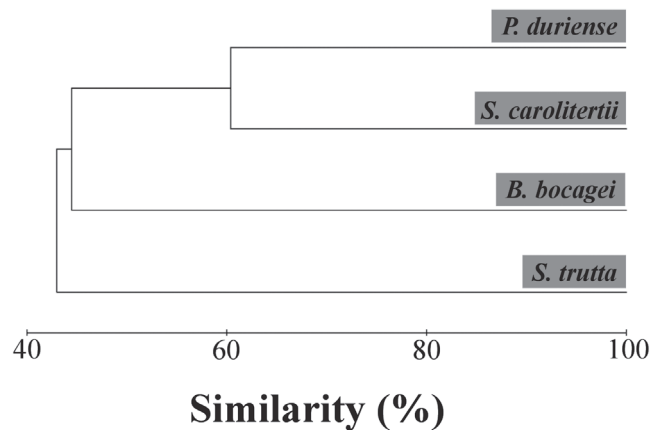


Fig. 2. Dendrogram resulting from the cluster analysis performed on stomach content data in terms of prey occurrence of the fish species.

Comparison among species

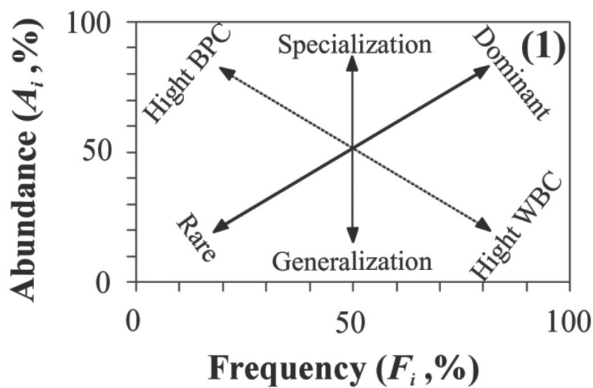
Cyprinids fed on several animal preys and also consumed detritus and plant material, showing that these species present typically omnivorous feeding

habits (Table 2). Plant material only was consumed by Northern straight-mouth nase. The dietary analyses, based on macroinvertebrates, showed high values of diet overlap using the Schoener's index (≥ 0.8 , even up to 1) (Table 3), and all the species showed a remarkable similarity in their prey utilization patterns. Thus, *Baetis* spp. constituted a significant proportion of the diet for *S. trutta*, *S. carolitertii* and *P. duriense* (56 %, 46.6 % and 42.1 %, respectively). In contrast, *B. bocagei*

fed chiefly on Chironomidae and *Rhyacophila* spp. (32.4 % and 21.6 % respectively).

Diet comparison among species shows that detritus are present in *P. duriense*, *B. bocagei* and *S. carolitertii*, although in different occurrence, being most frequently in the diet of Northern straight-mouth nase (85.1 % of occurrence) than Iberian barbel (77.8 % of occurrence) and Northern Iberian chub (57.9 % of occurrence). The diet composition of fish species also were analyzed using cluster analysis. Minimum bray-

curtis similarity between fish species was 29.4 % (Northern straight-mouth nase *versus* brown trout) and the most similar group was data from Northern straight-mouth nase and Northern Iberian chub (Table 4). Thus, the similarity index and cluster analysis carried out on frequency of occurrence data (Fig. 2) differentiated three feeding groups: 1) species feeding mainly on aquatic macroinvertebrates (*S. trutta*), 2) species feeding mainly on detritus but with aquatic invertebrates as an important complementary



— Feeding strategy
 — Prey importance
 Niche contribution

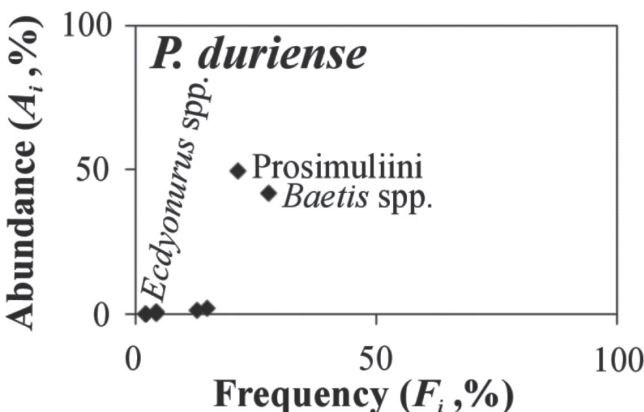
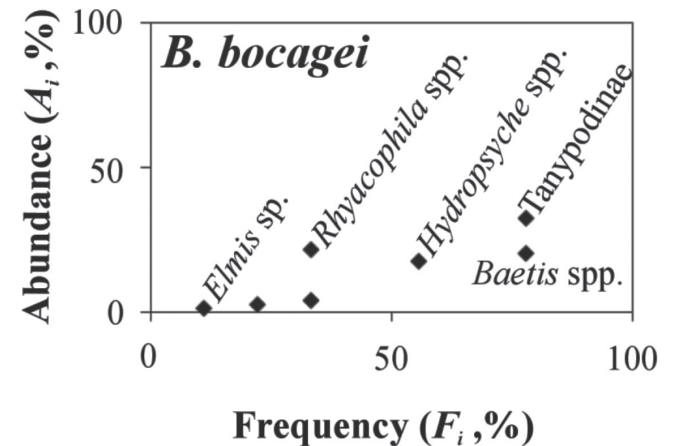
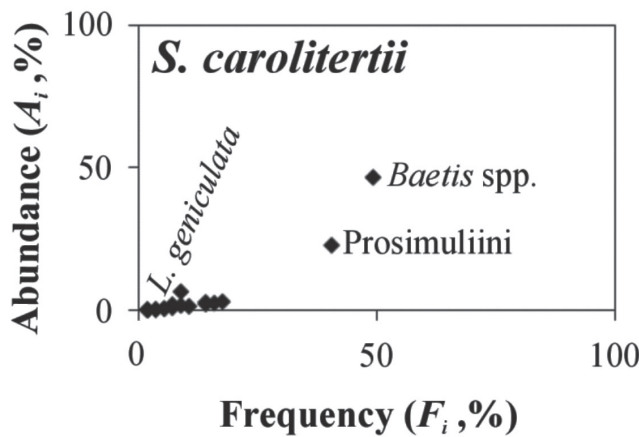
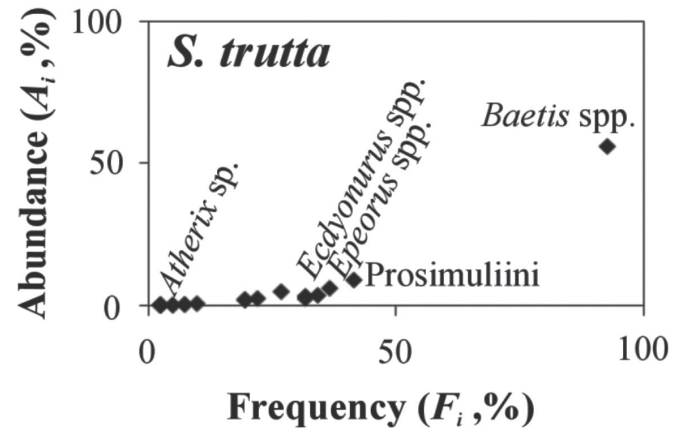


Fig. 3. Feeding strategy diagram. (1) Explanatory diagram of the modified Costello method according Amundsen et al. (1996). Data are presented for each fish species.

food category (*B. bocagei*), and 3) species feeding mainly on detritus but with invertebrates (aquatic and terrestrial) as an important complementary food category (*S. carolitertii* and *P. duriense*).

In all species, benthic prey constituted the most important prey in abundance terms, and terrestrial invertebrates

were only consumed by brown trout, Northern Iberian chub and Northern straight-mouth nase (11.8 %, 7.4 % and 1.4 % respectively, of the total abundance). The analysis of the feeding strategy of the species using Shannon diversity index indicated that brown trout had the largest niche breadth ($H' = 1.35 \pm 0.131$ SE), with lower values for *B. bocagei* ($H' = 1.07 \pm 0.166$ SE), *S. carolitertii* ($H' = 1.06 \pm 0.103$ SE) and *P. duriense* ($H' = 0.75 \pm 0.094$ SE). Differences among species were statistically significant (Kruskal-Wallis test: $H = 12.12, P < 0.05$). Similarly, the evenness index was higher in brown trout than in Iberian barbel, Northern Iberian chub or Northern straight-mouth nase (Table 5), being significant differences among species (Kruskal-Wallis test: $H = 11.14, P < 0.05$), Northern straight-mouth nase showed the most stenophagous diet. Regarding prey size (total length), there were differences

in the average prey size consumption among species (Kruskal-Wallis test: $H = 53.79, P < 0.05$). Brown trout fed on mean size $5.1 \text{ mm} \pm 0.19$ SE, being this size higher than that for Iberian barbel ($4 \text{ mm} \pm 0.32$ SE), Northern straight-mouth nase ($3.9 \text{ mm} \pm 0.11$ SE) or Northern Iberian chub ($3.7 \text{ mm} \pm 0.27$ SE).

The interpretation of the diagrams of the modified Costello graphical method (Amundsen et al. 1996) is shown in Fig. 3. The plot of prey-specific abundance (A_i) and frequency of occurrence (F_i) of the main components of the diet between fish species, showed a different feeding strategy developed by fish species, varying degrees of specialization and generalization on different prey types. In terms of prey importance, some aquatic prey (Fig. 3) presented a low F_i and a low A_i (lower left quadrant) for all species, displaying evidence of a generalist strategy. However, in brown trout *Baetis* spp. have been eaten by more than half the individuals ($F_i = 92.7\%$) and to have high contribution in specific abundance ($A_i = 56\%$). Similarly, other prey items have a prey importance for Iberian barbell (e.g. Tanypodinae), Northern straight-mouth nase (Prosimuliini and *Baetis* spp.) and Northern Iberian chub (*Baetis* spp. and Prosimuliini) (Fig. 3 and Table 2).

The results of dietary analysis using Tokeshi's (1991) graphical model demonstrated that despite the large range of population prey type diversity, the mean individual diet diversity was fairly stable. Thus, feeding patterns in all fish species were characterized by a mean individual diversity lower than population diversity, exhibiting generalist heterogeneous feeding strategies in all cases (Fig. 4).

Concerning macroinvertebrate trait analyses, the two first axes were sufficient to illustrate the relationships among faunal groups according to their combinations of traits ('eigenvalues' of Figs. 5 and 6), and accounted for > 65 % of the total variability in all cases. A general tendency that can be observed is the wider diversity of characteristics of *S. trutta* preys in comparison with those of *S. carolitertii*, *B. bocagei* and *P. duriense*. Regarding habitat traits, 'substratum' and 'flow exposure' traits showed no clear differences for preys of the four fish species (Figs. 5c, 5d). 'Macrohabitat' and 'current velocity' traits showed that Iberian barbel preferred to feed on epibenthic prey living in erosional macrohabitats with moderate current velocities, although overlap was higher between Northern Iberian chub and Northern straight-mouth nase (Figs. 5a, 5b). 'Diel drift behaviour', 'trajectory on the bottom substratum or in the drift', 'movement frequency', 'agility', 'aggregation tendency' and 'body flexibility' traits were similar for preys of the

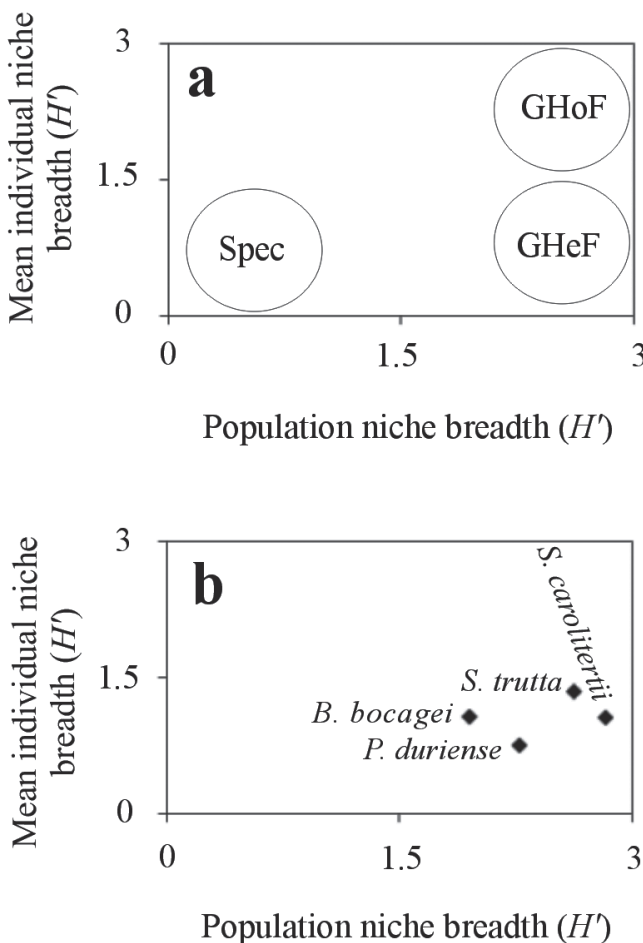


Fig. 4. a) Scheme for the interpretation of the Tokeshi graphical method, generalist homogeneous feeding strategies (GHoF), generalist heterogeneous feeding strategies (GHeF) and specific feeding strategies (Spec). b) Feeding strategy based on Tokeshi's (1991) graphical model, data are presented for each fish species.

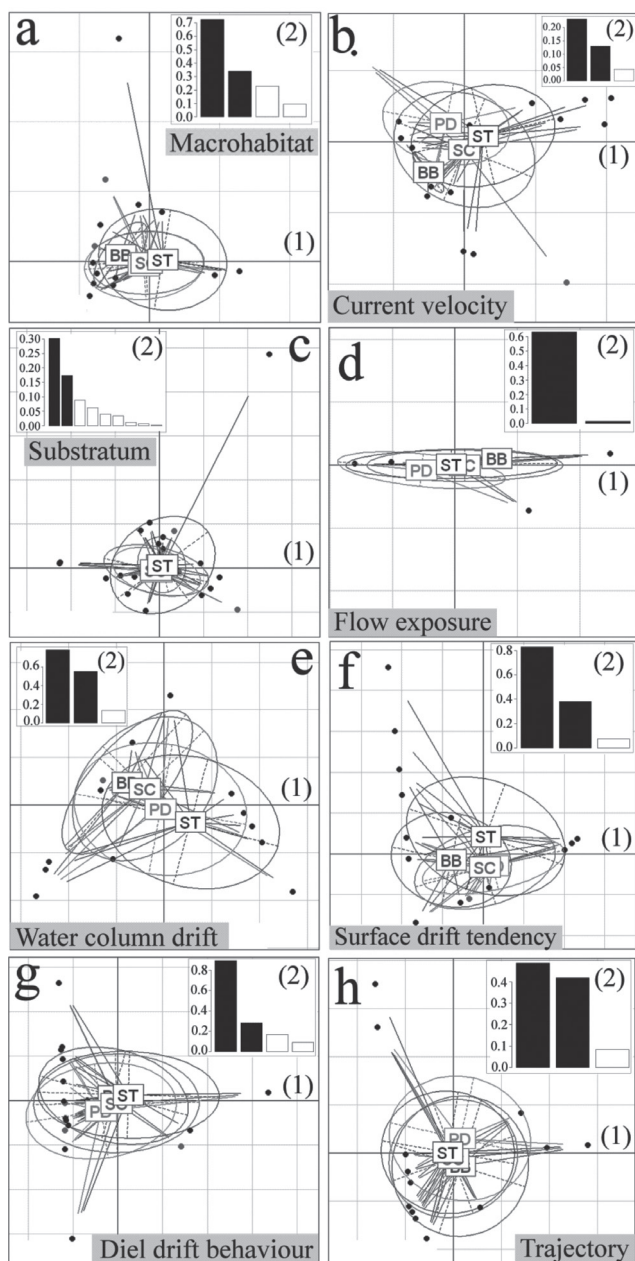


Fig. 5. Biplot of gut contents obtained from a fuzzy principal component analysis (FPCA). Distribution of each trait according to the gut contents (1) and histogram of eigenvalues (2, the first two values are in black). Data are presented for each fish species. BB: *B. bocagei*. SC: *S. carolitertii*. PD: *P. duriense* and ST: *S. trutta*. Ellipses envelop weighted average of prey taxa positions consumed by fish species; Labels (BB, SC, PD and ST) indicate the gravity centre of the ellipses. Filled lines link prey families (represented by a point) to their corresponding predator but are only 80 % of their total length for readability. Dotted lines represent the width and height of ellipses. Details and data needed for the elaboration of “a” to “h” graphics can be found in the Material and Methods section and Table 1.

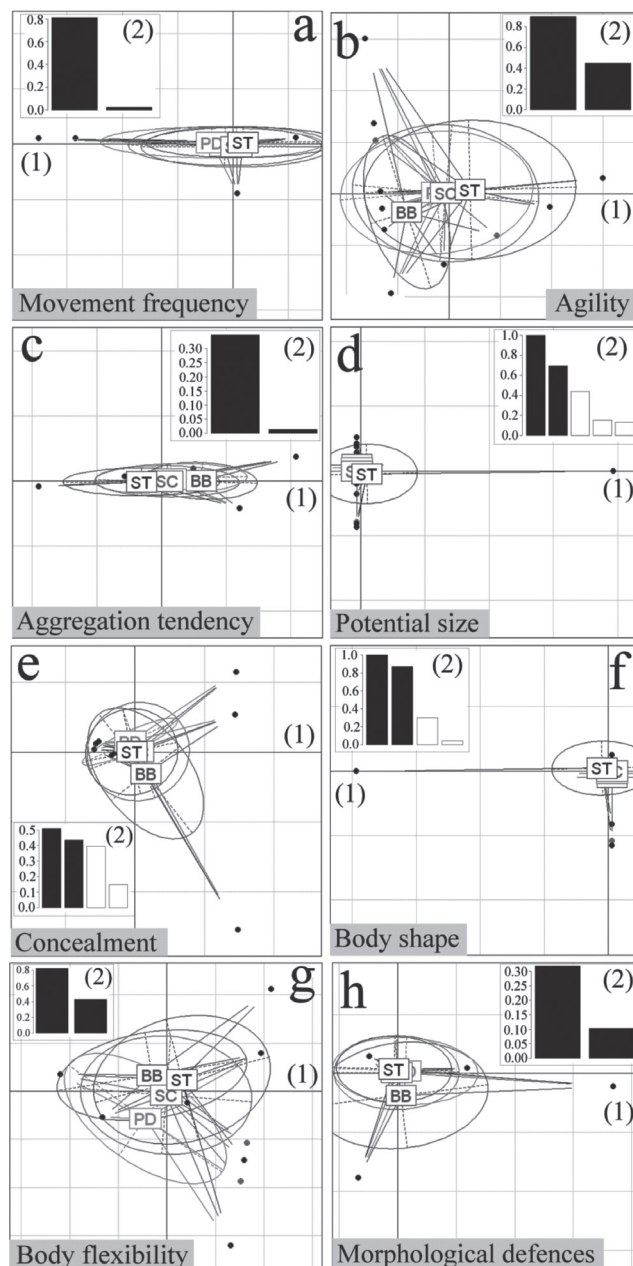


Fig. 6. Biplot of gut contents obtained from a fuzzy principal component analysis (FPCA). Distribution of each trait according to the gut contents (1) and histogram of eigenvalues (2, the first two values are in black). Data are presented for each fish species. BB: *B. bocagei*. SC: *S. carolitertii*. PD: *P. duriense* and ST: *S. trutta*. Ellipses envelop weighted average of prey taxa positions consumed by fish species; Labels (BB, SC, PD and ST) indicate the gravity centre of the ellipses. Filled lines link prey families (represented by a point) to their corresponding predator but are only 80 % of their total length for readability. Dotted lines represent the width and height of ellipses. Details and data needed for the elaboration of “a” to “h” graphics can be found in the Material and Methods section and Table 1.

four species (Figs. 5g, 5h, 6a-6c, 6g).

Finally, traits that best separated fish gut samples were those related to behavioural feeding habits ('tendency to drift in the water column' and 'tendency to drift at the water surface' traits) and morphological traits related to handling efficiency of fishes ('potential size', 'concealment', 'body flexibility' and 'morphological defences'). As it can be seen in the Fig. 5e, brown trout is clearly separated from the other three species. This is due to its preference to prey on organisms with high tendency to drift in the water column. *S. trutta*, *P. duriense* and *S. carolitertii* included in their diets macroinvertebrates that drift in the surface (Fig. 5f). Thus, although *S. carolitertii*, *B. bocagei* and *P. duriense* are omnivorous cyprinids, *B. bocagei* seems to feed exclusively on the bottom, eating detritus and macroinvertebrates. In contrast, *S. carolitertii* and *P. duriense* can include in their diets macroinvertebrates that drift in the surface. In relation to 'potential size', *S. trutta* showed a clear tendency to feed on potentially bigger preys than the rest of species (Fig. 6d). Concerning traits 'concealment' and 'morphological defences', Iberian barbel shows a higher spectrum of prey, which reveals a greater ability to prey on different concealments and morphological defences (Figs. 6e, 6h). Brown trout shows a higher spectrum of prey in the Fig. 6f, due to the preference to feed on cylindrical and conical preys.

Discussion

Previously, prey traits have been used to describe food partitioning between freshwater fish species in the Iberian Peninsula (Sánchez-Hernández et al. 2011b). In contrast with Sánchez-Hernández et al. (2011b), who studied the feeding habits of fish community in a Galician stream (NW Spain) during autumn, in our case sampling date was August. Moreover, important differences in habitat conditions (for example river flow or substrate characteristics) and fish community composition between our study site and theirs were found.

Concerning diet composition, results are broadly in accordance with previous studies. Thus, detritus and plant material were important food resources for Northern Iberian chub and Northern straight-mouth nase, presenting both species omnivorous feeding habits in which aquatic macroinvertebrates were an important food supply (Rodríguez-Jiménez 1987, Magalhães 1993a, b, Encina & Granado-Lorencio 1994, Coelho et al. 1997, Blanco-Garrido et al. 2003). Moreover, *S. carolitertii* and *P. duriense* feed at the bottom, the water column or surface column, similar

to finding in others cyprinids species (Rincón & Grossman 2001, Blanco-Garrido et al. 2003, Zamor & Grossman 2007). This study confirms previous research indicating that Iberian barbel feeds almost exclusively on aquatic invertebrates and detritus (Docampo & Vega 1990, Encina & Granado-Lorencio 1990, Encina & Granado-Lorencio 1994, Encina et al. 1999). Thus, results of trait analysis in the present study are in accordance with the bottom-feeding behaviour found in previous studies (Encina & Granado-Lorencio 1990, Encina et al. 2004). In relation with brown trout, Ephemeroptera nymphs seem to be the most important food items, as found by many researchers (e.g. Toledo et al. 1993, Lagarrigue et al. 2002, Oscoz et al. 2005). In addition, results of prey trait analyses are in accordance also with previous findings concerning for example prey diversity (de Crespín de Billy & Usseglio-Polatera 2002) or preference to feed on drifting organisms (Rader 1997, Rincón & Lobón-Cerviá 1999, Lagarrigue et al. 2002, Sánchez 2009).

Previous studies have demonstrated the generalist feeding strategy in numerous fish species using the graphical method of Costello (1990) modified by Amundsen et al. (1996) (e.g. Dominguez et al. 2002, Oscoz et al. 2006). In a recent study, Gabler & Amundsen (2010) have found that competitive coexistence with similar niches may be facilitated by a generalisation of niche width as predicted by optimal foraging theory, rather than the specialised niche width predicted by classic niche theory as a response to interspecific competition. Our findings, according the Amundsen's method and Tokeshi's (1991) graphical model, reinforce previous observations and the four fish species exhibited a generalist feeding strategies. In this study, diet analysis and dendrogram resulting from the cluster analysis performed on stomach content data differentiated three feeding groups: 1) macroinvertebrates (*S. trutta*), 2) omnivorous feeding regime with a remarkable bottom-feeding behaviour (*B. bocagei*) and 3) omnivorous feeding regime with a noteworthy drifting-feeding behaviour (*S. carolitertii* and *P. duriense*). Studies of food partitioning in fish communities have obtained contradictory results. Whereas, several authors have found differences in diet composition among species (Magalhães 1993a, Encina et al. 2004, Novakowski et al. 2008), others researchers conclude that the same food resource can be shared by several species (Hesthagen et al. 2004, Gabler & Amundsen 2010, Museth et al. 2010, Sandlund et al. 2010). In these cases, coexistence of fish species has been suggested to be related to food

partitioning at different levels, including different activity patterns (Kronfeld-Schor & Dayan 2003, Hesthagen et al. 2004, Sánchez-Hernández et al. 2011b), differences in prey size utilizations (Jepsen et al. 1997, Stevens et al. 2006, Sánchez-Hernández et al. 2011b) or differential use of space (Grossman et al. 1987a, b, Amarasekare 2003, Sandlund et al. 2010, Sánchez-Hernández et al. 2011b). A remarkable result of our study is that, although three of the four species analysed showed omnivorous feeding habits, there is a noteworthy high overlap among all of them concerning ingested macroinvertebrates. In fact, analysis of macroinvertebrate traits showed also a high overlap among the fish species. However, high overlap values may not indicate competition, since species can adopt different strategies to overcome competence. First, segregation of microhabitat is an important factor for reducing the effects of the competition by the trophic resource (Baker & Ross 1981, Yant et al. 1984, Haury et al. 1991). Indeed, the use of microhabitats is often distinguishable between species (Grossman et al. 1987a, b, Rincón & Lobón-Cerviá 1993), and in our case, for example, Iberian barbel preferred to feed on epibenthic prey living in erosional macrohabitats with moderate current velocities, whereas brown trout, Northern Iberian chub and Northern straight-mouth nase shows a high spectrum of prey, which reveals a great ability to prey on different substrata and different macroinvertebrates. Hence, differences were found among species on the ability to feed at different depths of the water column. Second, the ability of cyprinids to feed on detritus and plant material may have a high competitive value in environments with severe competition (Magalhães 1992), and may reduce the inter-specific competition in the area studied. Third, food partitioning may also occur at the level of prey size (Jepsen et al. 1997, Stevens et al. 2006, Sánchez-Hernández et al. 2011b). In most cases the high degree of digestion of the food impedes its prey length measurement, and

although this drawback can be overcome from the measurement of cephalic capsule width (see Rincón & Lobón-Cerviá 1999), this method will be useful if prey items have hard structures, but in softer prey items it will be only useful if these items are found in the beginning of the digestive tract. However, despite the above-mentioned problem, our findings showed that food partitioning occurs at the level of prey size. Fourth, terrestrial prey are present primarily on the stream surface and may constitute an important food resource. In the present study utilization of terrestrial prey by cyprinids (*S. carolitertii* and *P. duriense*) may reduce competition facilitating the partitioning of resources, as found Magalhães (1993b). Fifth, competition might get reduced also by differences in the diel activity patterns of fishes (Alanärä et al. 2001, David et al. 2007, Sánchez-Hernández et al. 2011b). In our case, no clear differences between fish species were found.

In conclusion, the present study provides important information about food partitioning in fish communities of temperate areas. Furthermore, analysis of prey traits provided us with few important clues for understanding the coexistence of fish species. Thus, feeding strategies concerning macrohabitat use, drift behaviour of prey and prey size seem to be important factors that explain the coexistence in this fish community, although seasonal variations in feeding strategies might occur as stated by Sánchez-Hernández et al. (2011b).

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